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# FLORIDA SCIENTIST

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*Biological Sciences*

## AMPHIBIANS AND REPTILES OF THE JOHN F. KENNEDY SPACE CENTER, FLORIDA: A LONG-TERM ASSESSMENT OF A LARGE PROTECTED HABITAT (1975–2000)

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**ABSTRACT:** *The Kennedy Space Center (KSC) is one of the largest areas of public land in eastern Florida. Here, we report the results of a 25-year assessment of the herpetofauna of the KSC, with specific emphasis on long-term changes in populations. Exclusive of marine turtles, we found 69 species of amphibians and reptiles. With one exception, all species found during earlier surveys in the 1970s were still present 25 years later and an additional 14 species were identified. There were no significant changes in the total number of snakes found on a road survey route, but there were significant changes in the relative species composition among snake species, especially for cottonmouths and Florida green water snakes. In addition, diamondback terrapin populations declined markedly, and introduced diseases and habitat alterations may be a threat to other species.*

**Key Words:** Amphibians, reptiles, monitoring, population changes, conservation

REPTILES and amphibians are important yet often ignored components of terrestrial and aquatic ecosystems (Gibbons, 1988; Vitt et al., 1990; Scott

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and Seigel, 1992). Even though the misconception that amphibians and reptiles are less economically and ecologically important than other vertebrates has been effectively dispelled over the past decade (e.g., Burton and Likens, 1975; Bennett and Gorman, 1979; Bury et al., 1980; Pough, 1980; Bury, 1988; Gibbons, 1988; Vitt et al., 1990; Scott and Seigel, 1992), the legacy of this attitude has important modern consequences. For example, although it is widely recognized that ecologically-sound land management requires at least a basic understanding of the presence and habitat requirements of resident species, such information is frequently lacking for amphibians and reptiles, especially on public lands. For instance, when resource managers on National Seashores in the United States were asked to rank their available information on the presence and distribution of various species, reptiles and amphibians placed last and next to last, respectively, behind vascular plants and all other groups of vertebrates (Stohlgren et al., 1994). These findings illustrate the need for better and more comprehensive data on the presence and distribution of amphibians and reptiles, especially on public lands protected from large-scale habitat development. Long-term data are especially important in assessing changes in species richness over time (Pechmann et al., 1991; Seigel et al., 1995).

The John F. Kennedy Space Center (hereafter, KSC) is one of the largest public land holdings along the Atlantic Coast of Florida (NASA, 1994). The 56,000-ha site is owned by the National Aeronautics and Space Administration (NASA) and is jointly managed by NASA, the U. S. Fish & Wildlife Service (USFWS), and the National Park Service (NPS). The site offers a broad array of habitats and a large number of state and federally-listed species (see Breining et al., 1998 and NASA, 1994 for reviews). Here, we report on a long-term (1975–2000) assessment of the presence, species richness, and distribution of the amphibians and reptiles of the KSC, with specific emphasis on long-term changes in populations.

**MATERIALS AND METHODS—History**—Initial assessments of the presence and distribution of amphibians and reptiles of the KSC were conducted from 1975–1977 under the direction of LME and FFS. These data consisted mainly of opportunistic observations, although specific efforts were made to permanently mark as many turtles as possible (using methods of Ernst and co-workers, 1974). Data collection was continued and augmented by RAS from 1977–1979, with added emphasis on assessing snake populations via standardized road surveys and studies of diamondback terrapin populations (*Malaclemys terrapin* [e.g., Seigel, 1980, 1984]). Studies by RBS began in 1987; in addition to making additional opportunistic observations, specific attention was focused on gopher tortoises (*Gopherus polyphemus*) and indigo snakes (*Drymarchon corais*) (e.g., Smith et al., 1997). In 1992, RAS began a systematic inventory of the amphibians and reptiles on the site, using a broader range of methods. These are described below.

**Collecting methods—Road surveys**—Initiated in 1977, road surveys focussed on the numbers of reptiles found along a 19.3- km- long segment of roads referred to as the Triangle (Rts. 402, 406, and Rt. 3; Fig. 1). This series of roads crossed a variety of habitats, including xeric scrub, brackish and freshwater wetlands, and roadside ditches. Road surveys were conducted 1–6 times per month, mainly between March and November, usually starting immediately at

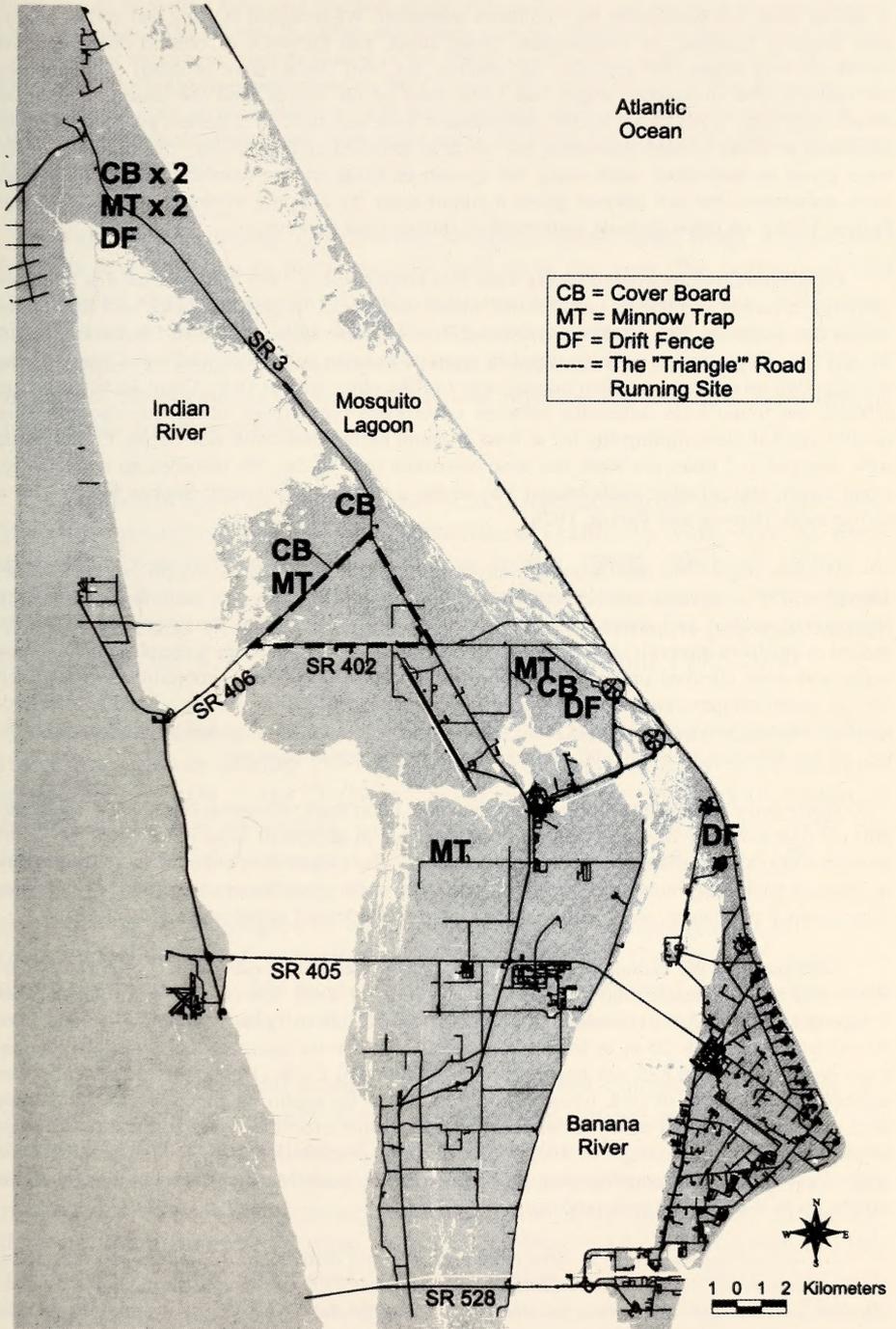


FIG. 1. Map of the Kennedy Space Center showing the location of sampling sites for the capture methods noted in the text. Abbreviations follow those in Table 1.

or before dusk and continuing for 1–2 hours thereafter. We recorded starting and ending times, total distance traveled, air temperature, cloud cover, and presence of rainfall during or just before surveys began. We recorded the species, sex, and status (alive or dead) of all reptiles encountered, the snout-vent length and body mass of all snakes, and the carapace, plastron length, and body mass of all turtles. Amphibians were recorded by numbers per species (only estimated in times of high numbers), but we also recorded calling activity by anurans. Turtles were given an individual mark using the system of Ernst and co-workers (1974) and snakes were sometimes (but not always) given a cohort mark by clipping ventral scales (Brown and Parker, 1976); no other animals were marked during road surveys.

*Coverboards*—Coverboard arrays were first established in 1993 and were used at five sites spanning a variety of habitats (xeric scrub, mesic hammocks, xeric hammocks, and adjacent to freshwater wetlands; Fig. 1). Each array had 20–24 coverboards, each board measuring  $91 \times 91 \times 5$  cm. Three arrays were arranged in pairs of wooden (plywood) and metal (tin) boards, whereas two arrays used wooden boards only (unlike other studies [e.g., Grant and co-workers (1992)], we found little difference between coverboard types [pers. obs.]). Coverboards were usually aged at the sampling site for at least a month before data collection began. Coverboards were checked 1–2 times per week but at no consistent time of day. We recorded air temperature, cloud cover, and whether each animal was under a wood or tin board. Snakes were given a cohort mark (Brown and Parker, 1976).

*Minnow traps*—We used commercially-available minnow traps (Memphis Net and Twine, Memphis, TN) at several sites selected for long-term sampling (Fig. 1), including both natural (freshwater swales) and altered sites (roadside ditches). Traps were set in groups of 10–20, spaced at ca. 10 m intervals, and operated for periods of 3–5 days. Traps were placed in shallow water and were checked once or twice per day to preclude incidental mortality. We recorded air and water temperatures using a digital thermometer and salinity using a hand-held refractometer. Snakes, turtles, and sirens were given a permanent mark by scale-clipping, shell notching, or toe clipping, respectively, and released at the point of capture.

*Turtle traps*—We used commercially-available hoop traps (Memphis Net and Twine, Memphis, TN) at a variety of aquatic sites. Traps were set in groups of 1–4, spaced at intervals of at least 10 m, and operated for periods of 2–5 days. Traps were checked once or twice per day to preclude incidental mortality. We recorded air and water temperatures as noted above. Turtles were given a permanent mark as described above and released at the point of capture.

*Drift fences*—We established drift fences near a wetlands-scrub habitat, in a xeric hammock, and along a beach sand dune community (Fig. 1). Drift fences were constructed either of aluminum flashing or plywood, set in either a straight-line or “plus” configuration, and were 60–80 cm high and 5–20 m in length. Most drift fences were equipped only with 2–4 funnel traps constructed of 0.635 cm hardware cloth, following Fitch (1987). One drift fence was equipped with a series of 19-L white plastic pitfall traps for capturing amphibians. Funnel traps were covered by a small board or other shading to reduce exposure to the sun and pitfall traps were equipped with a sponge to avoid desiccation of amphibians. Drift fences were checked daily during specified sampling periods throughout the year. Marking and handling methods follow those for road surveys (above).

*Anuran calling surveys*—To detect the presence and distribution of anuran breeding sites, we used automated data recorders (Peterson and Dorcas, 1992) to sample chorusing activity at selected wetland sites. We made no attempt to quantify chorus activity, but simply used this method to determine presence at sampling localities.

*Hand collecting*—We did not conduct time-constrained hand collecting during this study. However, many attempts were made to capture amphibians and reptiles by hand, especially

along levees bordering fresh and brackish water impoundments, and during night-time surveys along wetlands. Marking and handling procedures were as described for road surveys (above).

Voucher specimens were deposited in the Vertebrate Museum at the University of Central Florida and the collection maintained by the Canaveral National Seashore. For simplicity, only common names are given in the text, with both common and scientific names provided in the tables. All statistical comparisons were made using SYSTAT 7.0 (SYSTAT, 1992). All means are reported  $\pm$  one SD.

**RESULTS—*Sampling effort***—We sampled each year from 1992–2000 from as few as 10 to as many as 180 field days per year. We conducted 169 coverboard surveys, sampled with minnow traps 52 times for 3683 trap-nights, and conducted 3451 km of road surveys along our permanent sampling route. In addition, employees from Dynamac Corporation made many incidental observations of amphibians and reptiles and brought in numerous individuals for processing.

***Changes in species composition***—Exclusive of marine turtles, we identified 69 species of reptiles and amphibians (Table 1). Fifty-five of these species also were found during surveys in the 1970s (Ehrhart, 1976); an additional 14 species, not reported in Ehrhart's earlier summary, were found from 1992–2000 (Table 1). Only one species (the eastern hognose snake) known from the KSC in the 1970s was not found from 1992–2000.

***Long-term changes in numbers of snakes***—The mean number of snakes/km of road survey during 1977–1979 was  $0.159 \pm 0.262$  ( $N = 24$  surveys) compared to  $0.109 \pm 0.115$  ( $N = 78$  surveys) from 1992–2000. Although the overall counts of snakes was about 31% lower from 1992–2000, the difference between the samples was not statistically significant (ANOVA on square-root transformed data,  $F = 0.302$ ,  $df = 1, 100$ ,  $P = 0.584$ ). However, given the very high degree of variation within each sample period and within years (coefficients of variation of 100% or more), the lack of statistical significance could be due to insufficient statistical power to detect population trends (e.g., Hayes and Steidl, 1997) rather than to a lack of change in snake populations.

Although the overall counts of snakes did not change significantly between the sampling periods, Table 2 suggests that there were changes in the relative species composition of the snakes found during the road surveys, with two species (cottonmouths and Florida green water snakes) showing marked declines. A contingency table analysis of the differences in the relative numbers of the five most commonly observed snakes (cottonmouths, corn snakes, banded water snakes, ribbon snakes, and garter snakes) between the 1970s and the 1990s was strongly statistically significant ( $G = 25.9$ ,  $df = 4$ ,  $P < 0.001$ ). However, these differences were mainly due to the marked reduction in the relative counts of cottonmouths, which fell from 13% of the total sample in the 1970s to  $< 1.0\%$  in the 1990s. When cottonmouths

TABLE 1. Current inventory of amphibians and reptiles of the KSC. Data collected from 1992–2000 are compared with the list provided by Ehrhart (1976). Species marked with a “+” were found during the time period indicates; a “–” means that species was not found during that time interval. Species marked with a “\*” are known introductions. Species are grouped by major taxonomic lineage (e.g., crocodylians, turtles), then alphabetically by genus and species. Marine turtles are not listed here.

Species	Ehrhart, 1976	This study	Successful methods
<b>Crocodylians</b>			
<i>Alligator mississippiensis</i> (American alligator)	+	+	HC, RS, TT
<b>Turtles</b>			
<i>Apalone ferox</i> (Florida softshell turtle)	+	+	HC, RS, TT
<i>Chelydra serpentina</i> (snapping turtle)	+	+	RS
<i>Deirochelys reticularia</i> (chicken turtle)	+	+	DF, HC, RS, TT
<i>Gopherus polyphemus</i> (gopher tortoise)	+	+	HC, RS
<i>Kinosternon baurii</i> (striped mud turtle)	+	+	HC, RS
<i>Kinosternon subrubrum</i> (common mud turtle)	+	+	RR
<i>Malaclemys terrapin</i> (diamondback terrapin)	+	+	HC, RS
<i>Pseudemys nelsoni</i> (Florida redbelly turtle)	+	+	HC, RS
<i>Pseudemys peninsularis</i> (Florida cooter)	+	+	HC, RS, TT
<i>Sternotherus odoratus</i> (common musk turtle)	–	+	RS
<i>Terrapene carolina</i> (box turtle)	+	+	HC, RS
<b>Lizards</b>			
<i>Anolis carolinensis</i> (green anole)	+	+	CB, HC, RS
* <i>Anolis sagrei</i> (brown anole)	–	+	CB, DF, HC
<i>Cnemidophorus sexlineatus</i> (six-lined racerunner)	+	+	CB, DF, HC
<i>Eumeces egregius</i> (mole skink)	+	+	CB
<i>Eumeces inexpectatus</i> (southeastern five-lined skink)	+	+	CB, DF, HC
* <i>Hemidactylus garnotii</i> (Indo-Pacific gecko)	–	+	HC
** <i>Hemidactylus turcicus</i> (Mediterranean gecko)	–	+	HC
<i>Ophisaurus attenuatus</i> slender glass lizard	+	+	CB, HC, RS
<i>Ophisaurus compressus</i> (island glass lizard)	–	+	DF, HC, RS
<i>Ophisaurus ventralis</i> (eastern glass lizard)	+	+	DF, CB, HC
<i>Scincella lateralis</i> (ground skink)	+	+	CB, HC
<b>Snakes</b>			
<i>Agkistrodon piscivorus</i> (cottonmouth)	+	+	HC, RS
<i>Cemophora coccinea</i> (scarlet snake)	+	+	HC, RS
<i>Coluber constrictor</i> (racer)	+	+	CB, DF, HC, RS
<i>Crotalus adamanteus</i> (diamondback rattlesnake)	+	+	HC, RS
<i>Diadophis punctatus</i> (ring-necked snake)	+	+	CB, DF, HC, RS
<i>Drymarchon corais</i> (indigo snake)	+	+	HC, RS
<i>Elaphe guttata</i> (corn snake)	+	+	HC, RS
<i>Elaphe obsoleta</i> (yellow rat snake)	+	+	CB, HC, RS
<i>Farancia abacura</i> (mud snake)	+	+	MT, RS
<i>Heterodon platirhinos</i> (eastern hog-nosed snake)	+	–	—
<i>Lampropeltis getula</i> (common kingsnake)	+	+	HC, RS
<i>Lampropeltis triangulum</i> (scarlet kingsnake)	–	+	HC, RS
<i>Masticophis flagellum</i> (coachwhip)	+	+	DF, HC, RS
<i>Micrurus fulvius</i> (coral snake)	–	+	RS

TABLE 1. Continued.

Species	Ehrhart, 1976	This study	Successful methods
<i>Nerodia clarkii</i> (Atlantic saltmarsh snake)	—	+	HC
<i>Nerodia fasciata</i> (banded water snake)	+	+	MT, RS
<i>Nerodia floridana</i> (green water snake)	+	+	MT, RS
<i>Ophedrys aestivus</i> (rough green snake)	+	+	HC, RS
<i>Pituophis melanoleucus</i> (pine snake)	+	+	HC, RS
<i>Regina alleni</i> (striped crayfish snake)	+	+	MT, RS
<i>Rhadinaea flavilata</i> (pine woods snake)	—	+	CB
<i>Seminatrix pygaea</i> (black swamp snake)	—	+	MT
<i>Sistrurus miliarius</i> (pygmy rattlesnake)	+	+	RS
<i>Storeria dekayi</i> (brown snake)	+	+	RS
<i>Tantilla relicta</i> (coastal dunes crowned snake)	—	+	CB
<i>Thamnophis sauritus</i> (ribbon snake)	+	+	CB, DF, HC, MT, RS
<i>Thamnophis sirtalis</i> (garter snake)	+	+	CB, DF, HC, MT, RS
Salamanders			
<i>Amphiuma means</i> (two-toed amphiuma)	—	+	MT
<i>Notophthalmus viridescens</i> (red-spotted newt)	—	+	HC, MT
<i>Siren intermedia</i> (lesser siren)	+	+	MT
<i>Siren lacertina</i> (greater sire)	+	+	MT
Anurans			
<i>Acris gryllus</i> (southern cricket frog)	+	+	AC, HC, MT
<i>Bufo quercicus</i> (oak toad)	+	+	AC, CB, DF, HC
<i>Bufo terrestris</i> (southern toad)	+	+	CB, DF, HC, RS
* <i>Eleutherodactylus planirostris</i> (greenhouse frog)	+	+	CB, HC
<i>Gastrophryne carolinensis</i> (narrow-mouthed toad)	+	+	AC, CB, DF, HC
<i>Hyla cinerea</i> (green tree frog)	+	+	AC, DF, HC, MT, RS
<i>Hyla femoralis</i> (pinewoods tree frog)	+	+	AC, DF, HC
<i>Hyla gratiosa</i> (barking tree frog)	+	+	AC, HC
<i>Hyla squirella</i> (squirrel tree frog)	+	+	AC, DF, HC, MT, RS
<i>Pseudacris nigrita</i> (chorus frog)	+	+	AC
<i>Pseudacris ocularis</i> (little grass frog)	+	+	CB, HC, RS
<i>Rana capito</i> (gopher frog)	—	+	HC
<i>Rana grylio</i> (pig frog)	+	+	AC, HC, MT, RS
<i>Rana utricularia</i> (leopard frog)	+	+	AC, CB, DF, HC, MT, RS
<i>Scaphiopus holbrookii</i> (spadefoot toad)	+	+	DF

<sup>1</sup> Methods are as follows: AC = Anuran Calling, CB = coverboards, DF = drift fences, HC = hand-collecting, MT = minnow traps, RS = road surveys, TT = turtle traps.

are removed from the analysis there was no significant difference between the samples ( $G = 1.53$ ,  $df = 3$ ,  $P = 0.675$ ).

DISCUSSION—*Changes in species composition*—In addition to providing the first comprehensive species list for this protected habitat, the primary result of our study is that virtually all of the species of amphibians and reptiles found at KSC by Ehrhart (1976) are still present today. Indeed, we

TABLE 2. Differences in relative counts of snakes captured by road-collecting between the late 1970s and the 1990s. All records come from samples taken along the "triangle" formed by Rts. 3, 402, and 406. Numbers of each species are followed by percent of total sample in parentheses. Because of errors in recording data, some of the records shown here were not included in the statistical analysis of the differences in the numbers of snakes found per km between the 1970s and the 1990s.

Species	1977–1979	1992–2000
<i>Agkistrodon piscivorus</i> (cottonmouth)	13 (13.0)*	3 (0.95)*
<i>Cemophora coccinea</i> (scarlet snake)	1 (1.0)	2 (0.63)
<i>Coluber constrictor</i> (racer)	2 (2.0)	11 (3.5)
<i>Crotalus adamanteus</i> (diamondback rattlesnake)	2 (2.0)	2 (0.63)
<i>Diadophis punctatus</i> (ring-necked snake)	0 (0.0)	5 (1.6)
<i>Drymarchon corais</i> (indigo snake)	0 (0.0)	1 (0.3)
<i>Elaphe guttata</i> (corn snake)	4 (4.0)	15 (4.7)
<i>Elaphe obsoleta</i> (yellow rat snake)	1 (1.0)	3 (0.95)
<i>Farancia abacura</i> (mud snake)	2 (2.0)	3 (0.95)
<i>Lampropeltis getula</i> (common kingsnake)	1 (1.0)	0 (0.0)
<i>L. triangulum</i> (scarlet kingsnake)	0 (0.0)	1 (0.3)
<i>Nerodia fasciata</i> (banded water snake)	17 (17.0)	69 (21.8)
<i>Nerodia floridana</i> (green water snake)	5 (5.0)	5 (1.6)
<i>Regina alleni</i> (striped crayfish snake)	1 (1.0)	4 (1.3)
<i>Storeria dekayi</i> (brown snake)	1 (1.0)	0 (0.0)
<i>Thamnophis sauritus</i> (ribbon snake)	46 (46.0)	166 (52.4)
<i>Thamnophis sirtalis</i> (garter snake)	4 (4.0)	27 (8.5)
Number of snakes found (N)	100	317
Number of surveys (km driven)	24 (640)	78 (2811)

\* (percent)

documented an additional 14 species since the 1970s, likely due to a combination of more comprehensive collecting methods and recent species introductions. Some of these "new" species (e.g., brown anoles, Indo-Pacific geckos, and Mediterranean geckos) are exotics and probably represent recent introductions to the site, whereas others (e.g., black swamp snakes, island glass lizards, two-toed amphiumas, and red-spotted newts) probably were found in the 1990s because of the broader array of sampling methods employed during that period (see list of successful methods in Table 1). Examples of species that were strongly "method-specific" include black swamp snakes (commonly found using minnow traps but not found with any other method), pine woods snakes (found only under coverboards), and red-spotted newts (found mainly using minnow traps) (Table 1). Gibbons and co-workers (1997) found a similar "increase" in species richness over time on a large protected site in South Carolina. Our results showing a stable or higher species richness is particularly notable for amphibians, since some parts of the world are experiencing rapid losses in amphibian species (Vitt et al., 1990; Pounds et al., 1997).

The eastern hognose snake was the only species known from KSC that was not found from 1992–2000. However, this species was known from

only a single sighting in the 1970s (Ehrhart, 1976), so the absence of eastern hognose snakes in the 1990s could reflect either a true loss of the species, the lack of a reliable collecting method, or random chance (i.e., low abundance means the probability of an encounter is low at any given point in time).

*Long-term changes in numbers*—Although virtually all species of amphibians and reptiles present at the KSC in the 1970s are found there today, this does not mean that all species have stable populations. There has been a quantifiable (but not statistically significant) decrease in the numbers of snakes found on the permanent survey route, and a significant change in the relative counts of these snakes as well. Interpreting the apparent changes in snake numbers is difficult, but three possibilities represent likely explanations. First, the differences may merely represent sampling (statistical) error. However, our sample sizes are relatively large (a total of 102 samples), were conducted during periods of suitable weather conditions during both sampling periods, and were taken over a large number of years. Second, these changes may represent random temporal fluctuations unrelated to anthropogenic effects. Pechmann and co-workers (1991) and Seigel and co-workers (1995) (among others) have cautioned against interpreting changes in reptile and amphibian populations as human-caused without sufficient data. Finally, these changes may be the result of human effects, especially habitat modifications (e.g., fragmentation due to road construction and loss of freshwater habitats due to salt marsh restoration) and the cumulative effects of road mortality along our survey routes (Rosen and Lowe, 1994). However, except for changes in salinity due to salt marsh restoration (see below), we are unaware of any major habitat modifications along the routes surveyed, and cannot explain why cottonmouths showed such a strong decrease in numbers. Road mortality is very common at KSC, but other snakes species besides cottonmouths are killed by cars. Additional data assessing the effects of road mortality, and the effects of roads and impoundments on population fragmentation, would be highly desirable.

Other changes in herpetofauna of the KSC are also notable. For example, diamondback terrapins have undergone a dramatic reduction in numbers (likely due to raccoon predation, crab trapping, and habitat alterations), and are now uncommon to rare on the site (Seigel, 1993). In addition, gopher tortoises at the KSC have a high rate of infection with Upper Respiratory Tract Disease, a potentially fatal bacterial disease (Brown et al., 1994; Smith et al., 1998) that is suspected to have killed more than 40 adult tortoises at the KSC since 1998 (R. Seigel, unpubl. data). Finally, more exotic species may soon occur at the KSC, since both the tropical gecko (*Hemidactylus mabouia*) and the crested anole (*Anolis cristatellus*) were found in nearby Titusville in 1998 (Criscione et al., 1998; Seigel et al., 1999), and the Cuban treefrog (*Osteopilus septentrionalis*) has been found just south of the KSC (M. Epstein, 2000).

Changes in the status of amphibians and reptiles at the KSC are, obviously, a dynamic process that no single study can document adequately. For example, in conjunction with state agencies, the USFWS has recently undertaken a major initiative to convert human-created freshwater impoundments back to more natural brackish water marshes (M. Epstein, 2000). This restoration process has already caused noticeable changes in amphibian and reptile abundance at the KSC. One of our long-term monitoring sites for aquatic snakes and sirens went from freshwater to 42 ppt saltwater within a six month period in 1999. Consequently, sirens and aquatic snakes disappeared from this site and were absent as long as the water was brackish. Obviously, a long-term monitoring program is required to determine the effects of these and other changes in the herpetofauna of the KSC. NASA has committed to funding such a program for the foreseeable future.

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FIRST RECORD OF A WHITE TIGER SHARK, *GALEOCERDO CUVIER*, FROM THE NORTHEASTERN GULF OF MEXICO—*Steven J. Rider*<sup>(1)</sup>, *Michael Athorn*<sup>(2)</sup>, and *George O. Bailey*<sup>(3)</sup>, <sup>(1)</sup>Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, 350 Carroll Street, Eastpoint, FL 32328, USA, <sup>(2)</sup>F/V Margaritas, Scipio Creek Municipal Marina, Apalachicola, FL 32320, USA, <sup>(3)</sup>Florida Department of Environmental Protection, Apalachicola National Estuarine Research Reserve, 350 Carroll Street, Eastpoint, FL 32328, USA

ABSTRACT: A white female tiger shark, *Galeocerdo cuvier*, was caught on September 30, 1999, by a fishing vessel operating in the northeastern Gulf of Mexico. White specimens have been reported in several other species of elasmobranchs. However, this is the first documented record of a white specimen occurring in this species.

**Key Words:** Tiger shark, albino, coloration, chromatophores

ALBINO and white elasmobranch specimens are rare. Only twenty-five specimens composed of seventeen species from twelve families have been reported. Ten of these specimens from the following species: sevengill shark (*Notorynchus maculatus*), tawny nurse shark (*Nebrius concolor*), basking shark (*Cetorhinus maximus*), zebra shark (*Stegostoma fasciatum*), gray smoothhound (*Mustelus californicus*), Japanese topeshark (*Hemitriakis japonica*), spiny dogfish (*Squalus acanthias*), thornback skate (*Raja clavata*), common stingray (*Dasyatis pastinata*), and cownose ray (*Rhinoptera bonasus*), were reported as partial albinos (Traquair, 1893; Herald, 1953; Joseph, 1961; Cohen, 1973; Nakaya, 1973; Capape and Pontoustier, 1975; Froiland, 1975; Furata, 1985; Taniuchi and Yanagisawa, 1987). However, partial albino may be an inaccurate term. These aforementioned specimens were white in color, but the irises were reported as having pigment; thus, not albinos. White animals lack pigment in the chromatophores, while albino animals have colorless chromatophores. That is, their bodies were unable to form melanin because of one or several metabolic defects, which is albinism (King and Stansfield, 1996). This genetic trait has rarely been observed in elasmobranchs. Only eight elasmobranch albino specimens composed of four species from three families have been reported. These species were gray smoothhound (*Mustelus californicus*), leopard shark (*Triakis semifasciata*), scalloped hammerhead shark (*Sphyrna lewini*), common torpedo (*Torpedo torpedo*) and in each specimen the irises were pink, indicating colorless chromatophores (McKenzie, 1970; Talent, 1973; Follet, 1976; Brahim et al., 1998). Six specimens from the following species: nurse shark (*Ginglymostoma cirratum*), blue skate (*Raja batis*), cuckooray (*Raja naevus*), southern stingray (*Dasyatis americana*), and cownose ray (*Rhinoptera bonasus*), were reported as white specimens (Wilson, 1951; Schwartz, 1959; Schwartz and Safrit, 1977; Castro, 1998). Herald and co-workers (1960) reported the cap-

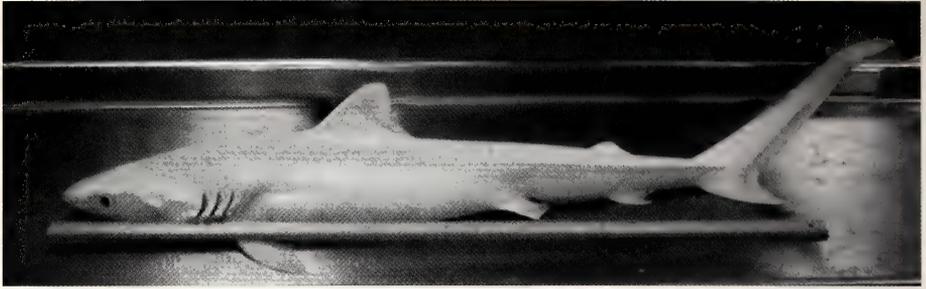


FIG. 1. A white female tiger shark, *Galeocerdo cuvier*, 124 cm total length, caught in the northeastern Gulf of Mexico.

ture of a white gray smoothhound, however it was unclear if this was a white individual or an albino. This note reports the collection of a white specimen from the family Carcharhinidae, or requiem sharks, captured in the Gulf of Mexico.

The white tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822), was caught on September 30, 1999. The locality was approximately 93-km southeast of Apalachicola, Florida along the 10-fathom curve (29.50° N, 85.21° W). The specimen was caught aboard the long-line fishing vessel, *F/V Margaritas*, while fishing for sharks. The specimen was verified as a tiger shark using the diagnostic characteristics as described by Castro (1996). The precaudal length of the white tiger shark was 124 cm and the weight was 7 kg.

The natural coloration was white, with the dorsal and ventral surfaces completely white (Figure 1). The dorsal dark spots, which give juvenile tiger sharks a mottled appearance were visible, although they were faint. Both irises were light brown in color. Based on reported length-at-ages by Branstetter and co-workers (1987), Castro (1996), and Winter and Dudley (2000), this specimen was less than 1 year of age. The white tiger shark was mounted and is currently on display at the Florida Department of Environmental Protection's Apalachicola National Estuarine Research Reserve in Apalachicola, Florida.

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## SEEDBANKS AND THEIR POTENTIAL ROLE IN THE VEGETATION DYNAMICS OF A NORTHERN EVERGLADES MARSH

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**ABSTRACT:** *The Florida Everglades, an ecosystem suffering from decades of human impact, will undergo hydrologic and nutrient restoration through surface water discharges from Stormwater Treatment Areas (STAs). The potential for vegetation change in response to these restoration efforts, as well as natural disturbances, may be influenced by the existing seedbank composition. Soils in Water Conservation Area 2A, which will receive STA discharges, were cored to a depth of 5 cm in May 1998 and to 5, 10, and 20 cm in October 1998. Seedling emergence assays were used to characterize the seedbank of these soils in relation to existing vegetation and restoration target species. In both assays, *Typha domingensis* seedlings only emerged from the 0–5 cm layer of soils collected from *Typha*-dominated sites. In contrast, two species that are primary indicators of unimpacted wet prairie/slough habitat (*Rhynchospora* spp. and *Eleocharis* spp.) were far more abundant in *Cladium jamaicense*-dominated soils. No emergence of *C. jamaicense* seedlings occurred in either assay. In addition, to observe natural seedbank recruitment from nutrient-enriched soils, vegetation was manually cleared from four 16m<sup>2</sup> field plots at three different *Typha*-dominated areas. In each plot, a virtually monospecific plant community comprised of *Amaranthus australis* became established. The results of this study indicate that seedbank recruitment of *T. domingensis* outside the boundaries of existing populations in this region may be quite limited. Furthermore, the contribution of the seedbank to restoration of *Rhynchospora*/*Eleocharis* wet prairie and *C. jamaicense* habitat may be negligible given that viable seeds of these species appear to be few and have a narrow distribution range in this region. The results are discussed in the context of vegetation management and restoration.*

**Key Words:** Everglades, *Typha domingensis*, *Cladium jamaicense*, seedling emergence, seedbank, plant communities

OVER the past half-century, the Florida Everglades have experienced large-scale alterations in hydrology and anthropogenic nutrient-enrichment, resulting in significant changes in wetland vegetation (Davis, 1994; Gunderson, 1994). One of the most conspicuous changes has been the gradual replacement of sawgrass (*Cladium jamaicense*, Crantz.) plains and wet prairie communities (characterized by an abundance of *Rhynchospora* spp. and *Eleocharis* spp.) with dense stands of cattail (*Typha domingensis*, Pers.) (Loveless, 1959; Gunderson, 1994; Craft et al., 1995; Doren et al., 1996). Preventing further expansion of *T. domingensis* is an important short-term

priority of Everglades restoration. A significant reduction in *T. domingensis* coverage, accompanied by re-establishment of *C. jamaicense* and *Rhynchospora/Eleocharis* spp. habitat, is a longer-term objective.

As part of the effort to restore hydrology and nutrient levels to historic Everglades conditions, a series of Stormwater Treatment Areas (STAs) have been constructed to deliver naturally filtered surface water to designated marsh regions. The western margin of Water Conservation Area 2A (WCA-2A) will be the recipient of discharge from Stormwater Treatment Area 2 (STA-2). Because natural water flows in WCA-2A have been severely altered by impoundment, this region tends to dry out for a substantial portion of the year (Smith et al., 2000). In addition, a gradient in water quality, soil chemistry, and macrophyte vegetation exists as a result of direct inputs of Hillsboro canal water that occurred during the 1990s (Fitz and Sklar, 1999; Rutchey and Vilchek, 1999). While total nitrogen content of the soil varies little with location or soil depth, total phosphorus (TP) exhibits a distinct gradient with decreasing concentrations towards the south and into the interior of the marsh (DeBusk et al., 1994; Smith et al., 2000) (Figure 1). This corresponds with a transition in vegetation from *T. domingensis* to *C. jamaicense* and finally to *C. jamaicense* interspersed with *Rhynchospora* spp. and *Eleocharis* spp. wet prairie.

Plant communities in this region may change as seedbank recruitment is stimulated by the addition of STA-2 outflow water to soils that are very dry for up to seven months out of the year. This, combined with natural disturbance events such as fires or drought, may provide an opportunity for vegetation changes through seed germination (Leck and Graveline, 1979; Pederson and van der Valk, 1983; Smith and Kadlec, 1984; Williges and Harris, 1995). However, the composition of the existing seedbank is unknown. Consequently, there is no basis to assess the potential for recruitment of undesirable (e.g., *T. domingensis*) vs. desirable (e.g., *C. jamaicense*, *Rhynchospora* spp., *Eleocharis* spp.) species into areas that lie outside their current distributions.

Seedling emergence assays are commonly used to analyze seedbank composition and predict vegetation changes (van der Valk and Davis, 1978; Smith and Kadlec, 1984; Leck and Simpson, 1995). As summarized by van der Valk and Rosburg (1997), who described seedbanks from eastern WCA-2A, seedling emergence assays that include 1) areas not previously assessed for seedbank composition, 2) seasonality, and 3) vertical distribution of seeds would be very useful in obtaining a complete understanding of Everglades seedbank communities and potential vegetation dynamics.

In this study, seedling emergence assays were conducted at two different times of the year (March and October, 1998) using soils from the STA-2 discharge receiving area of western WCA-2A. In the October assay, different depth increments were collected and assayed to encompass the historic seedbank. Our primary objective was to provide information on the existing seedbank composition, establish the distribution of seedbank species with



FIG.. 1. Map of South Florida depicting, WCA-2A (enlarged shaded area), sampling locations (open circles), approximate boundaries of vegetation communities, and site-specific soil TP concentrations.

respect to the existing vegetation gradient, and 3) identify persistent species within the seedbank. We hypothesized that since the reproductive output of *T. domingensis* is very high and seeds are wind-dispersed, seedling emergence of this species would be observed in soils collected from both *Typha* sites and non-*Typha* sites that are distant from existing stands. Conversely, emergence of *Cladium jamaicense*, *Rhynchospora* spp. and *Eleocharis* spp. whose seeds are dispersed by surface water flows may be restricted to sites closer to established populations. Such information may be useful in assessing the potential for vegetation changes and, therefore, addressing vegetation restoration and management strategies.

**METHODS—Study area**—Fifteen permanent sampling sites were established in western WCA-2A as part of an ongoing monitoring program to document changes associated with future STA-2 operation. A total of 15 sampling sites are located at 0.25, 0.5, 1.0, 2.0, and 4.0 km

away from the western boundary along three parallel transects (north-N, central-C, and south-S) oriented in the anticipated direction of water flow from future STA discharge (Figure 1).

Previous analyses of soils from this area revealed a TP concentration gradient corresponding with a transition in vegetation (Smith et al., 2000). For example, TP concentrations in the 0–2 cm soil layer under cattail communities averaged  $165 \pm 15 \mu\text{g}/\text{cm}^3$  while those under sawgrass averaged  $89 \pm 10 \mu\text{g}/\text{cm}^3$ . Soils from the sawgrass/wet prairie/slough community at the most interior site had a much lower TP-value of  $44 \mu\text{g}/\text{cm}^3$  (Figure 1). For reference, concentrations in unimpacted Everglades regions are typically  $< 40 \mu\text{g}/\text{cm}^3$  (Reddy et al, 1998).

*Sample collection and processing*—Soil samples were collected from each site in May and October of 1998 in an effort to include pre- and post-flowering/fruited periods for a large number of species, including those of most importance to restoration objectives—i.e., *Rhynchospora* spp. (spring/summer), *T. domingensis* (spring/summer), *E. cellulosa* (year-round), and *C. jamaicense* (summer/fall). Three replicate soil samples (0–5 cm layer) were collected from each of the 15 sites using a 10-cm diameter aluminum coring tube. In October, two additional soil layers (5–10 and 10–20 cm) were obtained and assayed to provide a rough depth profile. The cores were transported to a greenhouse facility where they were refrigerated for approximately 2 weeks before use.

Just prior to the assays, the soil samples were thoroughly mixed and any large plant debris removed to prevent vegetative reproduction from remnant roots/rhizomes. Each sample was then divided into three equal volumes and transferred to 1.1L pots (154 cm<sup>2</sup> surface area), which were randomly positioned in fiberglass tubs (1.2 × 1.2 × 0.3 m) and filled with tap water. Previous analyses of the tap water indicated TP concentrations of  $\sim 0.16 \text{ mg}/\text{L}$ , which is similar to or higher than concentrations found in surface waters of nutrient-enriched regions of the northern Everglades (Reddy et al 1993, Stewart et al 1997). High TP water was used to dampen the potentially confounding effect of soil nutrient levels on germination. In this way, we would be better able to identify seeds from oligotrophic sites that may not have germinated under low nutrient conditions.

Water levels were maintained to provide saturated conditions (water level at or very close to soil surface) representing near optimal germination conditions for *T. domingensis*, *C. jamaicense*, *Rhynchospora* spp, *Eleocharis* spp. as well as other wetland plants (Smith and Kadlec, 1984; van der Valk and Pederson, 1989; Vaithyanathan et al., 1997). Moreover, the temporal and spatial extent of soil saturation in this region of the Everglades is expected to increase as desiccated soils are rehydrated with STA outflow. The fiberglass tubs were placed underneath enclosures with screen sidewalls and clear Lexan<sup>®</sup> lids to allow light penetration while diverting precipitation and preventing contamination from airborne seed. The enclosures themselves were located outdoors in order to expose the soils to more natural conditions of temperature and irradiance.

Once identified, plants were removed before they could produce seed themselves. In a few cases, where identification could not initially be made, plants were removed and repotted in separate containers where they were grown until an inflorescence was produced and used for identification (Godfrey and Wooten, 1981; Tobe et al., 1998; Wunderlin, 1998). The numbers of seedlings of each species were counted as they emerged. Additionally, the date of emergence for the first seedling of selected species was recorded. Both assays were monitored until emergence ceased ( $\sim 6$  months).

*Natural seedbank recruitment*—In addition to these controlled assays, natural seedling emergence and plant community development was observed in three sets of four field plots (4m × 4m) located at sites N<sub>0.25</sub>, N<sub>0.5</sub>, and N<sub>1.0</sub> in *T. domingensis* communities (Figure 1). On February 17, 1999, the aboveground biomass in each plot was manually cleared. To prevent vegetative re-growth from belowground parts, the rootstocks and rhizomes were severed with a bush axe. In one of the four replicate plots at each site, the top 10 cm of soil was removed by shovel to allow recruitment from lower soil layers. After 60 days, the number of species and percent cover was recorded.

TABLE 1. Mean numbers of seedlings per m<sup>2</sup> and species per container by site for May and October 1998 assays.

Site	May seedlings	Oct seedlings	May species	Oct species
N.25	259 ± 112	1,147 ± 243	2.7 ± 0.88	4.7 ± 1.76
N.5	757 ± 151	1,688 ± 603	4.0 ± 0.58	6.3 ± 3.84
N1	389 ± 37	584 ± 99	2.3 ± 0.33	4.3 ± 1.33
N2	519 ± 198	389 ± 198	4.7 ± 1.20	4.0 ± 2.51
N4	43 ± 43	0	0.7 ± 0.66	0
C.25	281 ± 43	1,298 ± 487	3.0 ± 0.57	4.6 ± 2.18
C.5	562 ± 213	1,493 ± 245	2.3 ± 0.66	4.3 ± 2.96
C1	909 ± 694	952 ± 336	20 ± 1.52	4.7 ± 2.40
C2	194 ± 64	606 ± 255	20 ± 0.57	3.7 ± 2.02
C4	194 ± 163	173 ± 21	0.7 ± 0.33	1.7 ± 0.66
S.25	303 ± 177	649 ± 343	2.3 ± 0.66	2.3 ± 1.45
S.5	216 ± 21	670 ± 57	1.6 ± 0.33	5.0 ± 2.08
S1	389 ± 135	584 ± 234	2.3 ± 0.66	2.3 ± 0.88
S2	1,147 ± 727	822 ± 375	4.3 ± 0.33	4.7 ± 2.66
S4	173 ± 78	216 ± 86	1.3 ± 0.33	1.33 ± 0.66

*Data analysis*—All data were log-transformed to improve normality and homogeneity of variances. Data from the May assay were subjected to one-way ANOVA with location (site) as the primary source of variation. For the October assay, a two-way ANOVA was used to interpret location and soil depth effects. Least Significant Difference (LSD) tests ( $\alpha = 0.05$ ) evaluated differences between specific means. In addition, Sorenson's Index value (Morrison et al., 1992) was calculated to estimate species similarity between the two assays. All data are summarized in Appendices I and II.

**RESULTS—May assay—community**—Mean numbers of seedlings exhibited enormous spatial variation ranging between 43 seedlings/m<sup>2</sup> (N<sub>4.0</sub>) and 1,147 seedling/m<sup>2</sup> (S<sub>2.0</sub>) with the lowest numbers consistently occurring at the most interior (4.0-km) sites along each transect (Table 1). Because of high replicate variability, however, site differences for this measure were not statistically significant. The total number of species (all sites) observed in the assay was 17. Among sites, species richness varied significantly, ranging between 0.66 (C<sub>4.0</sub>) and 4.66 (N<sub>2.0</sub>) species per site (Table 1). The most interior marsh sites generated the fewest species; otherwise, no clear spatial trends were evident.

*Restoration target species*—*T. domingensis* was virtually absent in this assay as only one seedling emerged from one replicate sample. This occurred in soil collected from N<sub>0.25</sub>, which is a *Typha*-dominated area (Table 2). *C. jamaicense* did not emerge from any samples. *Rhynchospora* spp. seedlings were found in the highest numbers from the *Cladium*-dominated sites S<sub>1.0</sub> and S<sub>2.0</sub> (Table 2). *Rhynchospora divergens* Chapm. ex M.A. Curtis was the only species identified from this genus. When data were pooled by transect, *Rhynchospora* numbers were significantly higher in S- compared to N- or

TABLE 2. Mean numbers of seedlings/m<sup>2</sup> for selected species by site in the May assay.

Site	<i>Amaranthus</i>	<i>Typha</i>	<i>Rhynchospora</i>	<i>Eleocharis</i>
N.25	86 ± 57	21 ± 21	0	0
N.5	346 ± 78	0	21 ± 21	0
N1	173 ± 114	0	43 ± 43	0
N2	0	0	86 ± 57	0
N4	0	0	21 ± 21	0
C.25	43 ± 21	0	129 ± 37	0
C.5	0	0	0	0
C1	21 ± 21	0	0	0
C2	0	0	0	0
C4	0	0	194 ± 163	0
S.25	0	0	21 ± 21	0
S.5	0	0	64 ± 37	0
S1	0	0	281 ± 94	0
S2	0	0	735 ± 546	0
S4	0	0	86 ± 21	86 ± 86

C-transect soils (Table 4). *E. cellulosa* Torr. was found only in samples collected from the S<sub>4.0</sub> site (Table 2).

*Others*—*Amaranthus australis* (Gray) Sauer emerged from soils collected at many different sites but in significantly higher numbers from the *T. domingensis*-dominated sites (N<sub>0.5</sub> and N<sub>1.0</sub>) (Table 2). *Ammania coccinea* Rottb. emerged only from N-transect soils and was most abundant in samples from N<sub>0.5</sub> (Appendix I). *Ludwigia repens* Forst. dominated the soils from N<sub>2.0</sub>, C<sub>0.5</sub>, and C<sub>1.0</sub>. *Mitreolea petiolata* (J.F. Gmel.) T.&G., a species commonly found in disturbed wetlands (Tobe et al 1998), was dominant in C<sub>1.0</sub>, C<sub>2.0</sub>, S<sub>0.25</sub>, and S<sub>0.5</sub> soils. *Eustachys petrea* (Sw.) Desv., a grass that is abundant in upland habitats (Tobe et al 1998) emerged from soils of many different sites.

*Amaranthus australis* and *Rhynchospora* spp. were the first species to emerge after 16 and 15 days respectively (Appendix I). *Typha domingensis* emerged after 54 days. *E. cellulosa* emerged at the latest date, after 118 days.

*October assay—community*—Mean numbers of seedlings varied significantly among sites, ranging between 0 (N<sub>4.0</sub>) and 1,688 seedlings/m<sup>2</sup> (N<sub>0.5</sub>) within the 0–5 cm layer (Table 1). Similar to the May assay, the interior (4.0-km) sites generated the fewest plants. Numbers also decreased significantly with soil depth and were more similar among stations (Appendix II). A total of 23 different species was recorded in this assay. Among sites, mean numbers of species per site ranged between 0 (N<sub>4.0</sub>) and 6.33 (N<sub>0.5</sub>), although high replicate variability rendered these differences statistically insignificant (Table 1). Once again, however, the 4.0-km sites were the least diverse.

TABLE 3. Mean numbers of seedlings/m<sup>2</sup> for selected species by site in the October assay by site.

Site	<i>Amaranthus</i>	<i>Typha</i>	<i>Rhynchospora</i>	<i>Eleocharis</i>
N.25	151 ± 86	476 ± 57	64 ± 64	0
N.5	562 ± 323	129 ± 129	151 ± 120	0
N1	216 ± 78	216 ± 94	0	0
N2	0	0	0	0
N4	0	0	0	0
C.25	0	0	129 ± 37	0
C.5	0	0	21 ± 21	0
C1	0	0	0	0
C2	0	0	151 ± 120	0
C4	0	0	129 ± 37	0
S.25	0	0	43 ± 21	0
S.5	0	0	108 ± 21	0
S1	0	0	519 ± 224	0
S2	0	0	194 ± 37	0
S4	0	0	43 ± 43	173 ± 114

*Restoration target species*—*T. domingensis* seedlings emerged only from the 0–5 cm layer and only from *Typha*-dominated sites (N<sub>0.25</sub>, N<sub>0.5</sub>, N<sub>1.0</sub>), with the highest numbers (476 seedlings/m<sup>2</sup>) occurring in N<sub>0.25</sub> soils (Table 3). No seedlings of *C. jamaicense* emerged from any samples. *Rhynchospora* spp. grew from soils of many sites, but was much more abundant in those collected from S<sub>1.0</sub>. Pooled by transect, *Rhynchospora* seedling numbers were again significantly higher from the S-transect than the N-transect (Table 3). Three species of this genus were identified as *R. divergens*, *R. microcarpa* Balw. ex Gray, and *R. inundata* (Oakes) Fern. Similar to the May assay, *E. cellulosa* emerged only from S<sub>4.0</sub> samples (Table 3).

*Others*—*A. australis* emergence was restricted to *Typha*-dominated sites but was the most abundant species in N<sub>0.5</sub> and N<sub>1.0</sub> soils (Table 3; Appendix II). *A. coccinea* emerged only from N-transect soils. *Dichondra carolinensis* Michx., a plant common to disturbed wetlands (Tobe et al., 1998), was abundant in N<sub>0.25</sub> and N<sub>0.5</sub> soils but did not emerge from samples collected along the C- or S-transect. *Mitreola petiolata* was abundant throughout C- and S-transect soils.

The numbers and degree of spatial variation of both seedlings and species decreased significantly with soil depth (Appendix II). *T. domingensis*,

TABLE 4. Mean numbers of *Rhynchospora* spp. seedlings/m<sup>2</sup> by transect.

Transect	May	Oct
north	34 ± 15	47 ± 27
central	64 ± 35	95 ± 28
south	238 ± 117	181 ± 61

*D. carolinensis*, *Sagittaria lancifolia*, *A. coccinea*, *Cyperus* spp., *Pluchea odorata*, *Mikania scandens* and *R. inundata* seedlings were all restricted to the 0–5 cm. *E. cellulosa* seedlings did not grow from deeper layer soils. *Rhynchospora* spp. emerged from the 5–10 and 10–20 cm layers, although in significantly lower numbers compared to the 0–5 layer. *A. australis* emerged from both the surface (0–5) and deep layer (5–10, 10–20) soils at sites N<sub>0.25</sub>, N<sub>0.5</sub> and N<sub>1.0</sub>. *A. coccinea* appeared in the 2–10 and 10–20 cm layers collected from N<sub>0.25</sub>. *Polygonum hydropiperoides* Michx. germinated from all layers of the N- and C-transect samples (Appendix I).

Time until first emergence varied greatly among the different species but exhibited similarities to the May assay. *Amaranthus australis* and *Rhynchospora* spp. were the first species to emerge after 22 days. *T. domingensis* appeared after 69 days. *Dichromena colorata* and *E. cellulosa* required the longest times of 124 and 152 days, respectively.

*Assay comparison*—Only two species that were present in the May assay failed to appear in the October assay. These were *Eupatorium capillifolium* (Lam.) Small and *Eustachys petrea* (Sw.) Desv. However, nine new species were recorded in the October assay that were absent from the May assay including *Dichondra carolinensis*, *Lythrum alatum* Pursh., *Rorripa terres* (Michx.) Stuckey, *Kostelyskya virginica* (L.) Presl. Ex Gray, *Pluchea odorata* (L.) Cassini, *Ludwigia microcarpa* Michx., *Ludwigia peruviana* (L.) Hara, *Centella asiatica* (L.) Urban, and *Dichromena colorata* (L.) Hitchc. (Appendix II). Despite these differences, the Sorenson index value was 0.75, indicating that overall species similarity between the March and October assay was relatively high.

*Seedling emergence and plant community development in cleared field plots*—After approximately 14 days (March 2, 1999), *A. australis* had become the dominant species in every plot at all sites, including those in which the top 10 cm of soil had been removed. By May of 1999, these plants formed a tall, dense canopy > 2 m in height with only a few scattered *P. hydropiperoides* surviving in the under-story. At this time, canopy cover of *A. australis* was estimated to be 100% (Figure 2). This community persisted for 10 months until a large fire in June 1999 obliterated the vegetation and plot boundary markers. The plots themselves subsequently could not be relocated.

*DISCUSSION*—In comparing the results of this work to findings reported by van der Valk and Rosburg (1997) and Vaithyanathan (1997) from eastern WCA-2A, similarities exist with respect to *T. domingensis*, *A. australis*, *Rhynchospora* spp. and *Eleocharis* spp. Each study found that the emergence *T. domingensis* and *A. australis* was highest in *Typha*-dominated, P-enriched habitats and that *Rhynchospora* spp. and *Eleocharis* spp. seedlings were largely restricted to *Cladium*-dominated, unenriched habitats. However, van



FIG. 2. Natural seedbank recruitment approximately 3 months after plots were cleared of *T. domingensis*. Community is dominated by *A. australis* with no emergence seedlings or vegetative shoots of *T. domingensis*.

der Valk and Rosburg (1997) did observe some *Typha* emergence in soils collected from *Cladium*-dominated habitats, which did not occur in our study. One possible reason for this discrepancy is the large difference in hydroperiod between the two regions. Western WCA-2A is approximately 1 ft higher in elevation than the eastern portion and we suspect that prolonged desiccation in the former may have a negative effect on seed production, seed dispersal via surface water flow, and/or seed viability—a hypothesis that is currently under investigation.

An alternative explanation for the apparent limited distribution of viable *Typha* seed is that despite the presumed ability of seed to travel long distances by wind, dispersal may be geographically confined to areas within relatively close proximity to existing stands. With regard to soil-related effects on germination and emergence, we do not suspect that nutrient limitation contributed significantly to the absence of cattail emergence from lower TP soils from the C- and S-transect in this study. One reason is that the water used to saturate the soils in the experiment was enriched (~0.16 mg/L TP). In addition, Stewart et al. (1997) showed that the germination rate of *T. domingensis* is relatively constant over a wide range of P concentrations (0.200 to 0.008 mg/L).

Only one seedling of *T. domingensis* appeared in pre-flowering samples (May) and no seedlings emerged from deeper core layers suggesting a short period of seed viability. Seedlings were more abundant in October soils, which can probably be attributed to time of collection since seed maturity and dispersal peaks in July (Miao and Sklar, 1998). In contrast, seeds of *T.*

*latifolia* L. and *T. angustifolia* L. have been reported to retain viability for years (Leck and Graveline, 1979; Leck and Simpson, 1987). Differences in this trait may be genetic (McNaughton, 1966). It is also possible that environmental conditions such as high soil temperatures enhance the microbial degradation of seeds or that the experimental conditions of hydrology, temperature, and/or irradiance were sub-optimal for *T. domingensis* germination. Additionally, phytotoxic substances from decaying *T. domingensis* plants may inhibit the germination of their own seeds as well as other species (Gallardo-Williams et al., 2001). In any event, it appears that the potential for invasive population growth by seedbank recruitment may be quite limited for *T. domingensis* at certain times of the year.

*Amaranthus australis* emerged in high numbers and from deeper core layers—indicating a persistent seed bank—but also was largely restricted to *T. domingensis*-dominated, high TP sites. Van der Valk and Rosburg (1997) reported a similar trend for this species. Our field plot observations confirmed that which can be predicted from the seedling emergence assays—i.e. that *A. australis* is the dominant seedbank species in *Typha*-dominated habitats. *Typha* seedling emergence in these plots may have been suppressed by the rapid germination and growth of *A. australis*, a plant that would also be undesirable as a major part of the wetland plant community. However, the relative abundance of this species (an annual plant) may be fairly easy to manage using high water levels to eliminate the adult population and suppress seedbank recruitment. Given what appears to be the transient nature of *T. domingensis* seedbanks, the establishment of such non-*Typha* vegetation for a period of time may substantially diminish the potential for future seedbank recruitment of *T. domingensis*. Controlling plant community development in this way may prove useful in restoring important Everglades landscape features such as slough and wet prairie communities.

In addition to seedling emergence, absolute numbers of *A. australis* seeds (viable or not) in soils from eastern WCA-2A are reportedly much higher in cattail areas that have developed immediately downstream from canal discharge structures (van der Valk and Rosburg, 1997). A similar pattern was observed for the emergence of *A. coccinea*—a species that under certain conditions can exhibit rapid weed-like growth requiring chemical control (Byrd and McDaniel, 1998). Water supplied to the STAs comes from an extensive network of canals, which pass through areas of many different land uses. Consequently, STA discharge water may potentially contain species that are not associated with sawgrass and/or wet prairie communities. Secondly, there may be seed rain from plant species growing in the STAs and surrounding uplands into adjacent marsh areas that otherwise would not receive this material. In these assays, total numbers of seedlings and species were lowest at sites furthest from the perimeter levee that separates western WCA-2A from agricultural fields and drained wetlands. Furthermore, with the exception of *E. petrea* at N<sub>4,0</sub> (May 1999), these interior soils only produced seedlings of *Rhynchospora* and *Eleocharis*—species that are indica-

tors of pristine Everglades wet prairie communities. In contrast, peripheral sites generated seedlings of many species, including those normally associated with upland habitats *D. carolinensis*, *E. capillifolium*, and *E. petrea*.

*Rhynchospora* spp. and *Eleocharis* spp. historically comprised a substantial portion of the wet prairie/slough vegetation of WCA-2A (David, 1996; Jordan et al., 1997). It has been estimated that there has been a 20% reduction in this habitat type since the 1970s (White, 1994). In this study, only one species of *Rhynchospora* (*R. divergens*) grew from May soils and three from the October soils (*R. divergens*, *R. inundata*, *R. microcarpa*). *Rhynchospora divergens* and *R. microcarpa* also emerged from the deepest core layers of several October samples suggesting seeds of each species may be long-lived. *Rhynchospora* spp. seedlings emerged from many different sites, suggesting that there is viable seed distributed over a wide area. This may facilitate the process of population expansion during hydrologic and nutrient restoration. In both assays, however, *Rhynchospora* spp. appeared in the highest numbers from the S-transect (collectively) and *Eleocharis* spp. was restricted to the southernmost interior site. In general, this region is characterized by decreasing densities of *C. jamaicense* with increasing numbers of *Rhynchospora* spp. towards S<sub>4,0</sub> where *Eleocharis* spp. is encountered. This vegetation gradient corresponds with a reduction in soil TP concentrations. In eastern WCA-2A, van der Valk and Rosburg (1997) also observed no emergence of *E. elongata* or *Rhynchospora* spp. from *T. domingensis*-dominated (high TP) soils despite the presence of intact seed in these samples. Vaithyanathan et al. (1997) found a significant decrease in *Eleocharis* spp. emergence with increasing concentrations of soil TP.

Diminished adult populations of *C. jamaicense*, *Rhynchospora* spp., and *Eleocharis* spp., in WCA-2A (translating to lower seed production) and limited dispersal by surface water (as a consequence of higher plant densities in enriched soils) may be an explanation for these observations. However it is also possible that seed germination, in species that evolved under very oligotrophic conditions, is inhibited by one or several soil constituents in nutrient impacted zones including allelopathic substances from *T. domingensis* (McNaughton, 1968).

Although the May and October assays were similar with respect to overall species composition (as indicated by Sorensons Index), the seasonal variation in seedling emergence of certain species has potential value in developing indirect (water control) and direct (mechanical) vegetation management strategies. For example, it may be preferable to establish water depths that suppress *T. domingensis* recruitment in the fall (post-flowering) when the viable seedbank appears to be larger compared to the spring (pre-flowering) (Miao et al., 1999). In this regard, flooded or deep-water conditions have been reported to inhibit seed germination in *T. domingensis* and other emergent species (Smith and Kadlec, 1984; Vaithyanathan et al., 1997). On the other hand, recruitment of *Rhynchospora* spp. may be enhanced by managing water to provide optimal germination conditions in fall

rather than spring. Regardless, different seedling communities may be recruited from the seedbank depending not only on hydrologic conditions, but also when those conditions occur.

Although the times until first emergence may not be representative of actual germination rates, the relative differences among species may be important in the context of restoration. For example, *Eleocharis* required the longest duration to appear in both assays. Therefore, under all but optimal conditions, *Eleocharis* would presumably be rapidly outcompeted by faster-germinating species. Consequently, reestablishment of this species through the existing seedbank may prove difficult until such conditions are established.

*C. jamaicense* did not emerge from any of the assayed soil samples or cleared field plots. Thus, the maintenance of *C. jamaicense* within this region is likely to be dependent upon nutrient and hydrologic conditions that foster competitive superiority through vegetative reproduction. Other species such as *Panicum hemitomon* Schult., *Paspalidium geminatum* (Forssk.) Stapf, and *Pontederia cordata* L. that frequently occur in non-impacted sawgrass and wet prairie habitats of WCA-2A (Gunderson, 1994) were not observed in either of the assays or field plots. Within the existing vegetation of western WCA-2A, these species occur only in small patches or as scattered individuals—the original populations having been lost within what is now an uninterrupted expanse of dense cattail and sawgrass. Under-representation of these species in the seedbank may further lengthen the process of restoration.

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APPENDIX I. Mean numbers of seedlings/m<sup>2</sup>, standard errors, and summed numbers of seedlings/site for the May assay (dominant species of existing vegetation at each site is listed in parentheses).

Sampling location	Mean	STE	Sum
N 0.25 ( <i>Typha domingensis</i> )			
<i>Amaranthus australis</i>	1.3	0.9	4.0
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Ludwigia repens</i>	0.3	0.3	1.0
<i>Polygonum hydropiperoides</i>	1.3	0.9	4.0
<i>Sagittaria latifolia</i>	0.7	0.7	2.0
<i>Typha domingensis</i>	0.3	0.3	1.0
N 0.5 ( <i>Typha domingensis</i> )			
<i>Amaranthus australis</i>	5.3	1.2	16.0
<i>Ammania coccinea</i>	2.7	1.7	8.0
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Ludwigia repens</i>	2.3	1.9	7.0
<i>Polygonum hydropiperoides</i>	0.7	0.3	2.0
<i>Rhynchospora divergens</i>	0.3	0.3	1.0
N 1.0 ( <i>Typha domingensis</i> )			
<i>Amaranthus australis</i>	2.7	1.8	8.0
<i>Ammania coccinea</i>	1.0	0.6	3.0
<i>Ludwigia repens</i>	0.7	0.7	2.0
<i>Mikania scandens</i>	1.0	1.0	3.0
<i>Rhynchospora divergens</i>	0.7	0.7	2.0
N 2.0 ( <i>Cladium jamaicense</i> )			
<i>Ammania coccinea</i>	0.3	0.3	1.0
<i>Centella asiatica</i>	0.7	0.7	2.0
<i>Cyperus odoratus</i>	0.3	0.3	1.0
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Ludwigia alata</i>	1.3	0.9	4.0
<i>Ludwigia repens</i>	1.7	1.7	5.0
<i>Mikania scandens</i>	0.3	0.3	1.0
<i>Mitreolea petiolata</i>	1.0	0.6	3.0
<i>Rhynchospora divergens</i>	1.3	0.9	4.0
<i>Sagittaria lancifolia</i>	0.7	0.3	2.0
N 4.0 ( <i>Cladium jamaicense</i> )			
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Rhynchospora divergens</i>	0.3	0.3	1.0
C 0.25 ( <i>Cladium jamaicense</i> )			
<i>Amaranthus australis</i>	0.7	0.3	2.0
<i>Eupatorium capillifolium</i>	0.3	0.3	1.0
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Ludwigia alata</i>	0.7	0.7	2.0
<i>Polygonum hydropiperoides</i>	0.3	0.3	1.0
<i>Rhynchospora divergens</i>	2.0	0.6	6.0
C 0.5 ( <i>Cladium jamaicense</i> )			
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Ludwigia alata</i>	1.7	1.7	5.0
<i>Ludwigia repens</i>	5.7	1.9	17.0

## APPENDIX I. Continued.

Sampling location	Mean	STE	Sum
<i>Mitreolea petiolata</i>	0.7	0.7	2.0
<i>Polygonum hydropiperoides</i>	0.3	0.3	1.0
C 1.0 ( <i>Cladium jamaicense</i> )			
<i>Amaranthus australis</i>	0.3	0.3	1.0
<i>Cyperus odorata</i>	0.3	0.3	1.0
<i>Ludwigia alata</i>	2.7	2.7	8.0
<i>Ludwigia repens</i>	3.3	3.3	10.0
<i>Mitreolea petiolata</i>	7.3	4.3	22.0
C 2.0 ( <i>Cladium jamaicense</i> )			
<i>Amaranthus australis</i>	0.3	0.3	1.0
<i>Cyperus odorata</i>	0.3	0.3	1.0
<i>Eustachys petrea</i>	0.3	0.3	1.0
<i>Mitreolea petiolata</i>	1.7	0.9	5.0
<i>Prosperinica paulustris</i>	0.3	0.3	1.0
C 4.0 ( <i>Cladium jamaicense</i> )			
<i>Rhynchospora divergens</i>	3.0	2.5	9.0
S 0.25 ( <i>Cladium jamaicense</i> )			
<i>Amaranthus australis</i>	0.3	0.3	1.0
<i>Cyperus haspan</i>	0.3	0.3	1.0
<i>Cyperus odoratus</i>	0.3	0.3	1.0
<i>Ludwigia alata</i>	0.3	0.3	1.0
<i>Ludwigia repens</i>	0.3	0.3	1.0
<i>Mitreolea petiolata</i>	2.7	2.7	8.0
<i>Rhynchospora divergens</i>	0.3	0.3	1.0
S 0.5 ( <i>Cladium jamaicense</i> )			
<i>Mitreolea petiolata</i>	2.0	1.0	6.0
<i>Polygonum hydropiperoides</i>	0.3	0.3	1.0
<i>Rhynchospora divergens</i>	1.0	0.6	3.0
S 1.0 ( <i>Cladium jamaicense</i> )			
<i>Eupatorium capillifolium</i>	0.3	0.3	1.0
<i>Eustachys petrea</i>	0.7	0.7	2.0
<i>Mitreolea petiolata</i>	0.3	0.3	1.0
<i>Prosperinica paulustris</i>	0.3	0.3	1.0
<i>Rhynchospora divergens</i>	4.3	1.5	13.0
S 2.0 ( <i>Cladium jamaicense</i> )			
<i>Amaranthus australis</i>	0.7	0.3	2.0
<i>Cyperus odoratus</i>	0.7	0.7	2.0
<i>Ludwigia alata</i>	0.3	0.3	1.0
<i>Ludwigia repens</i>	0.7	0.3	2.0
<i>Mikania scandens</i>	0.3	0.3	1.0
<i>Mitreolea petiolata</i>	1.0	0.6	3.0
<i>Prosperinica paulustris</i>	2.7	2.7	8.0
<i>Rhynchospora divergens</i>	11.3	8.4	34.0
S 4.0 ( <i>Cladium jamaicense</i> )			
<i>Eleocharis cellulosa</i>	1.3	1.3	4.0
<i>Rhynchospora divergens</i>	1.3	0.3	4.0

APPENDIX II. October 1998 means, standard error and summed number of plants per station.

Sampling location	Mean	STE	Sum	Mean	STE	Sum	Mean	STE	Sum
N 0.25 ( <i>Typha domingensis</i> )									
<i>Amaranthus australis</i>	2.3	1.3	7.0	—	—	—	0.3	0.3	1
<i>Ammania coccinea</i>	—	—	—	0.3	0.3	1	0.5	0.5	1
<i>Dichondra carolinensis</i>	3.7	1.7	11.0	—	—	—	—	—	—
<i>Ludwigia repens</i>	—	—	—	—	—	—	0.3	0.3	1
<i>Lythrum alatum</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Polygonum hydropiperoides</i>	20	0.6	6.0	—	—	—	0.3	0.3	1
<i>Rhynchospora microcarpa</i>	1.5	1.5	3.0	—	—	—	—	—	—
<i>Rorripa teres</i>	—	—	—	1	0.6	3	—	—	—
<i>Sagittaria lancifolia</i>	0.7	0.3	2.0	—	—	—	—	—	—
<i>Typha domingensis</i>	7.3	0.9	22.0	—	—	—	—	—	—
<i>Kostelyskya virginica</i>	0.3	0.3	1.0	—	—	—	—	—	—
N 0.5 ( <i>Typha domingensis</i> )									
<i>Amaranthus australis</i>	8.7	5.0	26.0	0.3	0.3	1.0	0.3	0.3	1.0
<i>Ammania coccinea</i>	1.0	1.0	3.0	—	—	—	—	—	—
<i>Dichondra carolinensis</i>	1.3	0.7	4.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	2.7	1.2	8.0	0.3	0.3	1.0	—	—	—
<i>Ludwigia repens</i>	1.3	0.9	4.0	—	—	—	—	—	—
<i>Ludwigia peruviana</i>	1.7	1.7	5.0	—	—	—	—	—	—
<i>Mikania scandens</i>	0.7	0.3	2.0	—	—	—	—	—	—
<i>Pluchea odorata</i>	0.3	0.3	4.0	—	—	—	—	—	—
<i>Polygonum hydropiperoides</i>	8.0	3.2	24.0	2.7	0.9	8.0	0.7	0.7	2.0
<i>Prosperinica paulustris</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Rhynchospora divergens</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Rhynchospora microcarpa</i>	2.0	2.0	6.0	—	—	—	—	—	—
<i>Typha domingensis</i>	2.0	2.0	6.0	—	—	—	—	—	—
N 1.0 ( <i>Typha domingensis</i> )									
<i>Amaranthus australis</i>	3.3	1.2	16.0	0.3	0.3	1.0	0.3	0.3	1.0
<i>Dichondra carolinensis</i>	0.6	0.6	2.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	0.3	0.3	1.0	0.3	0.3	1.0	—	—	—
<i>Ludwigia repens</i>	0.3	0.3	1.0	0.7	0.7	2.0	—	—	—
<i>Polygonum hydropiperoides</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Prosperinica paulustris</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Rhynchospora divergens</i>	—	—	—	—	—	—	0.7	0.7	2.0
<i>Typha domingensis</i>	3.3	1.5	10.0	—	—	—	—	—	—
N 2.0 ( <i>Cladium jamaicense</i> )									
<i>Ammania coccinea</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Centella asiatica</i>	—	—	—	—	—	—	0.3	0.3	1.0
<i>Ludwigia alata</i>	1.7	1.2	5.0	—	—	—	—	—	—
<i>Ludwigia microcarpa</i>	1.0	1.0	3.0	—	—	—	—	—	—
<i>Lythrum alatum</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Mikania scandens</i>	1.3	1.3	4.0	—	—	—	—	—	—
<i>Polygonum hydropiperoides</i>	0.3	0.3	1.0	0.7	0.3	2.0	—	—	—
<i>Rhynchospora divergens</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Rorripa teres</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Sagittaria lancifolia</i>	0.3	0.3	1.0	—	—	—	—	—	—
N 4.0 ( <i>Cladium jamaicense</i> )									

## APPENDIX II. Continued.

Sampling location	Mean	STE	Sum	Mean	STE	Sum	Mean	STE	Sum
C 0.25 ( <i>Cladium jamaicense</i> )									
<i>Cyperus odorata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	11.7	6.2	35.0	1.0	1.0	3.0	—	—	—
<i>Ludwigia microcarpa</i>	0.7	0.7	2.0	—	—	—	—	—	—
<i>Ludwigia repens</i>	1.7	1.7	5.0	—	—	—	—	—	—
<i>Mitreolia petiolata</i>	1.0	0.6	3.0	—	—	—	0.3	0.3	1.0
<i>Pluchea odorata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Polygonum hydropiperoides</i>	0.7	0.3	2.0	1.7	1.7	5.0	1.7	1.7	5.0
<i>Prosperinica paulustris</i>	1.7	0.9	5.0	—	—	—	—	—	—
<i>Rhynchospora divergens</i>	2.0	0.6	6.0	—	—	—	—	—	—
<i>Rhynchospora microcarpa</i>	—	—	—	—	—	—	0.7	0.7	2.0
C 0.5 ( <i>Cladium jamaicense</i> )									
<i>Cyperus haspan</i>	0.7	0.7	2.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	1.7	1.7	5.0	—	—	—	—	—	—
<i>Ludwigia microcarpa</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Ludwigia repens</i>	9.7	2.4	29.0	0.3	0.3	1.0	—	—	—
<i>Lythrum alatum</i>	—	—	—	0.3	0.3	1.0	—	—	—
<i>Mikania scandens</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Mitreolia petiolata</i>	4.7	2.4	14.0	0.3	0.3	1.0	—	—	—
<i>Polygonum hydropiperoides</i>	3.7	3.2	11.0	—	—	—	—	—	—
<i>Prosperinica paulustris</i>	0.7	0.7	2.0	—	—	—	—	—	—
<i>Rhynchospora inundata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Sagittaria lancifolia</i>	0.7	0.3	2.0	—	—	—	—	—	—
C 1.0 ( <i>Cladium jamaicense</i> )									
<i>Centella asiatica</i>	—	—	—	0.3	0.3	1.0	—	—	—
<i>Cyperus haspan</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Dichondra carolinensis</i>	0.7	0.7	2.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	1.0	0.6	3.0	—	—	—	—	—	—
<i>Ludwigia microcarpa</i>	1.3	0.9	4.0	0.7	0.7	2.0	—	—	—
<i>Ludwigia repens</i>	0.3	0.3	1.0	0.3	0.3	1.0	—	—	—
<i>Lythrum alatum</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Mitreolia petiolata</i>	9.0	3.6	27.0	2.7	2.2	8.0	0.3	0.3	1.0
<i>Polygonum hydropiperoides</i>	1.0	0.0	3.0	—	—	—	—	—	—
<i>Prosperinica paulustris</i>	0.7	0.7	2.0	0.3	0.3	1.0	—	—	—
<i>Rorripa teres</i>	—	—	—	0.3	0.3	1.0	—	—	—
C 2.0 ( <i>Cladium jamaicense</i> )									
<i>Ludwigia alata</i>	1.0	1.0	3.0	0.3	0.3	1.0	—	—	—
<i>Mitreolia petiolata</i>	4.3	3.4	13.0	—	—	—	—	—	—
<i>Polygonum hydropiperoides</i>	0.7	0.3	2.0	0.3	0.3	1.0	—	—	—
<i>Prosperinica paulustris</i>	0.3	0.3	1.0	0.7	0.7	2.0	—	—	—
<i>Rhynchospora divergens</i>	2.3	1.9	7.0	0.3	0.3	1.0	—	—	—
<i>Rorripa teres</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Typha domingensis</i>	0.3	0.3	1.0	—	—	—	—	—	—
C 4.0 ( <i>Cladium jamaicense</i> )									
<i>Rhynchospora divergens</i>	0.7	0.7	2.0	—	—	—	0.3	0.3	1.0
<i>Rhynchospora inundata</i>	1.3	0.3	4.0	—	—	—	—	—	—
<i>Rhynchospora microcarpa</i>	0.7	0.3	2.0	0.3	0.3	1.0	—	—	—

## APPENDIX II. Continued.

Sampling location	Mean	STE	Sum	Mean	STE	Sum	Mean	STE	Sum
S 0.25 ( <i>Cladium jamaicense</i> )									
<i>Ludwigia alata</i>	1.7	1.2	5.0	—	—	—	—	—	—
<i>Ludwigia microcarpa</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Mitreolia petiolata</i>	5.7	2.3	17.0	0.3	0.3	1.0	—	—	—
<i>Prosperinica paulustris</i>	—	—	—	0.5	0.5	1.0	—	—	—
<i>Rhynchospora divergens</i>	0.7	0.3	2.0	—	—	—	—	—	—
<i>Rorripa teres</i>	1.7	1.7	5.0	—	—	—	—	—	—
S 0.5 ( <i>Cladium jamaicense</i> )									
<i>Cyperus haspan</i>	0.5	0.5	1.0	—	—	—	—	—	—
<i>Dichromena colorata</i>	—	—	—	2.3	2.3	7.0	—	—	—
<i>Ludwigia alata</i>	4.0	1.2	12.0	0.7	0.7	2.0	—	—	—
<i>Mitreolia petiolata</i>	3.0	1.5	9.0	0.3	0.3	1.0	—	—	—
<i>Prosperinica paulustris</i>	0.3	0.3	1.0	0.3	0.3	1.0	—	—	—
<i>Rhynchospora divergens</i>	1.3	0.7	4.0	—	—	—	—	—	—
<i>Rhynchospora microcarpa</i>	0.3	0.3	1.0	1.0	0.6	3.0	0.3	0.3	1.0
<i>Rorripa teres</i>	0.7	0.7	2.0	0.3	0.3	1.0	—	—	—
<i>Sagittaria lancifolia</i>	0.3	0.3	1.0	—	—	—	—	—	—
S 1.0 ( <i>Cladium jamaicense</i> )									
<i>Dichromena colorata</i>	—	—	—	4.7	3.7	14.0	—	—	—
<i>Mitreolia petiolata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Prosperinica paulustris</i>	0.7	0.7	2.0	—	—	—	—	—	—
<i>Rhynchospora divergens</i>	3.3	2.4	10.0	2.7	2.7	8.0	0.7	0.7	2.0
<i>Rhynchospora microcarpa</i>	4.7	4.7	14.0	—	—	—	—	—	—
S 2.0 ( <i>Cladium jamaicense</i> )									
<i>Cyperus haspan</i>	1.7	1.2	5.0	—	—	—	—	—	—
<i>Cyperus odorata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Ludwigia alata</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Ludwigia repens</i>	1.7	1.7	5.0	—	—	—	—	—	—
<i>Mitreolia petiolata</i>	1.7	0.9	5.0	0.3	0.3	1.0	0.3	0.3	1.0
<i>Prosperinica paulustris</i>	2.7	1.7	8.0	0.3	0.3	1.0	—	—	—
<i>Rhynchospora divergens</i>	0.3	0.3	1.0	—	—	—	—	—	—
<i>Rhynchospora inundata</i>	1.0	0.6	3.0	—	—	—	—	—	—
<i>Rhynchospora microcarpa</i>	1.7	0.9	5.0	—	—	—	0.3	0.3	1.0
<i>Rorripa teres</i>	1.3	0.9	4.0	—	—	—	—	—	—
S 4.0 ( <i>Cladium jamaicense</i> )									
<i>Eleocharis cellulosa</i>	2.7	1.8	8.0	—	—	—	—	—	—
<i>Rhynchospora divergens</i>	0.7	0.7	2.0	0.3	0.3	1.0	—	—	—
<i>Rhynchospora microcarpa</i>	—	—	—	0.7	0.7	2.0	—	—	—

## HERPETOFAUNA OF A LONG-UNBURNED SANDHILL HABITAT IN SOUTH-CENTRAL FLORIDA

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**ABSTRACT:** *The herpetofauna of an old-growth southern ridge sandhill site heavily invaded by species from adjacent sand pine scrub was monitored over a 15-year period beginning 52 years after the last fire. Twenty-two species of amphibians and reptiles were captured or observed on a 0.16-ha pitfall grid, and an additional seven species were recorded in similar habitat nearby. The two most frequently captured reptiles (Sceloporus woodi, Cnemidophorus sexlineatus) were xeric-adapted species most characteristic of sandhill habitats burned at normal 1–10 year intervals, and four other xeric-adapted species (Eumeces egregius lividus, Neoseps reynoldsi, Stilosoma extenuatum, Tantilla r. relicta) accounted for a combined 18.2% of all individuals captured during the study. Species richness and diversity were comparable to more frequently burned sandhill sites, and the only significant trend in the 15-year interval was a modest increase in overall diversity in 1984–88 and 1994 compared with 1979–83. Community similarity differed little between time periods. Xeric-adapted species were found in shrub-free openings in greater proportion than expected, and limited data on movements suggested that the large-bodied cursorial xeric species had relatively large home ranges incorporating multiple openings whereas smaller fossorial species had smaller home ranges including single or closely adjacent open patches. The results point to the presence of openings with sparse or no shrub cover as the critical factor allowing persistence of the xeric-specialists in the long unburned site. Consequently, where sandhill or other xeric habitats are developing uniformly dense woody cover and where conditions preclude burning either temporarily or permanently creation of openings by mechanical and/or chemical methods may be an effective management tool for maintaining viable populations of the herpetofauna and other biota characteristic of these habitats.*

**Key Words:** Conservation, fire, herpetofauna, sandhill

SANDHILL is one of the major pyrogenic xeric upland vegetation associations in Florida and is typically subject to low intensity fires at 1 to 10-year intervals (Myers, 1990). The herpetofauna of sandhill is diverse (e.g., Carr, 1940; Campbell and Christman, 1982; Mushinsky, 1985; Franz, 1995) and includes a distinctive assemblage of xeric-adapted species, several of which are endemic to Florida (Neill, 1957). Campbell and Christman (1982) stated that the effect of fire on the sandhill herpetofauna was to increase species diversity by opening the canopy and ground cover, permitting col-

onization by both the characteristic xeric-adapted species as well as more broadly habitat-tolerant species.

Sandhill along with other Florida xeric upland habitat types such as sand pine scrub and scrubby flatwoods has been greatly reduced and fragmented by development and agriculture, a consequence of which is reflected in the fact that more than two-thirds of the terrestrial species or subspecies of amphibians and reptiles listed as endangered, threatened, or species of special concern by the Florida Wildlife Conservation Commission or U.S. Fish and Wildlife Service (Wood, 1994) are closely associated with these habitats. An additional concern for the remaining tracts of these habitats is that the natural fire cycle has generally been suppressed, with resulting increased vegetation density and canopy coverage detrimental to the xeric-adapted species. The ability to persist in an isolated sandhill or other xeric upland site during intervals between fires is presumably most critical for those species with narrow habitat specificity and low vagility such as *Eumeces egregius*, *Neoseps reynoldsi*, *Tantilla relicta*, *Stilosoma extenuatum*, and *Sceloporus woodi*. From the standpoint of conservation and management of these species it is important to know how long they can maintain viable populations in isolated habitat patches in the absence of fire and what factors influence persistence times.

We studied the amphibians and reptiles of an isolated old-growth sandhill site near the southern end of the Lake Wales Ridge in south-central Florida over a 15-year period (1979–1994), beginning 52 years after the last fire. The objective was to assess the status of the herpetological community, particularly the xeric upland specialists, of a sandhill habitat with an unusually prolonged absence of fire.

DESCRIPTION OF THE STUDY AREA—The study was conducted on a pitfall grid in southern ridge sandhill (turkey oak phase) vegetation on the Archbold Biological Station (ABS), 12 km south of the town of Lake Placid, Highlands Co. (27° 11' N lat., 81° 21' W long.). The southern ridge sandhill association is restricted to the southern end of the Lake Wales Ridge and differs from typical sandhill vegetation in having south Florida slash pine (*Pinus elliotii* var. *densa*) rather than longleaf pine (*P. palustris*) as the primary overstory species and turkey oaks (*Quercus laevis*), the other characteristic tree species of sandhill habitat, that are generally stunted (Abrahamson, et al. 1984). The grid was in an approximately 86 ha-sandhill tract located at the highest elevation (53–61 m) in the general region and was surrounded at a slightly lower elevation by a broad zone of mature sand pine scrub with a nearly closed canopy. The study plot was 100 m from the nearest point of adjacent sand pine scrub and about 900 m from the nearest open water, a small artificial pond separated from the grid by paved roads.

In 1927 a high-intensity wildfire burned the sandhill, adjacent sand pine scrub, and other vegetation associations over an area of more than 400 ha. First-hand accounts of the fire (Cline, 1972; Kelsey, 1972) indicated that the

area was uniformly burned, with no islands of unburned or lightly burned vegetation remaining. Except for an occasional rain-extinguished spot burn around a lightning-struck slash pine, the sandhill and surrounding habitats had remained free of fire for 67 years by the end of the study in 1994.

A photograph (Myers, 1990; fig. 6.21A) of the sandhill habitat near the study site taken in 1929 two years after the fire shows an open pine stand; a sparse, low shrub layer of mainly turkey oak sprouts and palmettos; and a well-developed ground cover of wire grass. In the absence of fire, the sandhill association was subsequently invaded by sand pine (*P. clausa*), myrtle oak (*Q. myrtifolia*), Chapman's oak (*Q. chapmanii*), sand live oak (*Q. geminata*), and other species from the surrounding sand pine scrub. By 1957 development of the shrub layer was well advanced (Laessle, 1958, Fig. 9). Woody vegetative cover in quadrats sampled by Laessle (1958) ranged from 30 to 80%, with a mean of about 50%, although extensive open patches with wiregrass ground cover still persisted (JNL pers. obs.). At the beginning of this study in 1979 the vegetation consisted of an open overstory of slash and sand pines; a midstory of smaller trees, mostly oaks emerged from the shrub layer, and scrub hickory (*Carya floridana*); and a generally dense but patchy shrub layer dominated by myrtle oak, Chapman's oak, sand live oak, and palmettos (*Serenoa repens*, *Sabal etonia*). Ground cover consisted of wiregrass, gopher apple (*Licania michauxii*), reindeer moss (*Cladonia* spp.), and various forbs in open areas and sprouts of the shrub layer species in denser shrub thickets. The litter layer was well developed under larger trees and in shrub thickets but sparse, often with exposed sand, in more open sites.

The overall aspect of the vegetation did not change appreciably between 1979 and 1994, but the density and height of the shrub cover increased and openings were reduced. Frequency of occurrence of three major cover types at the 56 pitfall stations in 1979 (data from Sheehan, 1979) and 1994 reflect these trends: open areas devoid of shrubs—46% in 1979 vs. 30% in 1994; open shrub—23% in 1979 vs. 36% in 1994; dense shrub thickets—12% in 1979 vs. 34% in 1994. Vegetation surveys in 1969, 1979, and 1989 on a nearby plot in the same habitat documented a 114% increase in stem density in the shrub layer over the 20-year period (Menges et al., 1993). A photograph in 1988 of the same view as in 1929 (Myers 1990, fig. 6.21B) shows the greatly increased height, density, and coverage of the shrub layer and reduction of open patches and wiregrass ground cover resulting from 61 years of fire exclusion.

**METHODS**—The pitfall grid consisted of sunken 4.7-l (5 gal) plastic buckets spaced at 6.7 m intervals. A 6 × 6 array (0.09 ha) was established in July 1979 and expanded to a 7 × 8 array (0.16 ha) the following month. The buckets were covered with a 30 × 30 cm piece of 0.6 cm masonite or plywood elevated about 2 cm above the bucket by means of four wooden legs notched so that half rested on the rim of the bucket and half extended about 3 cm into the bucket, making it difficult to displace the lid from the side. The lids were held in place with a brick or a tightly stretched rubber shock cord. The covers were turned upside down to close

the buckets between sampling periods. The grid was usually checked in late afternoon. When the catch was low, the grid was checked at one- to three-day intervals. Relative abundance of a species in a given trapping period was expressed as the number of different individuals captured divided by the number of days the grid was open. Capture data for the 36-station pitfall grid trapped 14 days (504 pitfall days) in July 1979 were adjusted to a 56-station grid (784 pitfall days) by multiplying the number of captures by 1.5 (784/504).

Pitfalls were opened during 1 to 6 months (mean = 3.8) in each year from 1979 to 1988 and in 1994 for a total of 38 trapping periods ranging from 4 to 30 days (mean = 14.6) and a total of 570 days (31,640 pitfall days). Except for January 1981, 1984, and 1985 sampling was conducted only in the warmer months (March–October).

Animals were individually marked by toe clipping (amphibians and lizards other than *Rhineura* and *Neoseps*), notching ventral scales (snakes), and notching marginal scutes (turtle). About half of the *Neoseps* captured were marked for individual recognition by removal of the vestigial limbs in different combinations. Snout-vent length was routinely recorded.

Tests for differences among diversity indices ( $H'$ ) in different time periods followed Zar (1984). All other statistical tests were performed with the Statistica software package (StatSoft, 1994).

**RESULTS—Species composition**—Twenty-two species of amphibians and reptiles were recorded on the study plot, including 19 species (5 amphibians, 14 reptiles) captured in pitfalls (Table 1) and 3 species (*Hyla gratiosa*, *Drymarchon corais*, *Elaphe guttata*) observed on the grid but not captured. Active burrows of adult *Gopherus polyphemus* also were present on the grid throughout the study. Seven additional species recorded on the ABS in the sandhill association (*Hyla squirella*, *Heterodon platyrhinos*, *Masticophis flagellum*, *Opheodrys aestivus*, *Pituophis melanoleucus*, *Micrurus fulvius*, and *Crotalus adamanteus*) resulted in a total of 29 species for the old-growth habitat. The number of species captured in pitfalls and the total recorded from the study plot accounted for 66% and 76%, respectively, of the known sandhill herpetofauna of the ABS. *Virginia valeriae*, first reported from the region by Campbell (1962), has recently been collected from sandhill and scrub habitats within 5 km of our study site. A major difference in the species composition of southern ridge sandhill compared with most typical sandhill habitats elsewhere in Florida is the presence of *Sceloporus woodi*, rather than *S. undulatus*; *Eumeces egregius lividus*, endemic to the southern Lake Wales Ridge, rather than *E. e. onocrepis*; and *Tantilla r. relicta* rather than *T. r. neilli*.

Fifty-eight percent of all species captured in pitfalls was recorded in the first or second trapping period during the first year of the study (Fig. 1). First captures of the remaining species were evenly distributed over the interval from the 16th (year 3) to the 38th (year 15) trapping period. With the exception of *Eleutherodactylus planirostris*, these remaining species were difficult to capture in pitfalls because they were either arboreal or cryptic in habits, adults were large enough to escape from pitfalls (snakes), or individuals were unlikely to fall into a pitfall unless it was located at a burrow entrance (gopher tortoises).

A total of 325 individuals with 1055 recaptures was recorded in the

TABLE 1. Total numbers of individuals and recaptures (maximum for an individual in parentheses) and relative abundance (N individuals/100 grid days) in different time periods for 19 species of amphibians and reptiles on a pitfall grid in old-growth sandhill vegetation in south-central Florida. Number of grid days in each time period in parentheses at the top of the column.

Species	Number		Relative abundance			
	of indi- viduals	Number of recaptures	1979–83 (267)	1984–88 (206)	1994 (97)	1979–94 (570)
<i>Bufo quercicus</i>	2	0	0.75	0.00	0.00	0.35
<i>Hyla femoralis</i>	1	0	0.00	0.00	1.03	0.18
<i>Eleutherodactylus planirostris</i> <sup>1</sup>	12	1(1)	0.37	5.34	0.00	2.11
<i>Gastrophryne carolinensis</i> <sup>1</sup>	7	10(1)	1.50	0.00	3.09	1.23
<i>Rana capito aesopus</i> <sup>1,2</sup>	2	0	0.75	0.00	0.00	0.35
<i>Gopherus polyphemus</i> <sup>2</sup>	1	0	0.00	0.00	1.03	0.18
<i>Rhineura floridana</i>	1	0	0.37	0.00	0.00	0.18
<i>Anolis carolinensis</i> <sup>1</sup>	9	1	1.50	1.46	2.06	1.58
<i>Sceloporus woodi</i> <sup>1,2</sup>	81	749(37)	21.72	6.31	10.31	14.21
<i>Eumeces egregius</i> <sup>2</sup>	12	3(3)	1.87	2.43	2.06	2.11
<i>Eumeces inexpectatus</i> <sup>1</sup>	45	16(15)	4.87	10.19	11.34	7.89
<i>Neoseps reynoldsi</i> <sup>2</sup>	37	2(2)	9.36	3.40	5.15	6.49
<i>Scincella lateralis</i>	27	2(2)	2.62	3.88	12.37	4.74
<i>Cnemidophorus sexlineatus</i> <sup>1,2</sup>	72	271(30)	14.23	10.19	13.40	12.63
<i>Coluber constrictor</i> <sup>1</sup>	1	0	0.00	0.49	0.00	0.18
<i>Diadophis punctatus</i>	1	0	0.00	0.00	1.03	0.18
<i>Lampropeltis triangulum</i>	1	0	0.00	0.49	0.00	0.18
<i>Stilosoma extenuatum</i> <sup>2</sup>	1	0	0.00	0.49	0.00	0.18
<i>Tantilla relicta</i> <sup>2</sup>	12	0	1.12	3.40	2.06	2.11
Totals	325	1055(91)	61.05	48.06	64.95	57.02

<sup>1</sup> Species recorded by Lips (1991) from gopher tortoise burrows in similar habitat.

<sup>2</sup> Xeric-adapted species particularly characteristic of typical open sandhill habitat burned at normal intervals.

pitfalls. Amphibians comprised 7.4% of total original captures and reptiles 92.6%. *E. planirostris* accounted for 50% of all amphibians in pitfalls, its high frequency of occurrence being at least partly due to the fact that rather than being trapped in the buckets it used them as refuge sites. Although the pitfall grid was approximately 900 m from the nearest potential breeding site, *Gastrophryne carolinensis* was the second most abundant amphibian (29.2%). Among reptiles, lizards were the most frequently captured group, comprising 94.4% of all original captures compared with 5.3% for snakes, and 0.3% (1 individual) for turtles. Three species accounted for 71.8% of original lizard captures: *Sceloporus woodi*, 24.1%; *Cnemidophorus sexlineatus*, 21.2%; and *Eumeces inexpectatus*, 17.6%. Seventy-five percent of the snakes captured were *Tantilla relicta*, which was the only species with more than a single capture.

Among the reptiles, seven species characteristic of more open, xeric habitats (*G. polyphemus*, *S. woodi*, *Eumeces egregius*, *Neoseps reynoldsi*, *C. sexlineatus*, *Stilosoma extenuatum*, *Tantilla relicta*) accounted for 67.4% of the total number of original captures compared with 27.9% for six species

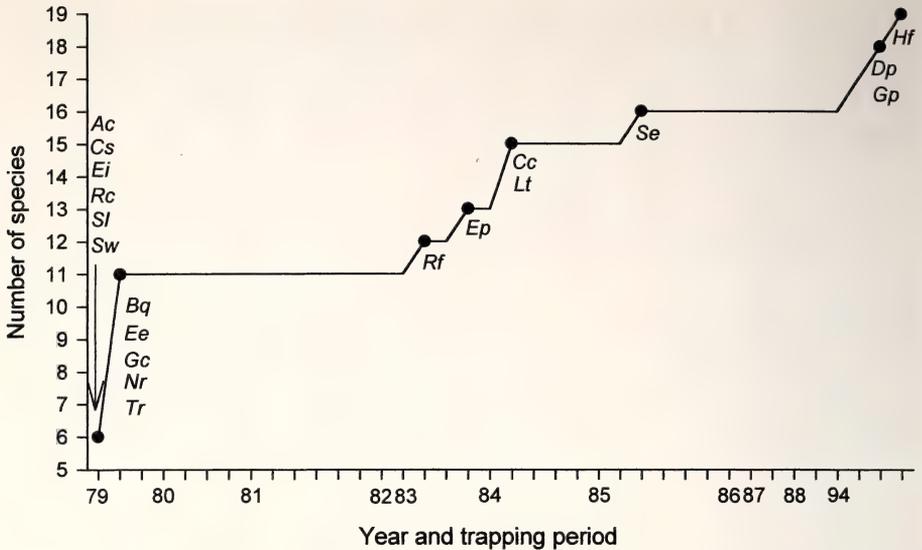


FIG. 1. Cumulative number of amphibian and reptile species captured on a pitfall grid in old-growth sandhill vegetation in south-central Florida during 38 trapping sessions from 1979 to 1994. Ticks on X-axis indicate number of trapping sessions in a given year. Species abbreviations as follows: Ac—*Anolis carolinensis*; Bq—*Bufo quercicus*; Cc—*Coluber constrictor*; Cs—*Cnemidophorus sexlineatus*; Dp—*Diadophis punctatus*; Ep—*Eleutherodactylus planirostris*; Ei—*Eumeces inexpectatus*; Ee—*Eumeces egregius*; Gc—*Gastrophryne carolinensis*; Gp—*Gopherus polyphemus*; Hf—*Hyla femoralis*; Lt—*Lampropeltis triangulum*; Nr—*Neoseps reynoldsi*; Rc—*Rana capito*; Rf—*Rhineura floridana*; Sl—*Scincella lateralis*; Sw—*Sceloporus woodi*; Se—*Stilosoma extenuatum*; Tr—*Tantilla relicta*.

with a broader habitat range (*Anolis carolinensis*, *E. inexpectatus*, *Scincella lateralis*, *Coluber constrictor*, *Diadophis punctatus*, *Lampropeltis triangulum*). Among lizards, the proportion of individuals recaptured in more than one month and mean and maximum periods of known residence on the grid were highest for *S. woodi*, and lowest for *Scincella* (Table 2).

Relative abundance of all species combined did not differ significantly between the time periods 1979–83, 1984–88, and 1994 ( $\chi^2_{df2} = 3.08$ ,  $p < 0.21$ ). Only four species of lizards had a sufficient number of captures in each time period to permit statistical testing of differences in relative abundance of individual species between intervals. Of these, relative abundance of *N. reynoldsi* and *S. woodi* decreased significantly over time (*N. reynoldsi*— $\chi^2_{df2} = 6.92$ ,  $p < 0.04$ ; *S. woodi*— $\chi^2_{df2} = 18.16$ ,  $p < 0.0001$ ), did not vary significantly for *C. sexlineatus* ( $\chi^2_{df2} = 1.39$ ,  $p < 0.50$ ), and showed a near-significant increase for *E. inexpectatus* ( $\chi^2_{df2} = 5.51$ ,  $p < 0.06$ ). Although sample sizes for *E. egregius* were too small for statistical testing, the data suggest no change in abundance of this species during the study.

Species diversity indices ( $H'$ ) and evenness values ( $J'$ ) for pitfall samples were relatively high overall and during each of the three time periods, with  $H'$  in the 1984–88 and 1994 periods being significantly greater than in

TABLE 2. Percentages of individuals known to have survived one or more months and average number of months known to be alive for six lizard species on a pitfall grid in old growth sandhill habitat in south central Florida.

Species	Number individuals	Number survived $\geq$ mo.	% survived	Number of months known alive	
				Mean $\pm$ S.E.	Range
<i>Sceloporus woodi</i>	81	17	21.0	9.7 $\pm$ 13.3	1.0–56.7
<i>Eumeces egregius</i>	12	2	16.7	4.7 $\pm$ 4.4	1.5, 7.8
<i>Eumeces inexpectatus</i>	60	7	11.7	4.7 $\pm$ 3.6	1.2–9.0 <sup>1</sup>
<i>Neoseps reynoldsi</i>	18 <sup>2</sup>	1	0.6	10.3 <sup>3</sup>	
<i>Scincella lateralis</i>	27	1	3.7	1.4	
<i>Cnemidophorus sexlineatus</i>	72	13	18.1	6.6 $\pm$ 4.8	1.0–11.8

<sup>1</sup> Excludes a questionable value of 58.4 months.

<sup>2</sup> Includes only marked individuals.

<sup>3</sup> Excludes a questionable value of 19.2 months.

1979–83 (Table 3). Because of interspecific differences in the probability of capture in pitfalls, these values must be considered as relative rather than absolute measures of the diversity of the herpetological community. On the assumption that lizards, with the exception of *Rhineura floridana*, were uniformly more trappable in pitfalls than any other group and thus were more likely to be captured in proportion to their actual abundance, diversity and evenness values for this component of the herpetofauna are presumably more reliable. As in the case of the total pitfall samples, diversity and evenness of lizards were higher in 1984–88 and 1994 than in 1979–83, but the differences were not significant in any case ( $p > 0.05$ ).

Horn's index of similarity (Horn, 1966) for total pitfall samples and lizards (excluding *R. floridana*) between different time periods during the study were as follows (values for lizards in parentheses): 1979–83 vs. 1984–88—0.84 (0.92); 1984–88 vs. 1994—0.88 (0.98); 1979–83 vs. 1994—0.87 (0.91). These values indicate a high level of similarity between time periods for both groups and no obvious trends over the 15-year period.

TABLE 3. Shannon-Wiener diversity index ( $H'_{\log \text{ base } 10}$ ) and evenness ( $J'$ ) based on total captures of amphibians and reptiles and lizards only (excluding *Rhineura floridana*) in pitfalls in old-growth sandhill habitat in south-central Florida during three time periods from 1979 to 1994. Significant differences ( $p < 0.05$ ) between indices in different time periods are indicated with different superscript letters.

Category	1979–1983	1984–1988	1994	All years
All species				
H'	0.810 <sup>a</sup>	0.935 <sup>b</sup>	0.918 <sup>b</sup>	0.926
J'	0.727	0.867	0.851	0.724
Lizards				
H'	0.686 <sup>a</sup>	0.772 <sup>a</sup>	0.770 <sup>a</sup>	0.752
J'	0.812	0.913	0.911	0.890

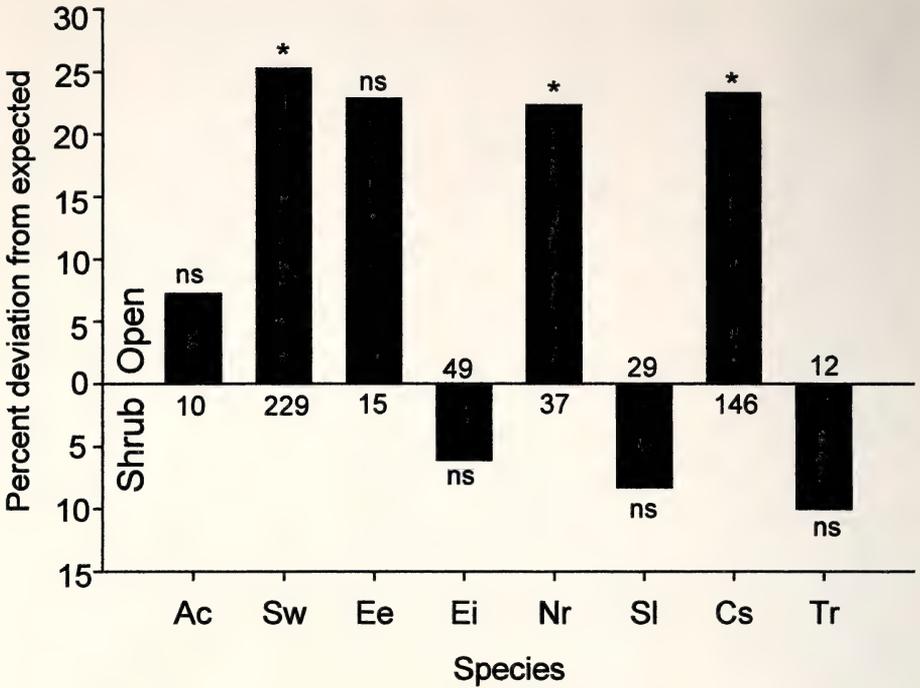


FIG. 2. Percentage deviation from expected (based on numbers of pitfall stations in each microhabitat category) of pitfall captures for eight reptile species in open and shrub-dominated sites in old-growth sandhill habitat in south-central Florida during 1979–94. Numbers at base of bars are total number of captures. Significant ( $p < 0.05$ ) and non-significant differences ( $\chi^2$  tests) are indicated above the bars by \* and ns, respectively. Abbreviations of species names as in Fig. 1.

*Microhabitat use*—Numbers of captures of seven lizard and one snake species during the study were sufficient to calculate  $\chi^2$  tests of observed versus expected frequencies of capture in pitfalls in openings without shrubs and in sites with moderate to heavy shrub density. *Anolis carolinensis*, *S. woodi*, *E. egregius*, *N. reynoldsi*, and *C. sexlineatus* were captured in open sites more frequently than expected based on numbers of pitfalls in open and shrub-dominated sites, whereas *E. inexpectatus*, *S. lateralis*, and *T. relicta* were captured more frequently than expected in shrub-dominated sites (Fig. 2). Although these results are generally consistent with predictions of the respective habitat preferences of the xeric-adapted and more mesic or broadly habitat tolerant species, the differences were significant ( $p < 0.05$ ) only for *S. woodi*, *N. reynoldsi*, and *C. sexlineatus*.

*Movements*—Mean distance between successive recaptures, assumed to be an index of home range size, could be calculated for 1 to 40 individuals of seven lizard species and minimum home range area for 2 to 19 individuals of three species with three or more nonlinear captures (Table 4). Although

TABLE 4. Distance (m) between successive recaptures and minimum home range area (m<sup>2</sup>) for adults of six species of lizards captured in pitfall traps in old-growth sandhill vegetation association in south-central Florida.

Species	Sex	Distance between successive recaptures (m)			Minimum home range (m <sup>2</sup> )		
		N <sup>2</sup>	Mean ± S.E.	Range	N <sup>2</sup>	Mean ± S.E.	Range
<i>Anolis carolinensis</i>	?	1/2	13.4				
	♂♂	19/94	12.1 ± 2.0	0-35.9	10/56	164.4 ± 60.3	23.4-592.9
	♀♀	16/95	15.0 ± 1.8	0-33.9	8/69	544.0 ± 178.5	63.4-1319.6
<i>Eumeces egregius</i>	Total <sup>1</sup>	40/206	12.7 ± 1.3	0-35.9	19/134	316.7 ± 91.2	22.2-1319.6
	♂♂	2/4	10.6 ± 3.9	6.7, 14.5			
	♀♀	1/2	6.7				
<i>Eumeces inexpectatus</i>	Total	3/6	9.3 ± 2.6	6.7-14.5			
	♂♂	12/31	15.4 ± 2.9	3.4-40.5	2/6	304.0 ± 214.1	89.8, 518.1
<i>Scincella lateralis</i>	?	2/4	13.7 ± 7.0	6.7, 20.8			
<i>Cnemidophorus sexlineatus</i>	♂♂	13/58	17.4 ± 2.8	0-40.2	6/42	515.4 ± 185.5	88.0-1165.0
	♀♀	8/26	24.3 ± 3.0	9.3-35.6	3/16	365.8 ± 288.4	64.9-942.4
	Total <sup>1</sup>	22/86	19.4 ± 2.1	0-40.2	9/58	465.5 ± 147.9	64.9-1165.0

<sup>1</sup> Includes individuals of questionable sex.

<sup>2</sup> Number of individuals/number of captures.

the small sample sizes for *A. carolinensis*, *E. egregius*, and *S. lateralis* preclude firm conclusions about movement patterns in these species, the data suggest that these small-bodied species have smaller home range size than the larger *S. woodi*, *E. inexpectatus*, and *C. sexlineatus*. A single *Neoseps* with two captures had a distance of 23.7m between captures. No significant sex differences existed in distance between successive recaptures in *S. woodi* and *C. sexlineatus*, the only two species with a sufficient number of captures for testing (t-tests. *S. woodi*:  $t_{df33} = -1.043$ ,  $p = 0.30$ ; *C. sexlineatus*:  $t_{df19} = 1.604$ ,  $p = 0.12$ ). However, minimum home range area of *S. woodi* was larger for females than males ( $t_{df16} = -2.203$ ,  $p = 0.04$ ), but there was no significant sex difference in *C. sexlineatus* ( $t_{df7} = 0.452$ ,  $p = 0.66$ ). Although *S. woodi*, *E. egregius*, *E. inexpectatus*, and *C. sexlineatus* differed significantly in distance between recaptures (ANOVA:  $F_{2,73} = 3.051$ ,  $p = 0.03$ ), only the difference between *S. woodi* and *C. sexlineatus* approached significance in post-hoc tests (Tukey HSD for unequal N:  $p = 0.07$ ), and minimum home range size of these two species did not differ significantly (t-test:  $t_{df26} = -0.892$ ,  $p = 0.38$ ).

DISCUSSION—Results of this study revealed the presence in the old-growth sandhill of all the xeric-adapted species typical of earlier post-fire stages of this habitat in peninsular Florida (Campbell and Christman, 1982) as well as unexpectedly high abundances of some of those species. Additionally, overall species richness was comparable to, or exceeded that reported for sandhill sites with a more typical fire history (Table 5). Diversity ( $H'$ ) was relatively high for all species and the lizard component alone, with a significant increase between 1979–83 and 1984–94 for total samples. Overall herpetofaunal diversity (0.926) in the old-growth study site during a 15-year period from 52 to 67 years after the last fire exceeded the values (converted to log 10) of 0.467 to 0.662 reported by Mushinsky (1985) for 1, 2, and 7 year-burned plots and a  $\geq 20$  year unburned control plot in sandhill habitat. Similarity of pitfall samples of all species and of only lizards, exclusive of *Rhineura*, in three time periods during the study remained high and exhibited no obvious long-term trends, indicating general stability of the herpetofaunal community, although predictable trends in abundance correlated with vegetation change occurred in individual species. Thus, the increase in shrub density and coverage over the 15-year period was reflected in a decrease in relative abundance of the xeric-specialists *N. reynoldsi* and *S. woodi* and an increase in relative abundance of *E. inexpectatus* and *S. lateralis*, two species with more mesic habitat preferences.

The somewhat counterintuitive finding of the persistence in the old-growth sandhill of xeric-adapted species usually associated with earlier post-fire vegetative conditions is best explained by the presence of openings, which were utilized by these species disproportionately to their prevalence on the grid. Thinning of oak shrub cover (Givens et al., 1984) contributed to the existence of shrub-free openings. Likewise, nearby fire lanes, 4-wheel

drive vehicle roads, and foot trails also provided open areas. Thus, a mosaic of open habitat patches persisted in the sandhill, even though reduced in extent, in the prolonged absence of burning and invasion by sand pine, oaks and other shrubs from the surrounding sand pine scrub association with the same fire history as the sandhill. Natural and human-mediated creation of open microhabitat as an explanation for persistence of these species in our old growth site is corroborated by findings of Campbell and Christman (1982) that loose soil rather than vegetation is probably the major factor determining the herpetofauna of xeric upland habitats, with the specialized sand-swimming *E. egregius* and *N. reynoldsi*, particularly, being restricted to microhabitats with sunny exposure, loose soil, and absence of roots (Mount, 1963; Christman, 1992a,b). Presumably, therefore, the persistence of open sandy patches free of roots in the old-growth sandhill benefited both the fossorial (*E. egregius*, *N. reynoldsi*, *S. extenuatum*, *T. relictus*) and terrestrial xeric-adapted species (*S. woodi*, *C. sexlineatus*), while at the same time the denser shrub cover with relatively well-developed litter layer provided conditions for more mesic and habitat-tolerant species such as *E. inexpectatus*, *S. lateralis*, and *D. punctatus*). The occurrence of the gopher frog (*Rana capito*) was dependent on the presence of burrows of the gopher tortoise (*Gopherus polyphemus*), another species which also tended to be situated in open patches.

The available data for xeric-adapted species, suggest that *S. woodi* had a smaller mean home range than *C. sexlineatus*, although the difference was not as pronounced as suggested by Hokit and co-workers (1999). It is possible that the size of the pitfall grid relative to the mobility of these and other larger species was too small to reveal their true home ranges. The three distances between recaptures recorded for *E. egregius* were comparable to the two (7 and 9 m) reported by Mount (1963) and suggest that this species has more restricted movements compared with the larger, cursorial terrestrial species. If this is the case, then the xeric-adapted species were exploiting open habitat patches differently, whereby *C. sexlineatus* and *S. woodi* incorporated multiple openings in their larger home ranges, and the smaller fossorial species with smaller home ranges occupied single or closely adjacent open patches.

In light of the 52-year gap between the last major fire and the beginning of this study, any conclusion as to the primary source of the initial post-burn populations—whether dispersal or residents that survived the burn—is obviously highly speculative. However, considering that the 1927 fire was apparently intense, uniform, and widespread together with the presumably low dispersal ability of the majority of the xeric-specialists, particularly *E. egregius*, *Neoseps*, *Tantilla*, *Stilosoma*, and probably *S. woodi*, most likely residents that survived the burn rather than long-distance dispersers from unburned or lightly-burned “islands” were the principal, even if not the sole, source of the early post-burn populations. This suggestion does not preclude the possibility that short-distance dispersal of animals from the

TABLE 5. Amphibians and reptiles (exclusive of aquatic or wetland species) reported from sandhill habitat in various Florida localities, as follows: Carr (1940)—statewide, includes species listed as characteristic or frequent in sandhill association; Campbell and Christman (1982)—Ocala National Forest; Mushinsky (1985)—Hillsborough County; Dodd (1992)—Putnam County; Franz (1995)—Putnam County; J.N. Layne (pers. obs.)—Alachua County; present study (Highlands County). Status codes: x = species present; o = locality not included in species' range.

Species	Campbell and		Mushin- sky	Dodd (1992) <sup>3</sup>	Franz (1995) <sup>1</sup>	Layne (pers. obs.) <sup>1</sup>	Present study <sup>2</sup>
	Carr (1940) <sup>1</sup>	Christman (1982) <sup>2</sup>					
<i>Scaphiopus holbrooki</i>	x	x	x	x	x	x	o
<i>Bufo quercicus</i>	x	x	x	x	x		x
<i>Bufo terrestris</i>	x	x	x	x	x	x	
<i>Eletherodactylus planirostris</i>			x	x	x		x
<i>Gastrophryne carolinensis</i>		x	x	x	x	x	x
<i>Hyla cinerea</i>		x	x			x	
<i>Hyla versicolor/chrysoscelis</i>				x		x	o
<i>Hyla crucifer</i>		x					
<i>Hyla femoralis</i>	x	x		x	x		x
<i>Hyla gratiosa</i>	x	x					x
<i>Hyla squirella</i>	x	x		x			x
<i>Rana capito</i>	x	x	x	x	x		x
<i>Gopherus polyphemus</i>	x	x	x		x		x
<i>Rhineura floridana</i>	x	x			x		x
<i>Ophisaurus</i> sp.	x	x		x			
<i>Anolis carolinensis</i>		x	x	x	x	x	x
<i>Sceloporus undulatus</i>	x	x		x	x	x	o
<i>Sceloporus woodi</i>		x	o	o	o	o	x
<i>Eumeces egregius</i>	x	x	o	x	x	x	x
<i>Eumeces laticeps</i>						x	o
<i>Eumeces inexpectatus</i>	x	x	x	x	x	x	x
<i>Neoseps reynoldsi</i>	x	x	o	o	o	o	x
<i>Scincella lateralis</i>		x	x	x	x	x	x
<i>Cnemidophorus sexlineatus</i>		x	x	x	x	x	x
<i>Cemophora coccinea</i>		x	x	x	x		
<i>Coluber constrictor</i>	x	x	x	x	x	x	x
<i>Diadophis punctatus</i>		x	x	x	x		x
<i>Drymarchon corais</i>	x	x	x			x	x
<i>Elaphe guttata</i>		x			x	x	x
<i>Elaphe obsoleta</i>		x				x	
<i>Heterodon platyrhinos</i>	x	x	x	x	x		x
<i>Heterodon simus</i>		x					o
<i>Lampropeltis triangulum</i>	x	x					x
<i>Masticophis flagellum</i>	x	x		x	x	x	x
<i>Opheodrys aestivus</i>		x					x
<i>Pituophis melanoleucus</i>	x	x			x		x
<i>Rhadinea flavilata</i>			x				o
<i>Storeria occipitomaculata</i>		x					o
<i>Stilosoma extenuatum</i>	x	x	x			x	x
<i>Tantilla relicta</i>	x	x	x	x	x		x
<i>Thamnophis sirtalis</i>				x	x		

TABLE 5. Continued.

Species	Campbell and Mushin-					Layne (pers. obs.) <sup>1</sup>	Present study <sup>2</sup>
	Carr (1940) <sup>1</sup>	Christman (1982) <sup>2</sup>	sky (1985) <sup>3</sup>	Dodd (1992) <sup>3</sup>	Franz (1995) <sup>1</sup>		
<i>Micrurus fulvius</i>		x		x	x	x	x
<i>Crotalus adamanteus</i>	x	x	x		x	x	x
<i>Sistrurus miliarius</i>		x		x	x		
Total number of species	23	39	21	25	27	20	29

<sup>1</sup> General list.

<sup>2</sup> Species recorded by pitfall/drift fence array or pitfall grid (individual species captured not designated by Campbell and Christman) and general observation.

<sup>3</sup> Species recorded only by pitfall/drift fence array.

adjacent scrub did not also contribute to early post-fire populations in the sandhill, but it can be assumed that these also represented *in situ* survivors of the same fire.

Our observations at the ABS following natural or prescribed fires in sandhill and other xeric habitats support the conclusion that burning does not cause high mortality of amphibians and reptiles and other vertebrates. For example, a survey on a 2.7-ha grid conducted the day following an intense burn in old-growth sandhill close to the present study site documented only five dead reptiles—a badly singed *C. constrictor* partly buried in ashes of thick duff around the base of a pine and four *N. reynoldsi* lying fully exposed in open areas. Live *S. woodi*, *C. sexlineatus*, and *E. inexpectatus* were observed and active *G. polyphemus* burrows were documented. Gopher tortoise burrows serve as important refugia for amphibians and reptiles in the sandhill habitat of the ABS (Lips, 1991), and burrows of the oldfield mouse (*Peromyscus polionotus*), cotton rat (*Sigmodon hispidus*), and nine-banded armadillo (*Dasyus novemcinctus*), as well as natural ground holes probably also afford protection from fires.

Fire also has been shown to have minimal direct impact on the herpetofauna in other Florida habitat types (Komarek, 1969; Means and Campbell, 1981; Hingten, 2000), and on a broader geographic scale Whelan (1995) concluded that fires result in “surprisingly little animal mortality.”

The results of this study demonstrate that under some conditions the xeric-adapted herpetofauna characteristic of open, early post-fire sandhill communities can persist for long periods in the absence of fire if sufficient openings devoid of woody vegetation are present. The frequent isolation of xeric upland habitats by other vegetation types and their continuing reduction and fragmentation by development and agriculture coupled with the low vagility of the xeric-specialists suggest that “relict” populations of these species in old-growth sandhill or scrub habitats are more likely to be the source of expanded post-fire populations than dispersal from other sites separated by unsuitable habitat types. This suggests that for old-growth sites that are developing a dense and homogeneous shrub layer and in which

prescribed burning is not an immediate option artificial creation of openings by mechanical or chemical methods may extend the survival times of populations of xeric-adapted species until burning is possible. In such cases the effectiveness of prescribed burning may be enhanced by prior mechanical or chemical treatment (Brockway and Outcalt, 2000). Where burning is completely excluded for reasons of public safety, as in densely populated areas with small, isolated sandhill or scrub sites, the habitats might be managed for xeric-adapted species by artificial methods alone (Greenburg et al., 1994; Zedacker, 2000).

Our site provided an extreme case of prolonged absence of fire in a sandhill association in which natural and artificially-created open patches contributed to the persistence of xeric-adapted herpetofauna. In light of the continuing loss and fragmentation of pyrogenic xeric upland habitats in Florida together with increasing practical difficulty in approximating the natural historic fire regime through prescribed burning, the results of this study underscore the need for further testing of the effectiveness of artificial management techniques as a means of maintaining conditions favorable to the xeric-adapted herpetofauna and other biota characteristic of these habitats until they can be returned to earlier successional stages through prescribed burning or as an alternative to fire in sites where use of prescribed fire is not feasible.

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## FIRE INTENSITY AND SHRUB REGENERATION IN PALMETTO-DOMINATED FLATWOODS OF CENTRAL FLORIDA

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**ABSTRACT:** *Fire intensity variation has the potential to affect vegetation dynamics in Florida ecosystems, but this has been little studied. In a south-central Florida pine flatwoods, we manipulated fuel loads before a prescribed fire. We then monitored maximum temperatures in the soil during the burn and characterized shrub stem dynamics before and periodically postfire for four years. Added fuel biomass exceeded the biomass of naturally occurring fuels, which varied significantly among sites. The addition of fuel significantly elevated maximum soil temperatures during the burn. All 12 shrub species found prefire persisted in our plots, and nine new shrub species appeared postfire but remained uncommon in our plots. Fuel additions did not affect the plot-level shrub species richness, overall shrub stem density, or species' stem densities. Richness initially decreased following the fire, then rapidly increased to prefire levels and remained fairly constant for four years. Overall shrub stem density increased from one to nine months after the fire, and subsequently stabilized. *Quercus minima* and *Ximenia americana* increased rapidly in stem numbers postfire and *Helianthemum nashii* showed a delayed increase. Other species such as the two palmettos (*Serenoa repens* and *Sabal etonia*) were fairly stable. Our results emphasize that only very intense fires should be expected to markedly alter the stability of postfire responses of pine flatwoods.*

**Key Words:** Hot spots, Florida flatwoods, fire intensity, postfire shrub response

FIRES are one of the predominant ecological disturbances in Florida (Robbins and Myers, 1992) and in many parts of the world (Whelan, 1995). Many plant species possess traits that allow recovery of populations after fires via resprouting, clonal spread, or seedling recruitment (Menges and Kohfeldt, 1995; Schimmel and Granstrom, 1996; Benwell, 1998; Hoffman, 1998; Bond and Midgley, 2000). With fire suppression, shifts in vegetation structure can occur (Menges et al., 1993) and many fire-adapted species may decline (Leach and Givnish, 1996; Harrod et al., 2000).

Besides the mere occurrence of fire, aspects of the fire regime such as fire frequency, fire intensity, and season of burn can affect plant communities (Robbins and Myers, 1992; Glitzenstein et al., 1995; Collins, 2000; Harrod

et al., 2000). Most of these components have not been studied for Florida ecosystems.

Fire intensity is an estimate of fireline intensity, the rate of heat produced per unit length of a fire front (Byram, 1959). Fire intensity can be assayed by maximum temperature, residence time, crown scorch, water evaporation, and residual twig diameter (van Wagner, 1973; Rice, 1993; Perez and Moreno, 1998; Odion and Davis, 2000). The intensity of fire can affect postfire vegetation recovery (Rice, 1993; Ashton and Martin, 1996; Williams et al., 1999; but see D'Antonio et al., 2000). Intense patches or "hot spots" can create additional mortality (Schimmel and Granstrom, 1996) and provide opportunities for invasion of weedy species (Milberg and Lamont, 1995) or rapid expansion of resident species (Cole and Taylor, 1995; Romagni and Gries, 2000). Patterns of intensely burned areas and lightly burned or unburned areas may affect the recovery of large areas in mosaic burns (Turner et al., 1997; 2000).

Pine flatwoods vegetation is subject to frequent fires (Stout and Marion, 1993; Menges, 1999) which may cause little vegetation change (Abrahamson, 1984a) or may temporarily increase the proportions of herbaceous species (Gilliam and Christensen, 1986; Lewis et al., 1988; Maliakal and Menges, 2000). Many pine flatwoods are dominated by *Serenoa repens* (saw palmetto), which has low mortality and turnover rates (Abrahamson, 1995) and recovers rapidly by resprouting after fire (Abrahamson, 1984b; Schmalzer and Hinkle, 1992; Menges and Kohfeldt, 1995). When left unburned, flatwoods sites may show increasing levels of saw palmetto (Maliakal and Menges, 2000), show declines in herbs (Edmisten, 1963) or may be invaded by hardwoods such as bayhead trees (Peroni and Abrahamson, 1986; Menges et al., 1993; Stout and Marion, 1993). Flatwoods tend to burn nearly completely in most burns (Abrahamson, 1984a). Unlike some other frequently-burned areas such as sandhills, flatwoods often burn at high fire intensity (Abrahamson, 1984b; Menges and Deyrup, 2001). Such variation in fire intensity can affect patterns of postfire mortality of south Florida slash pine (Menges and Deyrup, 2001).

In this study, we have attempted to manipulate fire intensity by fuel additions prior to prescribed fire in one Florida flatwoods site. As well as estimating fire intensity, we document pre- and postfire shrub vegetation, and assay changes in shrub communities with time and as a function of variation in fire intensity.

**METHODS—Study area**—Research was conducted at Lake Placid Scrub Wildlife and Environmental Area in south-central Florida, 5 km northwest of Archbold Biological Station (27° 11' N, 81° 21' W, Highlands County). Climate is characterized by hot, wet summers and mild, dry winters, with most rain falling from June to September (Abrahamson et al., 1984). Soils are Satellite Sand, Archbold Sand and Basinger Fine Sand (Carter et al., 1989). The flatwoods vegetation is dominated by palmettos (*Serenoa repens* and *Sabal etonia*; nomenclature follows Wunderlin, 1998). Less abundant shrubs include *Quercus minima*, *Ilex glabra*, *Ximenia americana*, and *Lyonia fruticosa*. Natural and human-induced fires have been common in this land-

TABLE 1. Loads of both naturally occurring fuel and fuel added to treated plots, fire temperatures at 5-cm depth in the soil, and plot-level richness and stem densities before the prescribed fire measured in the three sites. Data are means  $\pm$  SE for three plots (fuel loads and fire temperatures) and six plots (richness and stem density) per site. Temperatures  $< 66^\circ\text{C}$  were considered as  $65^\circ\text{C}$  for analysis.

Variable	Site 1	Site 2	Site 3
Natural fuel ( $\text{g m}^{-2}$ )			
Leaves and miscellaneous	469.2 $\pm$ 142.1	1173.2 $\pm$ 273.3	630.3 $\pm$ 219.7
Pine needles	5.6 $\pm$ 5.0	33.7 $\pm$ 12.4	4.9 $\pm$ 27
Stems $< 6$ mm	5.2 $\pm$ 8.9	45.3 $\pm$ 13.0	49.4 $\pm$ 16.5
Stems $> 6$ –25 mm	146.2 $\pm$ 79.8	359.6 $\pm$ 69.6	97.5 $\pm$ 43.5
Stems $> 25$ –76 mm	0	0	13.3 $\pm$ 13.3
Total	636.2 $\pm$ 153.4	1611.5 $\pm$ 297.1	795.3 $\pm$ 258.1
Added fuel ( $\text{g m}^{-2}$ )			
Duff and pine needles	900	900	900
Stems $< 6$ mm	700	700	700
Stems $> 6$ –25 mm	1900	1900	1900
Stems $> 25$ –76 mm	3700	3700	3700
Stems $> 76$ mm	4900	4900	4900
Total	12100	12100	12100
Fire temperature ( $^\circ\text{C}$ )			
Control plots	65 $\pm$ 0	88.3 $\pm$ 9.3	65 $\pm$ 0
Treated plots	121 $\pm$ 0	134.8 $\pm$ 13.8	127.2 $\pm$ 4.7
Species richness ( $\text{sp m}^{-2}$ )	1.0 $\pm$ 0.2	0.5 $\pm$ 0.1	0.7 $\pm$ 0.1
Stem density ( $\text{stems m}^{-2}$ )	4.0 $\pm$ 0.9	3.5 $\pm$ 3.7	4.9 $\pm$ 0.9

scape. Climate, soils, vegetation, and fire history of the palmetto flatwoods association have been described by Abrahamson et al. (1984), Abrahamson and Hartnett (1990) and Stout and Marion (1993). Prior to this study, the last fire in our study area was a prescribed burn occurring in 1987.

*Experimental design and sampling*—In March 1996, we selected three flatwood sites in an area planned for prescribed burning. At each site, we randomly located three pairs of 2-m  $\times$  2-m plots, with each plot in the pair separated by 2 m. We added additional fuel, collected from nearby sites, to one randomly selected plot of each pair and left the other untreated. Added fuel included duff and pine needles, and dead woody debris (twigs and stems) partitioned into size classes based on the standard time lag classes used in fire modeling (Deeming et al., 1977, Table 1).

At each plot pair, we also estimated naturally occurring fuel loads by collecting all dead fuel within a 0.5-m  $\times$  1-m quadrat located between paired plots. Dead fuels were separated into the following categories: leaves and miscellaneous, pine needles, and woody debris partitioned into the time lag classes (Table 1). Fuel was then oven-dried to constant weight at  $65^\circ\text{C}$ .

We estimated fire intensity using pyrometers made with temperature-sensitive paints (ranging from  $66^\circ\text{C}$  to  $204^\circ\text{C}$ ) on aluminum tags. Two pyrometers per plot, located at 5-cm depth in the soil, were randomly located in both control and treated plots. To assess effects of fire intensity on shrub regeneration, we counted number of stems of each woody species within plots previous to fire and subsequently at 1, 3, 6, 9, 12, 24, 36, and 48 months postfire. At the seedling stage, individual species of the two palmettos could not be determined and were recorded collectively as palmetto seedlings.

*Statistical analyses*—We evaluated differences in naturally occurring fuel loads, mean fire temperatures, shrub richness and total stem density among sites and between control and treat-

ment plots with Kruskal-Wallis tests. Fire temperatures below 66 °C were considered to have a value of 65 °C. Variations through time in plot-level shrub species richness, total stem density, and stem density of more abundant species were analyzed using repeated-measures analysis of variance on square-root transformed data, and its non-parametric equivalent, the non-parametric, split-plot analysis (Koch et al., 1980; Potvin et al., 1990). We used Huynth-Feldt criterion to evaluate compound symmetry in ANOVAs. Since this assumption was violated, we report only non-parametric results. For each sampling time, mean values of control and treated plots per site were used in the analyses ( $n = 3$  sites). Analyses of stem density of individual species were performed for the most common shrubs sampled in more than one site and for three plots of *Helianthemum nashii* (found in only one site). Throughout this manuscript, data are given as the mean  $\pm$  SE. Computations were conducted with SPSS 9.0 (SPSS Inc., 1999).

**RESULTS—Naturally occurring fuel loads**—Natural fuel biomass varied nearly three-fold, but not significantly, among sites (Table 1;  $\chi^2_2 = 4.62$ ,  $P = 0.1$ ). Added fuel biomass exceeded total biomass in untreated plots and also exceeded individual fuel categories in all but one case (Table 1). We added coarse woody debris to treatment plots, but no woody debris  $>76$  mm diameter was observed for natural fuel biomass (Table 1).

**Fire temperatures**—Maximum fire temperatures at a 5-cm depth in the soil were significantly hotter in fuel-added plots than in control plots ( $\chi^2_1 = 3.97$ ,  $P < 0.05$ ; Table 1). Differences in fire temperature among sites were significant for control plots ( $\chi^2_2 = 7.71$ ,  $P < 0.05$ ), but not for treated plots ( $\chi^2_2 = 1.17$ ,  $P = 0.56$ ; Table 1). Both natural fuel load and fire temperature were highest in site 2 (Table 1). The natural logarithm of fuel load explained a 90% of the variation in the natural logarithm of fire temperature ( $P < 0.0001$ ,  $n = 18$  plots, Fig. 1). Although all plots burned, temperatures in the soil indicated a light to moderate fire intensity.

**Richness, total stem density, and stem density of more abundant species**—Before prescribed fire, sites were similar in terms of total stem density ( $\chi^2_2 = 2.15$ ,  $P = 0.34$ ), but differed in the species richness ( $\chi^2_2 = 6.36$ ,  $P < 0.05$ ; Table 1). All 12 woody species sampled prior to fire also were observed postfire. In contrast, nine species were recorded only during post-fire sampling (Table 2). None of the newly appearing species became common in our plots.

Although fire temperatures were significantly higher in treated than in control plots, the fire treatment had no effects on number of shrub species or shrub stem density at the plot level ( $P > 0.1$  for all comparisons). In contrast, richness and total stem density changed significantly through time ( $\chi^2_8 = 28.13$ ,  $P < 0.001$  and  $\chi^2_8 = 22.43$ ,  $P < 0.005$ , respectively). Plot-level richness initially decreased, then rapidly increased to prefire levels, then continued fairly constant for four years (Fig. 2). Stem density of all shrub species combined had a clear increase from one to nine months after the fire, and was then stable through four years (Fig. 3).

Stem densities of some but not all common shrubs changed with time. Variations with time in stem densities of *S. repens*, *S. etonia*, and *Rhus*

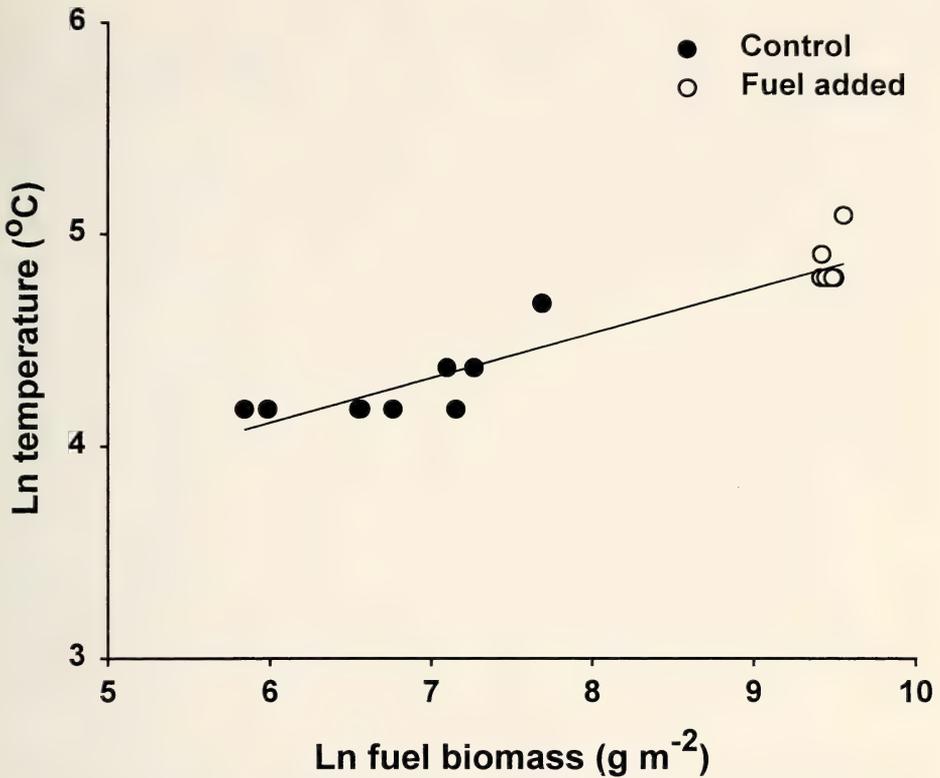


FIG. 1. Relationship between fire temperature and fuel load after natural log transformation of both variables ( $n = 9$  for both control and treatment plots). The regression line predicts  $\ln \text{ temperature} = 2.85 + 0.21(\ln \text{ fuel biomass})$ ;  $r^2 = 0.90$ ,  $S_{y,x} = 0.11$ ,  $n = 18$ .

TABLE 2. Woody species found before and after the fire.

Species found before and after	Species found only after
<i>Baccharis halimifolia</i>	<i>Asimina reticulosa</i>
<i>Ilex glabra</i>	<i>Carya floridana</i>
<i>Licania michauxii</i>	<i>Gaylussacia dumosa</i>
<i>Lyonia fruticosa</i>	<i>Helianthemum nashii</i>
<i>Myrica cerifera</i>	<i>Hypericum edisonianum</i>
<i>Palafoxia feayi</i>	<i>Quercus chapmanii</i>
<i>Pinus palustris</i> (sapling)	<i>Quercus geminata</i>
<i>Quercus minima</i>	<i>Rhus copallinum</i>
<i>Quercus myrtifolia</i>	<i>Vaccinium myrsinites</i>
<i>Sabal etonia</i>	
<i>Serenoa repens</i>	
<i>Ximena americana</i>	

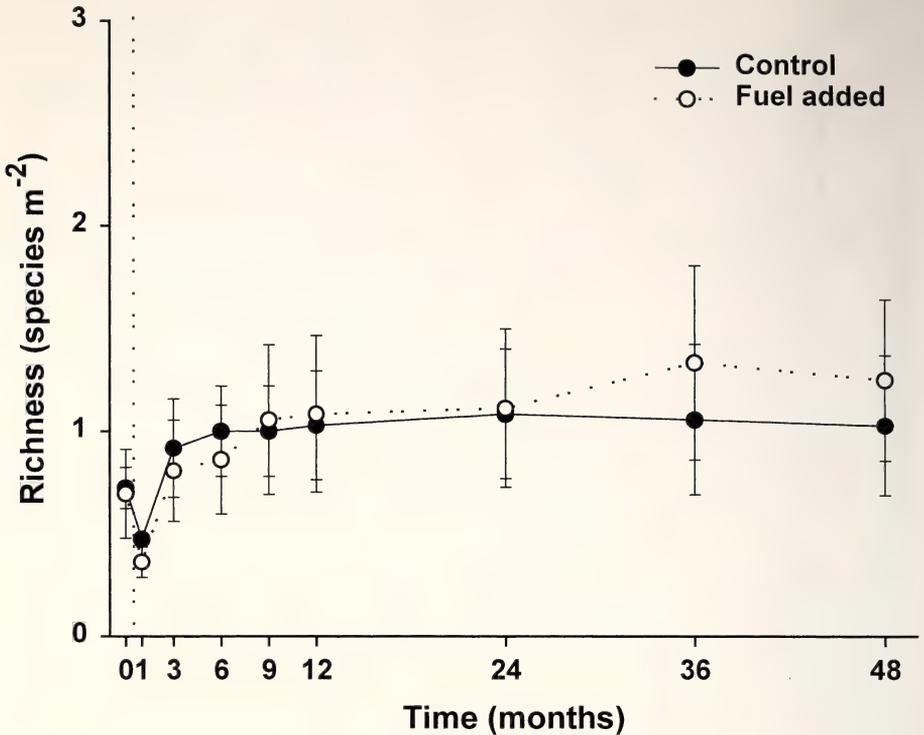


FIG. 2. Richness of woody plants before and through 48 months after fire in control and treatment plots. Data are means  $\pm$  SE for three sites. Vertical dotted line indicates fire occurrence. In the "Time" axis, 0 is equal to prefire.

*copallinum* were not significant ( $\chi^2_8 = 11.22$ ,  $P = 0.19$ ;  $\chi^2_8 = 14.32$ ,  $P = 0.07$ , and  $\chi^2_8 = 4.99$ ,  $P = 0.76$ , respectively; Fig. 4). Conversely, *Q. minima*, *X. americana*, and palmetto seedlings showed significant temporal changes ( $\chi^2_8 = 33.24$ ,  $P < 0.001$ ;  $\chi^2_8 = 19.41$ ,  $P < 0.05$ , and  $\chi^2_8 = 17.95$ ,  $P < 0.05$ , respectively; Fig. 4). *Q. minima* increased from one to 12 months postfire, and then had no important changes. *X. americana* was almost absent from the prefire sampling to three months postfire, then increased considerably through 24 months postfire. Although differences were not significant ( $\chi^2_1 = 0.05$ ,  $P = 0.83$ ), this increase was more important in treated than in control plots. Seedlings of palmettos peaked nine and 36 months after fire. *H. nashii* had no stems before the fire and then had a substantial increase during the second and third postfire years ( $\chi^2_8 = 44.86$ ,  $P < 0.001$ , Fig. 4).

DISCUSSION—Added fuels created significantly more intense fires in flatwoods plots. Maximum temperatures were significantly elevated in plots with added fuel, and these soil temperatures were positively correlated with the amount of fuel in the plots. Although there was a short-term delay in the resprouting of the two dominant palmettos, overall there were no longer-

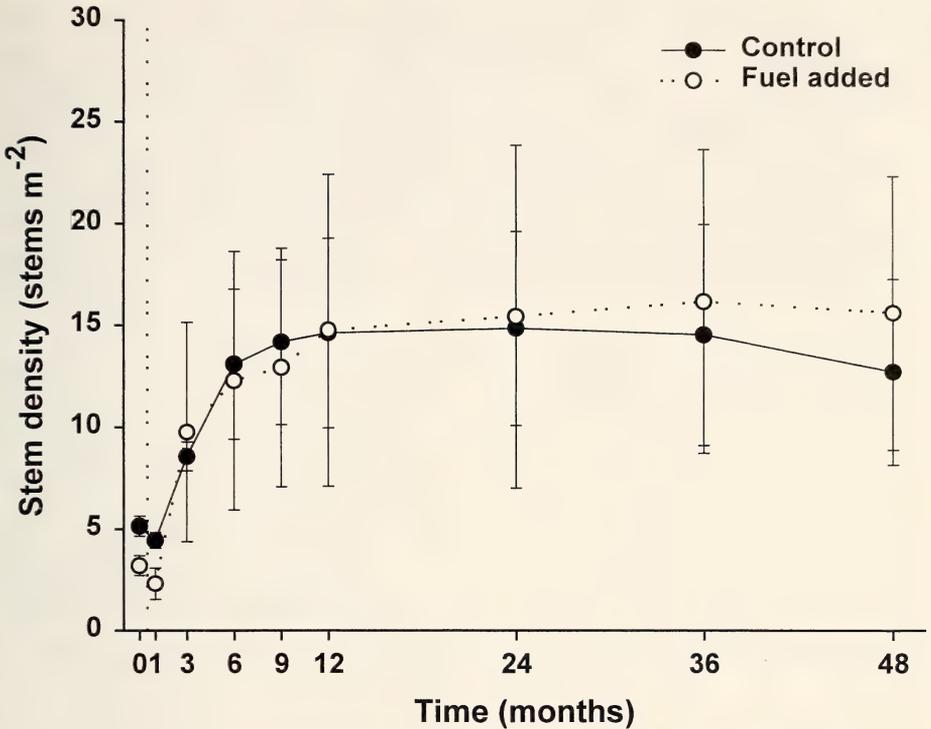


FIG. 3. Changes in stem density of all shrub species before and through 48 months after fire in control and treatment plots. Data are means  $\pm$  SE for three sites. Vertical dotted line indicates fire occurrence. In the "Time" axis, 0 is equal to prefire.

term effects of additional fuels on the density or species richness of pine flatwoods shrubs.

The lack of significant shrub response to added fuel suggests the moderate nature of this fire as well as the stability of pine flatwoods vegetation. The added fuel may have been insufficient to create hot spots and cause mortality of the dominant shrubs. Residual, unburned added fuel was evident in those plots postfire. Perhaps if weather conditions had been more extreme or lighting patterns different, those added fuels would have been consumed.

Flatwoods vegetation may often burn intensely relative to other types of Florida vegetation (Abrahamson, 1984b; Menges and Deyrup, 2001). However, flatwoods shrubs seem well adapted to a range of fire intensities. Across dozens of fires at Archbold Biological Station, we have observed patches of killed (non-resprouting) palmettos and oaks in only a few instances, after extreme fires in deep duffs and heavy fuels under pines or snags. If fire-induced shrub mortality is required for gap formation in flatwoods, this must occur only rarely.

No species were lost from these flatwoods sites with the passage of the fire. This observation is consistent with the fire-adapted nature of this veg-

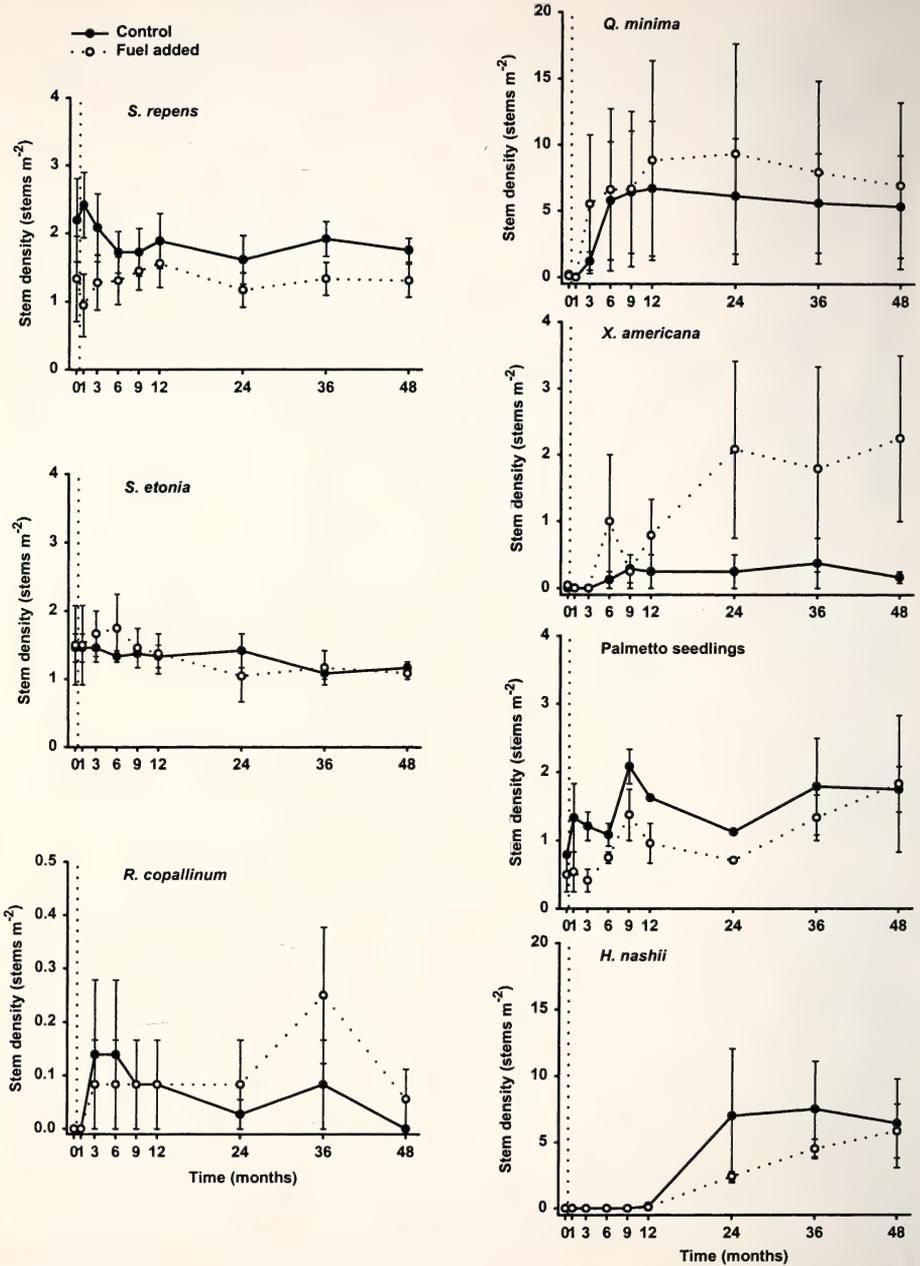


FIG. 4. Stem density dynamics of the most common shrubs before and through 48 months after fire in control and treated plots. Data are means  $\pm$  SE for three sites (*S. repens*, *R. copallinum*, *Q. minima*), two sites (*S. etonia*, *X. americana*, palmetto seedlings), and three plots in one site (*H. nashii*). Vertical dotted lines indicate fire occurrence. In the "Time" axis, 0 is equal to prefire.

etation (Abrahamson, 1984a). However, new species appeared in our plots and other shrub species increased dramatically in stem densities. The increases included an increase, maintained for four years, in the resprouting shrubs *Q. minima* and *X. americana*. *R. copallinum*, absent before the fire, showed up in large numbers in some locations. Based on the morphology of these plants, we believe that these are unlikely to be seedlings, but may represent sprouting from dormant buds. The clonal subshrub *H. nashii*, which showed a delayed increase postfire, is capable of recovering postfire via resprouting, clonal spread, and seedling recruitment (Menges and Kohfeldt, 1995).

Structural responses in the flatwoods shrub community were characterized by increases in stem numbers during the first postfire year, created largely by major increases in *Q. minima* in some plots. In contrast, other dominants such as the dwarf palms *S. repens* and *S. etonia* recovered from the burn in near-identical densities as prefire. The stability of palmetto responses is consistent with the findings in other community studies (Schmalzer and Hinkle, 1992) and in more detailed demographic research (Abrahamson, 1995). However, *S. repens* may gradually increase between fires during the first 30 years (Maliakal and Menges, 2000). Beyond this point, trends in *S. repens* are variable and may differ by vegetation type (Menges et al., 1993; Menges and Kohfeldt, 1995).

A short-term loss of plot-level diversity disappeared within a year, but there was an increase in study-level species richness as more species occurred in the plots postfire than prefire. The increase in representation of subordinate species contrasts with similar diversity found across wiregrass flatwoods sites varying in postfire age (Maliakal and Menges, 2000). The lower study-level species richness prefire may be partly an artifact of the small sample sizes of this study and the presence of dormant plants of some species in flatwoods. Nonetheless, these results emphasize the basic stability of the pine flatwoods shrub community with fire, while showing that subtle shifts with fire are likely. Fire intensity effects are likely only with extremely intense burns.

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## REMARKS ON THE CURRENT STATUS OF THE NON-MARINE HERPETOFAUNA OF EGMONT KEY, FLORIDA

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**ABSTRACT:** *The present, non-marine herpetofauna of Egmont Key consists of three (possibly four) snakes, two (possibly five) lizards, two turtles, and three frogs. Three species (Cuban Treefrog, *Osteopilus septentrionalis*; Indo-Pacific Gecko, *Hemidactylus garnotii*; Cornsnake, *Elaphe guttata*) are reported for the first time. The Cuban Treefrog and Indo-Pacific Gecko likely arrived with construction material; the sole Cornsnake may have been a released captive. There are no recent records of three species (Green Treefrog, *Hyla cinerea*; Mole Skink, *Eumeces egregius*; Eastern Diamond-backed Rattlesnake, *Crotalus adamanteus*). The Green Anole (*Anolis carolinensis*), thought extirpated, was resighted in 1998. This species may have recently recolonized or been transported to the island rather than have persisted unseen for more than 90 years.*

**Key Words:** Egmont Key, Tampa Bay, Non-indigenous species, Herpetofauna, Island, Colonization, Extirpation

EGMONT Key (27°36' N, 82°45' W) is an elongate continental island located at the mouth of Tampa Bay, Hillsborough County, Florida. In the early 1990s, the island contained ca.180 ha of a mostly mixed forest and scrub, consisting primarily of Brazilian pepper (*Schinus terebinthifolius*), Australian pine (*Casuarina equisetifolia*), and cabbage palm (*Sabal palmetto*). Since then, however, considerable erosion has taken place on the western (Gulf) side of the island, thus reducing its size. In addition, the Florida Park Service, which administers the island in cooperation with the U.S. Fish and Wildlife Service, has girdled many of the pines and cut or applied herbicides (Garlon 4®) to much of the Brazilian pepper. Vegetation on the buildings surrounding historic Fort Dade, mostly in the north, has been cleared, and extensive landscaping has been undertaken in anticipation of opening the island to increased numbers of tourists. Franz and co-workers (1992) and Dodd and co-workers (1994) provided an overview of the island's history and vegetative communities, respectively.

Herpetologically, the island is probably best known for its large population of gopher tortoises (*Gopherus polyphemus*) (Mushinsky and McCoy,

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1994). However, a large population of Florida box turtles (*Terrapene carolina bauri*) also is present and a long-term study of the life history of *T. c. bauri* was initiated in 1991 (reviewed by Dodd, 2001, and references therein). Between January 1991 and April 1993, 9 three to five day research trips were made to the island. All parts of the island were visited, and both diurnal and nocturnal searches were conducted. During the course of field observations, 12 species of amphibians and non-marine reptiles were observed (Franz et al., 1992; Smith et al., 1993). Franz and co-workers (1992) reviewed the history of herpetological collections on the island, dating back to 1869–1870. We follow the recommendations of Crother and co-workers (2000) when using common names of amphibians and reptiles and in capitalizing these names.

**NEW RECORDS**—Since the earlier reports by Franz and co-workers (1992) and Smith and co-workers (1993), we have collected further observations on the occurrence of herpetofaunal species on Egmont Key during an additional 24 sampling periods on the island (May 1993 to May 2001). These are summarized as follows:

*Osteopilus septentrionalis* (Cuban Treefrog). On 11 October 1999, we first observed substantial numbers of tadpoles of the Cuban Treefrog at the north end of the island behind the lighthouse and on the south end in a swale south of the Tampa Bay Pilot's Association (TBPA) compound (4 tadpoles: UF 119720). We have since observed juveniles (UF 123134, 16 mm snout-urostyle length) and adults (UF 12521–12528) in the ruins of Fort Dade and in a concrete catchment pool under the lighthouse diesel storage tank, both at the northern end of the island, on 2 November 2000, 11 April 2001, and 22 May 2001. Large numbers of tadpoles also were seen in the diesel catchment pool on 11 April.

Cuban Treefrogs probably colonized the island via introduction on building supplies during the extensive conversion of the old Fort Dade guard house into a visitor center. A large amount of building materials (wood, pipes, concrete blocks, roofing supplies) was brought to the northern end of the island (the only location with sufficient docking facilities) in the summer of 1999, and Cuban Treefrogs were noted shortly thereafter in the vicinity of the construction site. The fact that tadpoles were found in a swale ca. 1.5 km to the south does not preclude introduction through the TBPA compound, or even for dual points of introduction, however. We do not know if a population still exists in the south because pools of freshwater sufficient for tadpole development have not been available since the initial sighting.

*Anolis carolinensis* (Green Anole). Green Anoles were documented from Egmont Key based on collections in 1869–1870 and 1904 (reviewed by Franz et al., 1992), but have not been recorded since. On 7 April 1998, we photographed an adult Green Anole (photograph UF 123130) on a horizontal limb ca. 1.6 m above the substrate in dense Brazilian pepper on the southern end of the island. The lizard was observed at ca. 17:00 hr (air temperature

28°C, 61% relative humidity, clear weather). This has been the only record of a Green Anole between January 1991 and April 2001, despite intensive searches throughout the island by different observers at various times of the year and during all daylight hours. This species may have recently recolonized or been transported to the island rather than have persisted unseen for more than 90 years.

*Hemidactylus garnotii* (Indo-Pacific Gecko). Despite repeated nocturnal searches of buildings during 31 visits between January 1991 and November 2000, no geckos were observed. On the evening of 9 April 2001, we observed a single specimen on a house in the TBPA compound on Egmont's east-central coast. The specimen was found ca. 21:30 hr approximately 4 m above the ground on a wall brightly illuminated by a security light. The specimen (UF 123135) measures 58 mm SVL. This species probably colonized Egmont Key recently as a result of human-mediated transport associated with the ongoing construction of visitor's facilities or the delivery of supplies to the TBPA compound. Inasmuch as the lizard was found in the TBPA compound, it seems likely that it was brought to the island in supplies for the pilots. Whether a self-sustaining population will become established cannot be determined at present.

*Elaphe guttata* (Cornsake). The only Cornsnake recorded on Egmont Key was captured under palm litter on the west side of the Old Fort Trail just north of the TBPA compound on 25 April 2000 (air temperature 25°C, substrate temperature 22°C, 58% relative humidity, clear weather). The specimen, an adult male (92 cm SVL; 109 cm total length; 205 g body mass), was photographed (UF 123131) and released. The Cornsnake probably was a deliberately released animal, especially given its proximity to the TBPA compound.

*Crotalus adamanteus* (Eastern Diamond-backed Rattlesnake). Eastern Diamond-backed Rattlesnakes were reported by soldiers stationed on Egmont Key during the Fort Dade era (1898–1924) (Franz and co-workers, 1992; Hurley and Mohlman, 2000). In 1991–1992, Franz and co-workers (1992) noted that several adults were still on the island (photographic records: UF 123132, 123133). The last individual seen by us was in February 1992. A small (ca. 45–50 cm) Eastern Diamond-back washed up on the eastern shore near the TBPA compound after a severe storm in 1997 (R. Baker, 2001), but no further sightings have been recorded. It seems likely that the Eastern Diamond-backed Rattlesnake has been extirpated. However, Eastern Diamond-backs may occasionally recolonize the island, although source populations on the highly urbanized adjacent mainland must be very few. It is unlikely that a self-sustaining population could be maintained because there are no native or feral mammals on the island, and ground-nesting birds are available only during a limited season, thereby severely limiting food resources. Colonizing snakes would also face human persecution. At least two diamondbacks present in the early 1990s were killed either by tourists or the boat pilots (Baker, 1993).

OTHER SPECIES—The Green Treefrog (*Hyla cinerea*) was heard calling in June 1993, but there have been no further records of this species. It seems unlikely that a breeding population became established on the island, although additional introductions may be expected considering the proximity of Egmont Key to the mainland and the many visitors to the island. Both the Squirrel Treefrog (*Hyla squirella*) and the Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*) are known from recent observations; the latter has been seen on nearly every field visit, where it is found in the central portions of the island under palm logs and other debris that retain moisture.

Two lizard species appear to be firmly established (Brown Anole, *Anolis sagrei*; Southeastern Five-lined Skink, *Eumeces inexpectatus*). Brown Anoles, especially, are extremely abundant, and all size classes of Southeastern Five-lined Skinks have been observed repeatedly through the years. The Mole Skink (*Eumeces egregius*) is still known only from a single specimen (Smith et al., 1993). Both the biological and taxonomic status of this phenotypically unique specimen remains enigmatic.

There are three well-established species of snakes on the island: Eastern Racer (*Coluber constrictor*), Yellow Ratsnake (*Elaphe obsoleta*), and Kingsnake (*Lampropeltis getula*) (Franz et al., 1992; Smith et al., 1993). Eastern Racers and Yellow Ratsnakes are commonly observed, but Kingsnakes are only infrequently observed.

BIOGEOGRAPHY—Many variables naturally govern the distribution of species on islands, including island size and habitat complexity, proximity to a colonizing source (mainland, larger island), the dispersal capabilities of colonizers, weather, and currents (reviewed by Laerm et al., 2000, for the herpetofauna of the Georgia barrier islands). Each of these factors historically may have influenced the composition of the herpetofauna of Egmont Key. However, human activity, through deliberate or passive transfer, is most likely the main factor governing the composition of Egmont's herpetofauna today. The native vegetation community of Egmont Key was removed over the course of more than 150 years of intensive human occupation (see Hurlley and Mohlman, 2000), and human activity remains intensive. It comes as no surprise that three of the species currently found on the island are non-indigenous, and that humans may have hastened the extirpation of the island's largest resident reptile predator. The historical biogeography of the island remains intriguing, however, because the Mole Skink, Eastern Racers, and Kingsnakes show taxonomic affinities with mainland populations to the south and north of the Tampa Bay region, rather than to the nearest likely source populations (Smith et al., 1993).

In summary, the non-marine herpetofauna of Egmont Key presently consists of three (possibly four) snakes, two (possibly five) lizards, two turtles, and three frogs. At least two species (*Osteopilus septentrionalis*, *Hemidactylus garnotii*), and possibly four (if *Anolis carolinensis* and *Elaphe guttata* are included), have colonized the island since 1998 in association with the

construction of visitor's facilities, with the delivery of supplies, or by deliberate release. Two species (*Hyla cinerea*, *Crotalus adamanteus*) likely no longer occur on the island, and the biological status of one species (*Eumeces egregius*) remains obscure. Taken together, these observations suggest that colonization and extirpation are ongoing dynamic processes affecting the herpetofauna of the islands off Florida's west coast, particularly those subject to high human activity, and point to the desirability of periodic surveys of island biodiversity.

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## HERPETOFAUNAL DRIFT-FENCE SURVEY OF TWO SEEPAGE BOGS IN OKALOOSA COUNTY, FLORIDA

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**ABSTRACT:** *Two seepage bogs in Blackwater River State Forest, Okaloosa County, Florida, were surveyed using funnel traps along drift fences for 165 trapping days from 23 September 1998 to 1 September 1999. Fourteen amphibian and 23 reptile species were trapped, and two additional anuran species were heard calling in bogs. Bogs were used by some species from the surrounding pine uplands and provided ideal habitat for Pine Barrens treefrogs (*Hyla anderssonii*), dwarf salamanders (*Eurycea cf. quadridigitata*), southern coal skinks (*Eumeces anthracinus pluvialis*), and several snake species. Most species were apparently more common in the herbaceous than the shrub portions of bogs. The species composition of amphibian and reptile communities differed between bogs and often between shrub and herb portions of the same bog. Much of this difference was probably due to incomplete sampling of the herpetofaunal community, but some of the difference was due to habitat variation. The warmest months, June and August, produced the greatest diversity of species. Stream temperatures in shrub bogs never dropped below 10°C during the sampling period. Herpetofauna inhabiting seepage bogs is primarily threatened by improper fire frequency or timing, alteration of hydrology, and siltation from and impoundment by roads.*

**Key Words:** amphibian, reptile, community, seepage bog, Florida

ABUNDANT rainfall percolating through the deep, porous sands of Florida's Panhandle accumulates in reservoirs of perched ground water when it encounters relatively impermeable layers of silty marl, clay, or limestone. When gentle slopes intersect these perched water tables, the ground water trickles out laterally over a broad zone and forms wetlands called seepage bogs (Folkerts, 1991). Boggy meadows on or at the bases of slopes, which are sometimes called herb bogs, were historically maintained by periodic, lightning-started fires that swept downslope from the longleaf pine (*Pinus palustris*) uplands every five years or less. Wiregrass (*Aristida beyrichiana*) and other pyrophytic vegetation help carry fire into these herbaceous wetlands, which characteristically contain insectivorous plant species, such as pitcher plants (*Sarracenia* spp.) and sundews (*Drosera* spp.). An herb bog is the floristically richest of pitcher plant habitats (Folkerts, 1991) and may contain more plant species per unit area than any other community in the Florida Panhandle (Clewell, 1981). In the prolonged absence of fire, fire-sensitive evergreen shrub species typically invade upslope, where they shade out much of the herbaceous vegetation and may eventually dry up much of

the bog through increased evapotranspiration, creating a shrub bog (Means and Moler, 1979; Means, 1990). Shrub bogs are often present downslope of herb bogs, where fire is usually inhibited by permanently saturated soil and small stream channels that drain the bog.

Prior to European settlement, longleaf pine communities covered more than 60% of the upland areas in the southeastern Coastal Plain (Wahlenberg, 1946), but today they cover < 2% of their original area due to agriculture, urbanization, and intensive forestry (Means and Grow, 1985; Ware et al., 1993). Similarly, an estimated 97% of the acreage of Gulf Coast bogs has been destroyed or severely altered through drainage for pine monoculture or agriculture, fire suppression, alteration of fire periodicity and seasonality, grazing, pond construction, and urbanization (Folkerts, 1982). Since 1982, the rate of bog destruction has increased significantly, and additional damage has been done by off-road vehicle traffic and increased herbicide use in forests and along highways (Folkerts, 1991). Some of the largest and best remaining examples of longleaf pine-dominated sandhill communities, and most of the remaining seepage bogs in Florida, occur on Blackwater River State Forest and Eglin Air Force Base.

This study was the first in Florida to use drift fences to survey the herpetofaunal community of bogs. Although Florida is apparently not experiencing the dramatic declines in amphibian populations seen in some parts of the world (e.g., Blaustein and Wake, 1990; Wyman, 1990; Blaustein et al., 1994; Phillips, 1994), some dusky salamander (*Desmognathus* spp.) populations may be inexplicably declining (Dodd, 1998; Means, 1999), and one of three disjunct populations forming the fragmented geographic distribution of the Pine Barrens treefrog (*Hyla andersonii*) overlaps the region of this study. The collection of baseline data on the species composition and relative abundance of bog herpetofauna provides comparative information for future monitoring studies and the opportunity to identify species that might be affected adversely by logging, road construction, grazing, stream impoundments, trash dumping, fertilizer and biocide applications, and excessive human recreational use of vulnerable bog habitats.

**METHODS**—The two seepage bogs I surveyed were in different river drainages despite being situated only about 12.4 km apart in Blackwater River State Forest, Okaloosa County, Florida. Godman's Bog drains into Reedy Creek, a tributary of the Yellow River, whereas Open Bog drains into Bull Pen Branch, a tributary of the Blackwater River. The bogs were selected because they were known breeding sites for Pine Barrens treefrogs (Godwin, 1998) and had an herb and a shrub bog in close proximity.

In September 1998, I installed one drift-fence array in the herb portion (30°53'57.45"N, 86°44'31.25"W) and one array in the shrub portion (30°53'55.05"N, 86°44'33.25"W) of Open Bog. I also installed one array in the herb portion (30°53'44.28"N, 86°36'44.96"W) and one array in the shrub portion (30°53'42.13"N, 86°36'46.81"W) of Godman's Bog. Each drift-fence array consisted of three silt fences (see Enge, 1997b) that met at a center point at 120° angles. Each array had six double-opening (86 cm long, 20 cm diameter) and six single-opening (86 cm long, 25 cm diameter) funnel traps constructed of aluminum window screen fastened together with office staples. A single-opening funnel trap was placed on each side of the fence

at the end of each arm of the array. A double-opening funnel trap was placed on each side of the fence near the midpoint of each arm. Traps situated in streams in shrub bogs were held in place by sticking an L-shaped wire stake through the bottom of the front of the trap (Engel, 1997b).

The pine stand surrounding Open Bog was  $\approx 62$  years old and was typically burned every four years during the cool season; it had last been burned in February 1995. The pine stand surrounding Godman's Bog was  $\approx 57$  years old and was also typically burned every three years during the cool season; it had last been burned in February 1998. The uplands around both bogs had a canopy of longleaf (*Pinus palustris*) and slash (*P. elliotii*) pines, a shrub layer containing mostly gallberry (*Ilex glabra*) and persimmon (*Diospyros virginiana*), and a ground cover of predominantly wiregrass and bracken fern (*Pteridium aquilinum*). The oak species (*Quercus* spp.) in the uplands differed between the two sites, with Open Bog having a shrub layer of sand post (*Q. margaretta*), laurel (*Q. hemisphaerica*), and live (*Q. virginiana*) oaks. Uplands near Godman's Bog had a subcanopy of water (*Q. nigra*) and southern red (*Q. falcata*) oaks, and a shrub layer of southern red, laurel, and bluejack (*Q. incana*) oaks.

The array situated in the extensive herbaceous portion of Open Bog had scattered slash pines nearby and only about 5% shrub cover, predominantly gallberry, largeleaf gallberry (*Ilex coriacea*), and black titi (*Cliftonia monophylla*). The dense ground cover consisted of ca. 75% graminaceous species, including wiregrass, beakrush (*Rhynchospora* spp.), nut-rush (*Scleria* spp.), and giant white-top sedge (*Dichromena latifolia*). Trumpet (*Sarracenia flava*) and white-topped (*S. leucophylla*) pitcher plants were conspicuous, but total forb coverage was probably only 10% and included parrot pitcher plant (*S. psittacina*), pink sundew (*Drosera capillaris*), dew-threads (*D. tracyi*), bladderwort (*Utricularia* spp.), hatpins (*Eriocaulon* spp.), yellow-eyed grass (*Xyris* spp.), drumheads (*Polygala cruciata*), meadowbeauty (*Rhexia alifanus* and *R. lutea*), flat-topped goldenrod (*Euthamia minor*), bracken fern, and asphodel (*Tofieldia racemosa*). Woody ground cover was ca. 15% and consisted mostly of St. Johns-wort (*Hypericum* spp.), gallberry, and woolly-berry (*Gaylussacia mosieri*).

The other array in Open Bog was situated 91 m away and entirely encompassed by a shrub bog along the seepage stream, which was 0.6–2.3 m wide and 2–15 cm deep. One arm intersected the stream, and another arm partially abutted the stream, which often bifurcated as it wound among trees and root hummocks. The shrub bog had a dense canopy  $\leq 10$  m high composed mainly of black titi with lesser amounts of bayberry (*Myrica heterophylla*), sweetbay (*Magnolia virginiana*), and greenbriar (*Smilax* spp.). Ground cover was only 10% and consisted mostly of woody species, primarily black titi and bayberry, although scattered white-topped pitcher plants, hatpins, yellow-eyed grass, and bladderwort were present. Approximately 90% of the surface was covered in titi leaves, and sphagnum moss (*Sphagnum* spp.) covered about 2%.

The herbaceous portion of Godman's Bog differed from Open Bog in being smaller, having a steeper slope, and lacking white-topped pitcher plants. Seepage occasionally ceased around the array, unlike the continuously saturated soil in Open Bog. The array lacked canopy cover, although widely scattered slash and longleaf pines were present in the bog. Shrub coverage by largeleaf gallberry was only 2%. Grassy ground cover was ca. 90%, consisting mainly of wiregrass with lesser amounts of panicum (*Panicum* spp.), bluestem (*Andropogon* spp.), beakrush, nut-rush, spikerush (*Eleocharis* spp.), and giant white-top sedge. Herbaceous ground cover consisted of trumpet and parrot pitcher plants, pink sundew, dew-threads, bachelor's button (*Polygala lutea*), milkwort (*P. ramosa*), drumheads, yellow-eyed grass, hatpins, sneezeweed (*Helenium* spp.), flat-topped goldenrod, blazing-star (*Liatriis* sp.), and meadowbeauty. Woody ground cover was ca. 5%, primarily gallberry, woolly-berry, St. Johns-wort, wax myrtle (*Myrica cerifera*), and greenbriar. Sphagnum moss and clubmoss (*Lycopodium appressum*) covered ca. 2% of the ground. The end of one arm of the array was 2 m from a patch of largeleaf gallberry, and the end of the arm farthest downslope was 3 m from the edge of a narrow shrub bog.

The other array in Godman's Bog was 82 m away in a shrub bog that had burned in February 1998, killing most of the aboveground portions of shrubs, although regeneration was occurring. One arm of the array intersected the stream and the other arms traversed both burned

and unburned portions of the shrub bog. This shrub bog differed from that in Open Bog by being much narrower, having a slope bordering one side, and containing few seepage areas adjacent to the stream. Slash pine, sweetbay, and swamp titi (*Cyrilla racemiflora*) provided 20% canopy cover. Overall shrub cover was 30%, ranging from 90% in the unburned portion along the stream to 5% in the burned areas. Predominant shrubs near the stream were swamp titi, largeleaf gallberry, sweetbay, swamp bay (*Persea palustris*), hazel alder (*Alnus serrulata*), and greenbriar, whereas gallberry predominated away from the stream because more fire-sensitive shrubs, primarily swamp titi, had been killed. Overall woody ground cover was 50%, partly because of shrub regeneration in burned areas, and included woolly-berry, swamp titi, largeleaf gallberry, bayberry, buttonbush (*Cephalanthus occidentalis*), sweetbay, swamp bay, and slash pine. Grassy ground cover was 5%, mostly bushy broom grass (*Andropogon glomeratus*) and panicum. Forbs covered only 1–2% of the surface and included bachelor's button, cinnamon fern (*Osmunda cinnamomea*), meadowbeauty, white-topped pitcher plant, yellow-eyed grass, and redroot (*Lachnanthes caroliniana*). Sphagnum moss coverage was only 1% and confined to the stream margins.

Godman's Bog experienced substantial surface runoff after heavy rains, which sometimes knocked down the fence intersecting the stream. The stream in the shrub bog was typically 0.5–1.0 m wide and 5–12 cm deep, and it flowed continuously throughout the study. However, when I visited the site on 25 September 1999 after the study ended, the stream had ceased flowing and contained only a few shallow pools.

Traps were open for a total of 165 days from 23 September to 1 November 1998, 1 February to 6 March 1999, 31 March to 1 May 1999, 31 May to 1 July 1999, and 1 August to 1 September 1999. I typically checked traps every five days, but trap-check intervals ranged from three to eight days. Traps were provided with a moistened sponge and tempered masonite or tileboard shade covers to minimize mortality of trapped animals. I marked and released captured animals  $\geq 2$  m away on the opposite side of the fence using the methodology recommended by Enge (1997a). I did not mark small snakes because of the possibility of deleterious injury. Larval amphibians are not included in capture totals.

I recorded precipitation from a rain gauge at each bog each time traps were checked. Air temperatures in the shade were recorded every hour in the shrub portion of Open Bog using a StowAway<sup>®</sup> XTI temperature data logger. Each time the site was visited, I also recorded the air temperature from a mercury maximum-minimum thermometer affixed to a tree trunk 1 m above the ground in the shrub portion of Open Bog. I recorded relative stream depths in the shrub bogs from permanently placed PVC pipes marked in centimeters, and I recorded stream temperatures using a handheld, pocket case mercury thermometer. In April, June, and August 1999, I collected vegetative data within a 15-m radius of the center point of each array using ocular estimation of percent cover in four layers: canopy (> 5 m tall), shrub (1–5 m tall), ground cover (< 1 m high), and moss.

Herpetofaunal species composition between different areas was compared using the Jaccard similarity coefficient:  $C_j = c/(a + b - c)$ , where  $c$  = the number of species shared by both habitats,  $a$  = the number of species in Habitat A, and  $b$  = the number of species in Habitat B (Magurran, 1988). For these comparisons, I included species observed along fences or anurans heard calling in bogs, but I omitted anuran species heard calling from nearby upland areas.

**RESULTS AND DISCUSSION—Temporal variation in abiotic variables and captures**—Water levels in the low-volume first-order streams in shrub bogs varied 15.5 cm in Godman's Bog and 8 cm in Open Bog during the course of the study (Table 1). The steeper slopes at Godman's Bog probably contributed to greater surface runoff into the stream. The highest water level was recorded in Godman's Bog after Hurricane Georges dropped at least 16.0 cm of rain, whereas the highest water level in Open Bog was recorded

TABLE 1. Maximum and minimum readings for abiotic variables recorded in shrub portions of Open Bog and Godman's Bog, Okaloosa County, Florida. Stream depths are relative.

Site	October 1998		February 1999		April 1999		June 1999		August 1999	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Open Bog										
Stream depth (cm)	17.5	15.0	19.0	15.5	17.0	16.0	18.0	17.0	23.0	18.0
Water temperature (°C)	21.1	18.3	17.8	10.0	19.7	16.1	22.7	19.7	25.0	22.9
Air temperature(°C)	30.6	2.8	26.1	-5.0	32.8	-0.6	33.3	13.3	36.7	19.4
Godman's Bog										
Stream depth (cm)	29.0	16.0	25.5	13.5	15.0	13.5	19.0	13.5	21.0	17.0
Water temperature (°C)	25.6	18.6	15.6	11.5	20.3	16.9	23.9	20.9	29.7	23.5

after 6.2 cm of rain in August 1999. Precipitation between bogs was often variable, especially during summer thunderstorms.

Stream temperatures fluctuated much less than did air temperatures. Air temperatures of  $< 0^{\circ}\text{C}$  occurred in bogs, but stream temperatures never dropped below  $10.0^{\circ}\text{C}$  in shrub bogs (Table 1). Air temperatures in the shadiest shrub bog reached  $36.7^{\circ}\text{C}$  (Table 1), and higher temperatures were undoubtedly attained elsewhere in more open shrub and herb bogs. During the months of trapping, air temperatures varied  $41.7^{\circ}\text{C}$  in the shrub portion of Open Bog, with a maximum daily variation in air temperature of  $23.7^{\circ}\text{C}$  on 19 April 1999.

Traps were opened on 23 September 1998 and first checked on 30 September or 1 October after Hurricane Georges deluged the Panhandle on 27–28 September with 76.2 cm of rain in Crestview and 40.6 cm of rain in Pensacola. On 29 September, the Blackwater River at Baker, Okaloosa County, crested at a record 8.76 m, which was 5.41 m above flood stage. At Open Bog, the rain gauge had 12.4 cm, whereas the rain gauge at Godman's Bog had  $> 16.0$  cm (the rain gauge was full). Despite damage to arrays and displaced traps from the hurricane, I trapped a total of 47 amphibians during the first week; thus, 18.5% of all amphibians ( $n = 254$ ) were trapped during 4.2% of the study's time.

The warmest months of sampling, June and August, were the most productive for catching a diversity of reptile species. Ten reptile species were trapped during each of these months in Open Bog, whereas in Godman's Bog, 12 reptile species were trapped in June and 13 in August. For all bogs combined, 15 reptile species were trapped in both June and August. June was also the most productive month for trapping a diversity of amphibian species; eight species were trapped in each bog (a total of nine species). The coolest month, February, was the least productive for trapping amphibians and reptiles, but this was the only month when a northern spring peeper and rough earth snake were captured.

*Rare taxa*—I trapped five taxa that are listed by the Florida Fish and Wildlife Conservation Commission (1999) or the Florida Committee on Rare and Endangered Plants and Animals (Moler, 1992): Pine Barrens treefrog, southern coal skink (*Eumeces anthracinus pluvialis*), mimic glass lizard (*Ophisaurus mimicus*), mole kingsnake (*Lampropeltis calligaster rhombomaculata*), and Florida pine snake (*Pituophis melanoleucus mugitus*).

The Pine Barrens treefrog, a Species of Special Concern (Florida Fish and Wildlife Conservation Commission, 1999), is known from  $\approx 150$  sites in four Florida counties and 22 sites in two Alabama counties; this disjunct population is  $\approx 900$  km from the nearest definitely known populations in the Carolinas (Means, 1992). I trapped one Pine Barrens treefrog along the edge of each shrub bog, whereas I trapped 13 in herb bogs (Table 2). The five treefrogs trapped in the herbaceous portion of Godman's Bog were along the fence farthest downslope near a shrub-lined drain, and seven of eight

treefrogs trapped in the herbaceous portion of Open Bog were along the fence farthest downslope, where standing, shallow water was often present. Five males and 10 females were trapped, and none was recaptured. Six frogs were trapped on 5 April after 5.5 cm of rain, and the remaining nine frogs were trapped on three different occasions in June after rainfall ranging from 1.4 to 6.1 cm. This species was apparently trapped only after descending to the ground to breed. One trap contained one male and three females, and twice females spawned in traps. One trap contained developing eggs and a male treefrog, but the female had apparently escaped. Males measured  $37.4 \pm 1.44$  mm SVL (range 35–43 mm) and weighed  $3.50 \pm 0.197$  g (range 2.8–4.0 g), whereas eight females measured  $39.8 \pm 0.96$  mm SVL (range 36–44 mm) and weighed  $4.44 \pm 0.714$  g (range 3.7–5.5 g). Females were significantly heavier than males ( $t = 2.98$ , 11 df,  $P = 0.012$ ). Two females were not measured, because one had been killed by fire ants, and another had been recently eaten by an eastern garter snake (*Thamnophis sirtalis sirtalis*), which was forced to regurgitate it.

Southern coal skinks were most common in herb bogs, although three were trapped (one was a recapture) in the shrub portion of Godman's Bog (Table 2). Those trapped in shrub bogs were in areas of low shrubs regenerating after fire, not in the taller, denser shrubs along the stream. At both arrays in herb bogs, coal skinks were trapped along all three fences, ranging from drier upslope areas to wetter downslope areas. One individual was trapped in February, one in April, seven in June, five in August, and two in October. Of the 16 captures, three were recaptures. Seven adults measured  $50.9 \pm 1.72$  mm SVL (range 45–58 mm) and weighed  $3.64 \pm 0.465$  g (range 2.2–5.9 g).

In Godman's Bog, a male Florida pine snake (*Pituophis melanoleucus mugitus*) was trapped on 5 June in the herbaceous portion, and a female was trapped on 1 September in the shrub portion. Both snakes measured 138 cm SVL, but the male weighed 980 g and the female 800 g. The anterior half of the dorsum of each snake had a dark brown wash that obscured most of the blotches. Another unusual capture was a male mole kingsnake (*Lampropeltis calligaster rhombomaculata*) (61 cm SVL; 98 g), which was trapped in the upslope herbaceous portion of Open Bog on 1 July. A mimic glass lizard (*Ophisaurus mimicus*) was also trapped here on 27 October.

Most or all of the dwarf salamanders (*Eurycea* cf. *quadridigitata*) trapped were an undescribed species that is morphologically and biochemically distinct from the nominate species (Palis and Jensen, 1995; Means, 1999). This undescribed species is characterized by an orange dorsal stripe and a bright yellow underside of the tail. Dwarf salamanders were apparently gravid from October through possibly 10 April. A larval dwarf salamander ready to metamorphose was trapped on 10 April, and a recent metamorph was trapped on 22 April.

*Community composition*—The amphibian community of bogs consisted predominantly of southern cricket frogs (*Acris gryllus gryllus*), eastern nar-

TABLE 2. Herpetofauna captured 23 September 1998–September 1999 in herb and shrub bogs in Blackwater River State Forest, Okaloosa County, Florida (X indicates taxon observed but not captured).

Taxon	Open Bog		Godman's Bog	
	Herbaceous	Shrub	Herbaceous	Shrub
<b>Anurans</b>				
Southern cricket frog ( <i>Acris gryllus gryllus</i> )	14	2	19	13
Southern toad ( <i>Bufo terrestris</i> )	7	0	1	3
Eastern narrowmouth toad ( <i>Gastrophryne carolinensis</i> )	9	6	11	6
Pine Barrens treefrog ( <i>Hyla andersonii</i> )	8	1	5	1
Pinewoods treefrog ( <i>H. femoralis</i> )	0	0	X	X
Northern spring peeper ( <i>Pseudacris crucifer crucifer</i> )	0	0	1	0
Southern chorus frog ( <i>P. nigrita nigrita</i> )	X	0	0	0
Bullfrog ( <i>Rana catesbeiana</i> )	2	1	0	0
Bronze frog ( <i>R. clamitans clamitans</i> )	3	9	2	8
Southern leopard frog ( <i>R. sphenoccephala</i> )	0	1	1	0
Unidentified	1	0	2	2
<b>Salamanders</b>				
Spotted dusky salamander ( <i>Desmognathus fuscus conanti</i> )	0	0	0	1
Southern two-lined salamander ( <i>Eurycea cirrigera</i> )	1	8	0	0
Three-lined salamander ( <i>E. guttolineata</i> )	0	1	0	0
Dwarf salamander ( <i>E. cf. quadridigitata</i> )	37	6	15	6
Southeastern slimy salamander ( <i>Plethodon grobmani</i> )	0	0	0	1
Southern red salamander ( <i>Pseudotriton ruber vioscai</i> )	6	21	27	5
<b>Turtles</b>				
Eastern mud turtle ( <i>Kinosternon subrubrum subrubrum</i> )	2	7	1	1
Gulf Coast box turtle ( <i>Terrapene carolina major</i> )	0	1	1	0
<b>Lizards</b>				
Green anole ( <i>Anolis carolinensis</i> )	0	0	1	0
Southern coal skink ( <i>Eumeces anthracinus pluvialis</i> )	8	0	5	3

TABLE 2. Continued.

Taxon	Open Bog		Godman's Bog	
	Herbaceous	Shrub	Herbaceous	Shrub
Broadhead skink ( <i>E. laticeps</i> )	0	10	2	10
Mimic glass lizard ( <i>Ophisaurus mimicus</i> )	1	0	0	0
Eastern glass lizard ( <i>O. ventralis</i> )	3	0	5	2
Ground skink ( <i>Scincella lateralis</i> )	5	2	15	4
Snakes				
Cottonmouth ( <i>Agkistrodon piscivorus</i> )	0	0	1	1
Northern scarlet snake ( <i>Cemophora coccinea copei</i> )	2	3	2	1
Southern black racer ( <i>Coluber constrictor priapus</i> )	3	2	17	8
Southern ringneck snake ( <i>Diadophis punctatus punctatus</i> )	3	1	0	3
Corn snake ( <i>Elaphe guttata guttata</i> )	1	0	2	2
Mole kingsnake ( <i>Lampropeltis calligaster rhombomaculata</i> )	1	0	0	0
Banded water snake ( <i>Nerodia fasciata fasciata</i> )	0	1	2	2
Florida pine snake ( <i>Pituophis melanoleucus mugitus</i> )	0	0	1	1
Gulf crayfish snake ( <i>Regina rigida sinicola</i> )	4	7 <sup>1</sup>	1	2
Dusky pigmy rattlesnake ( <i>Sistrurus miliarius barbouri</i> )	0	X	1	1
Florida redbelly snake ( <i>Storeria occipitomaculata obscura</i> )	1	0	1	1
Southeastern crowned snake ( <i>Tantilla coronata</i> )	0	0	0	1
Eastern ribbon snake ( <i>Thamnophis sauritus sauritus</i> )	0	2	0	2
Eastern garter snake ( <i>T. sirtalis sirtalis</i> )	6	2	2	0
Rough earth snake ( <i>Virginia striatula</i> )	1	0	0	0
Unidentified	1	0	1	0
Grand total	130	94	145	91

<sup>1</sup> An adult female and six neonates apparently born in the trap.

rowmouth toads (*Gastrophryne carolinensis*), dwarf salamanders, and southern red salamanders (*Pseudotriton ruber vioscai*). Bronze frogs (*Rana clamitans clamitans*) and two-lined salamanders (*Eurycea cirrigera*) were relatively common, especially in shrub bogs. Southern toads (*Bufo terrestris*), southern leopard frogs (*Rana sphenoccephala*), and young bullfrogs (*R. catesbeiana*) were occasionally captured in both types of bogs, but spotted dusky (*Desmognathus fuscus conanti*), three-lined (*Eurycea guttolineata*), and southeastern slimy (*Plethodon grobmani*) salamanders were apparently confined to shrub bogs. Thirteen of 15 Pine Barrens treefrogs came from herb bogs. One-half of all amphibian taxa trapped are at or near the southern terminus of their geographic ranges (Conant and Collins, 1991), and most are tied closely to aquatic systems.

Upland snake species—southeastern crowned snake (*Tantilla coronata*), northern scarlet snake (*Cemophora coccinea copei*), corn snake (*Elaphe guttata guttata*), mole kingsnake, and pine snake—occasionally traveled through bogs or entered them to drink or forage. Arrays in bogs occasionally trapped hispid cotton rats (*Sigmodon hispidus*) and young marsh rabbits (*Sylvilagus palustris*), which are potential prey items for large snake species. The saturated soil of bogs was not aversive to most reptile species, and the vegetative physiognomy of herbaceous portions of bogs did not differ much from the surrounding sandhill habitat in that both had a dense, grassy ground cover and scattered shrubs and pine trees.

Reptile species that probably do equally well in uplands and bogs are the box turtle (*Terrapene carolina*), green anole (*Anolis carolinensis*), broad-head skink (*Eumeces laticeps*), ground skink (*Scincella lateralis*), mimic glass lizard, eastern glass lizard (*Ophisaurus ventralis*), southern black racer (*Coluber constrictor priapus*), corn snake, dusky pigmy rattlesnake (*Sistrurus miliarius barbouri*), Florida redbelly snake (*Storeria occipitomaculata obscura*), and rough earth snake. Species that probably prefer the wetter conditions or more abundant amphibian prey present in bogs are the eastern mud turtle (*Kinosternon subrubrum subrubrum*), coal skink, cottonmouth (*Agkistrodon piscivorus*), southern ringneck snake (*Diadophis punctatus punctatus*), banded water snake (*Nerodia fasciata fasciata*), Gulf crayfish snake (*Regina rigida sinicola*), garter snake, and eastern ribbon snake (*T. sauritus sauritus*). Coal skinks were more abundant in herb bogs, whereas the more arboreal broadhead skinks were more abundant in shrub bogs because trees provided vertical structure, although two neonates were trapped in herb bogs. The two *Thamnophis* species apparently segregated the habitat, with garter snakes primarily inhabiting herb bogs and semiarboreal ribbon snakes primarily inhabiting shrub bogs.

The lack of leaf litter and woody debris in herb bogs provides seemingly little surface cover for herpetofauna, although clumps of dense wiregrass and other ground cover may provide above-ground refugia. The sunny aspect of herb bogs would appear to provide stressful environmental conditions for amphibians, which prefer shadier and cooler conditions than do most reptile

species. Some non-burrowing amphibians in herb bogs probably move into adjacent shrub bogs to escape high temperatures, at least during the daytime. Many amphibians and reptiles, however, probably use the abundant burrows of crayfish as refugia. I occasionally observed red salamanders peering from and entering crayfish burrows in herb bogs. Sufficient rainfall occurred during my study to maintain continuously saturated soil conditions in most portions of the bogs, but during seasonal or extended droughts, when the soil of bogs may dry (Wolfe et al., 1988), crayfish burrows may provide important refugia for moisture-dependent animals (Enge, 1997a). Seepage bogs remain saturated longer than most other pitcher plant habitats (Folkerts, 1991), but during droughts, some bog animals are probably forced to move downslope to find permanent water in stream channels.

*Community comparisons*—Fourteen amphibian species and 23 reptile species were trapped in seepage bogs. At Open Bog, the amphibian species composition was somewhat similar between the herb and shrub portions ( $C_j = 0.67$ ), but the reptile species composition was dissimilar ( $C_j = 0.39$ ). In contrast, at Godman's Bog, both amphibian ( $C_j = 0.67$ ) and reptile ( $C_j = 0.70$ ) communities were somewhat similar between the herb and shrub portions. The dissimilarity in reptile species composition between herb and shrub portions of Open Bog was probably due to the array in the shrub bog being situated completely in the shady interior, with its tall, dense shrubs. In contrast, two fences of the shrub bog array at Godman's Bog were situated in more sunny, open conditions where shrubs were regenerating from a recent fire. This area of shrub regeneration provided reptiles with conditions more similar to those present in herb bogs.

Herbaceous portions of Open Bog and Godman's Bog did not have very similar amphibian ( $C_j = 0.41$ ) or reptile ( $C_j = 0.48$ ) communities. Shrub portions of the two bogs also did not have very similar community composition for amphibians ( $C_j = 0.38$ ) or reptiles ( $C_j = 0.47$ ). I believe that most of the differences in species composition between the two bogs were not due to their location in different river drainages but instead to differences in topography, vegetative structure and density, and seepage flow. Additional trapping would probably have produced more similar species lists for the two bogs because nine species at Open Bog and eight species at Godman's Bog were represented by only a single capture (Table 2). Some of these "rare" species were undoubtedly present in both bogs and would have been detected during longer or more intensive sampling. I heard calling pine-woods treefrogs (*Hyla femoralis*) in Godman's Bog and southern chorus frogs (*Pseudacris nigrita nigrita*) in Open Bog but failed to trap any. The variability in species composition between the two bogs indicates that more bogs would need to be sampled in order to develop a comprehensive list of species utilizing bogs.

If species lists from herbaceous portions of the two bogs are combined and compared with species lists from shrub portions, the similarity of the

community composition of herb and shrub bogs increased for amphibians ( $C_j = 0.69$ ) and reptiles ( $C_j = 0.74$ ), which probably indicates incomplete sampling of each habitat type. The overall species composition of Open Bog versus Godman's Bog (shrub and herb portions combined) was more similar for reptiles ( $C_j = 0.62$ ) than for amphibians ( $C_j = 0.50$ ).

The only comparable drift-fence survey of seepage bogs along the Gulf Coast was conducted in five bogs and adjacent upland pine forests in the Angelina National Forest in eastern Texas (Reid and Whiting, 1994). Eleven species of amphibians and 17 species of reptiles were trapped in Texas bogs, whereas 14 amphibian and 23 reptile species were trapped in Florida bogs. Comparisons of the species composition of Florida and Texas seepage bogs can be made if one allows for species differences due to geographic ranges (e.g., *Bufo*, *Thamnophis*). Bogs in Florida and Texas were not very similar in amphibian species composition ( $C_j = 0.47$ ). Most of the species trapped in Texas bogs were also found in Florida bogs, but Texas had a depauperate salamander fauna in that it lacked dusky, two-lined, three-lined, slimy, and red salamanders. The dwarf salamander was the most common amphibian species in both Florida (23.5%;  $n = 272$ ) and Texas (47.0%;  $n = 89$ ) bogs. The second and third most common amphibian species in Texas bogs were the narrowmouth toad (15.7%) and bronze frog (14.5%), which were also common in Florida bogs (11.8% and 8.1%, respectively).

Bogs in Florida and Texas were dissimilar in reptile species composition ( $C_j = 0.33$ ). However, if eight reptile species that were trapped only in Texas upland forests are included, the similarity between Florida and Texas bogs increases ( $C_j = 0.41$ ). Ground skinks constituted 50.3% of reptile captures ( $n = 324$ ) in Texas bogs, followed by coal skinks (18.5%), six-lined racerunners (*Cnemidophorus sexlineatus sexlineatus*; 8.6%), green anoles (*Anolis carolinensis*; 7.7%), and southern fence lizards (*Sceloporus undulatus undulatus*; 4.6%). Ground and coal skinks were the second and fourth most frequently trapped reptile species in Florida bogs. I failed to trap racerunners and fence lizards in bogs, although they were common in adjacent uplands and undoubtedly entered bogs occasionally, especially during dry conditions.

*Potential threats and management implications*—The most obvious threats to bogs in Blackwater River State Forest are inadvertent damming of the seepage streams that drain bogs upslope of roads, and siltation of bogs downslope of roads. Bogs are sometimes silted in by runoff of clay, silt, and sand from unpaved roads, especially after heavy rains and recent road-grading activities.

I could not determine whether groundwater seepage in bogs was affected by surface excavations or groundwater extraction in the area. Seepage wetlands can be threatened by stormwater ponds, borrow pits, man-made lakes, and mining operations in upland areas up to 1.6 km away (Bacchus, 1995). These large excavations can permanently reduce groundwater levels by extensively increasing the "void space" previously occupied by the ground

water, increasing evaporational losses due to conversion of ground water to surface water, and permanently reducing recharge (Bacchus, 1995). Seepage wetlands are also threatened by active groundwater withdrawals for irrigation of golf courses and agricultural fields, and by residential, industrial, and municipal wells (Bacchus, 1995). Even shallow firelines that are trenched parallel to the margins of seepage-slope habitats can significantly alter the lateral flow of ground water by converting it to surface water, which is subject to higher rates of evaporation (Bacchus, 1995; Hermann, 1995). Reduction in ground water feeding seepage bogs will shorten the hydroperiod and, thus, affect herpetofaunal populations (particularly amphibian species that breed in seepage pools and streams) and allow encroachment of upland plant species. Fortunately, this area of Florida has the highest annual average surplus (46 cm) of rainfall over potential evapotranspiration (Winsberg, 1992).

Herb bogs on seepage slopes are dependent upon the frequent fires characteristic of surrounding longleaf pine-wiregrass communities to maintain their open conditions (Folkerts, 1982; Means, 1990). Without fire, hardwood encroachment into herb bogs leads to increased evapotranspiration and lower groundwater levels, eliminating seepage pools that provide larval habitat for species like the Pine Barrens treefrog (Means and Moler, 1979; Means, 1990). Growing-season fires are more natural and are more effective at killing hardwoods (Robbins and Myers, 1992; Hermann, 1995). Initial cool fires in winter may be necessary to reduce fuel loads in bogs that have become degraded through fire suppression, but winter fires and annual burning are apparently detrimental to pitcher plants (Hermann, 1995; Johnson and Hipes, 1997). The two bogs I studied had typically burned when the surrounding uplands were prescription burned from September through February every three or four years since at least 1978 (Klempa, 1999).

Much of Blackwater River State Forest and Eglin Air Force Base remains heavily forested, and most of the pine forests are managed by prescribed burning. In upland pine forests with high tree densities, most bog flora and fauna would probably benefit from selective logging if it was conducted above the seepage zone and if ground-cover disturbance was minimal. Opening up the canopy would encourage wiregrass growth (Means, 1997) and might increase downslope seepage through reduced evapotranspiration. Care needs to be taken that the use of heavy equipment does not alter the hydrology of the bogs or cause erosional runoff and subsequent siltation of bogs.

Fragmentation of upland habitats and loss of bogs decrease local herpetofaunal diversity. Bog species (e.g., Pine Barrens treefrog) that have undergone local population extinctions, possibly as a result of severe droughts or habitat degradation due to fire suppression, may be precluded from recolonizing suitable habitat because of unfavorable surrounding habitat and large distances between bogs. Another threat to bog herpetofauna is red imported fire ants (*Solenopsis invicta*), which primarily prey upon eggs,

hatchlings, and small species with limited mobility (Allen et al., 1997, 1998). Fire ant colonies were present in pine uplands in Blackwater River State Forest, but ant colonies appeared to be most numerous on seepage slopes. Trapped animals were sometimes killed by fire ants, and fire ants have been suggested as a possible factor in declines of certain herpetofaunal species in the southeastern Coastal Plain (Mount, 1981). I did not observe any damage to bogs by rooting feral hogs (*Sus scrofa*); however, this is a problem in seepage habitats elsewhere (Printiss and Hipes, 1999).

I conducted only a limited herpetofaunal survey of seepage bogs, and more intensive surveys are needed to document differences in herpetofaunal composition within and among bogs and to better understand how the community composition is affected by the surrounding landscape, fire history, vegetative cover, and hydrology. Additional studies are also needed of the habitat use of the Pine Barrens treefrog, especially outside the breeding season. The small size, dispersed distribution, and sensitivity of bogs to human alteration make bog-dwelling herpetofauna especially vulnerable to extirpation, particularly those taxa with small geographic ranges that reside continuously within this habitat.

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- (2) **FAS site:** [www.floridaacademyofsciences.org](http://www.floridaacademyofsciences.org) (select "Florida Scientist").

It is possible to search for papers and abstracts of papers for the past six years: Go to the FAS site (above) and select "Allen Press". When the link is complete, select "Advanced Search" and follow the directions.

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