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Detection Probabilities and Site Occupancy Estimates for Amphibians at Okefenokee National Wildlife Refuge

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ABSTRACT.—We conducted an amphibian inventory at Okefenokee National Wildlife Refuge from August 2000 to June 2002 as part of the U.S. Department of the Interior's national Amphibian Research and Monitoring Initiative. Nineteen species of amphibians (15 anurans and 4 caudates) were documented within the Refuge, including one protected species, the Gopher Frog *Rana capito*. We also collected 1 y of monitoring data for amphibian populations and incorporated the results into the inventory. Detection probabilities and site occupancy estimates for four species, the Pinewoods Treefrog (*Hyla femoralis*), Pig Frog (*Rana grylio*), Southern Leopard Frog (*R. sphenocephala*) and Carpenter Frog (*R. virgatipes*) are presented here. Detection probabilities observed in this study indicate that spring and summer surveys offer the best opportunity to detect these species in the Refuge. Results of the inventory suggest that substantial changes may have occurred in the amphibian fauna within and adjacent to the swamp. However, monitoring the amphibian community of Okefenokee Swamp will prove difficult because of the logistical challenges associated with a rigorous statistical assessment of status and trends.

INTRODUCTION

Okefenokee Swamp is one of the largest freshwater wetlands in the southeastern United States. The swamp lies within the coastal plain of Georgia and Florida and encompasses an area more than 200,000 ha in size. Approximately 158,000 ha of the 200,000 ha swamp were designated as a National Wildlife Refuge (NWR) in 1937 and more than 95% of the Refuge has been declared a National Wilderness Area. Human activity in the swamp has included logging, dredging, peat mining and water impoundment at the Suwannee River Sill (McQueen and Mizell, 1926; Trowell and Izlar, 1984; Loftin, 1998). Fires (both natural and anthropogenic) have played a large role in shaping the character of the swamp.

Despite past land use alterations, the Okefenokee Swamp is one of the most significant wetlands on U.S. public lands. The swamp is well-known for its unique bog-like wetlands as well as a diverse fauna. In particular, there is a long history of amphibian research in and around the swamp (reviewed by Gibbons, 2002). The earliest investigations of the amphibians of the Okefenokee Swamp were undertaken in the early 1900s by A.H. Wright and students from Cornell University (Harper, 1932; Wright, 1926, 1932). These investigations were extremely comprehensive and resulted in publication of Wright's seminal work, *Life Histories of the Frogs of Okefinokee Swamp, Georgia* (Wright, 1932). Unfortunately, no companion work on salamanders was ever published (Dodd, 1995). In the late 1970s historic amphibian collections from the region were summarized by Laerm *et al.* (1980). Later work included surveys for three protected species previously recorded from the swamp, the Flatwoods Salamander (*Ambystoma cingulatum*; federally listed as threatened), Striped Newt (*Notophthalmus perstriatus*; candidate for federal listing) and Gopher

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Frog (*Rana capito*; a species of special concern in Georgia and Florida) (Dodd and LaClaire, 1995; Jensen, 1995). Yet, beyond these targeted surveys, recent comprehensive published amphibian surveys within the swamp are lacking.

The lack of current information on the status of amphibian populations in the Okefenokee Swamp is of concern given the recent accounts of amphibian population declines around the world (Alford and Richards, 1999; Daszak *et al.*, 1999; Houlahan *et al.*, 2000). In 2000 the U.S. Department of the Interior initiated the Amphibian Research and Monitoring Initiative to address concerns about the status of amphibian populations on federal lands (Hall and Langtimm, 2001). Okefenokee National Wildlife Refuge was one of the initial southeastern sites chosen for inclusion in the national program. Our approach to the amphibian inventory and monitoring initiative at the Refuge included: (1) targeted surveys of historic localities for rare species; (2) short-term sampling to determine species presence and distribution throughout the Refuge; and (3) intensive repeated sampling at permanent monitoring sites within the Refuge to estimate detectability and site occupancy of select species. Results of the inventory and monitoring effort are presented here.

STUDY AREA

The mean annual rainfall in the Okefenokee area is ca. 127 cm and the average minimum and maximum temperatures are ca. 13 C and 27 C, respectively (Southeast Regional Climate Center). Average monthly rainfall is typically 5–10 cm/mo from November through May and is slightly higher (13–18 cm/mo) from June through September. Forested wetlands comprise 57% of the habitat within the Refuge and contain pond cypress (*Taxodium ascendens*), titi (*Cyrilla racemiflora*), loblolly bay (*Gordonia lasianthus*), blackgum tupelo (*Nyssa sylvatica*), hurrahbush (*Lyonia lucida*) and dahoon (*Ilex cassine*) (Wright and Wright, 1932; Loftin, 1998). Most large pond cypress were logged out of the swamp in the early 1900s. Dense shrub thickets of titi, hurrahbush and fetterbush (*Leucothoe racemosa*) cover 29% of the swamp. Wet prairies with yellow-eyed grass (*Xyris* sp.), Walter's sedge (*Carex walteri*), spatterdock (*Nuphar luteum*), fragrant water lily (*Nymphaea odorata*) and golden club (*Orontium aquaticum*) cover 8% of the swamp. Narrow man-made boat trails and natural lakes transect the wetland habitats of the swamp. The remaining 5% of the Refuge consists of forested uplands with slash pine (*Pinus elliottii*), longleaf pine (*P. palustris*), saw palmetto (*Serenoa repens*) and gallberry (*I. glabra*). Upland forests on the east side of the Refuge consist of mesic pine flatwoods and scrubby flatwoods. Those on the southern and western periphery of the Refuge are mesic pine flatwoods. The numerous (ca. 70) islands within the swamp also contain pine flatwoods. A number of small ponds and cypress strands occur within the pine flatwoods, particularly in the western part of the Refuge.

METHODS

Targeted surveys for rare amphibians were conducted at ephemeral ponds within the Refuge from September to January in 2000 and 2001. If standing water were present in the ponds, we dip-netted extensively for Flatwoods Salamander, Striped Newt and Gopher Frog larvae. If ponds were dry, we conducted litter/cover searches for adult salamanders in and around the ponds. Funnel traps were placed in Gopher Tortoise (*Gopherus polyphemus*) burrows in fall 2001 in an attempt to capture adult Gopher Frogs.

We conducted 116 surveys (80 1-d surveys and 36 3-d surveys) from August 2000 to June 2002 at different localities in the Refuge (Fig. 1). We used a variety of sampling techniques to detect amphibians, depending on conditions at the site. For the 1-d surveys, if standing water were present, we employed dip-nets to collect aquatic amphibians and larvae (Shaffer

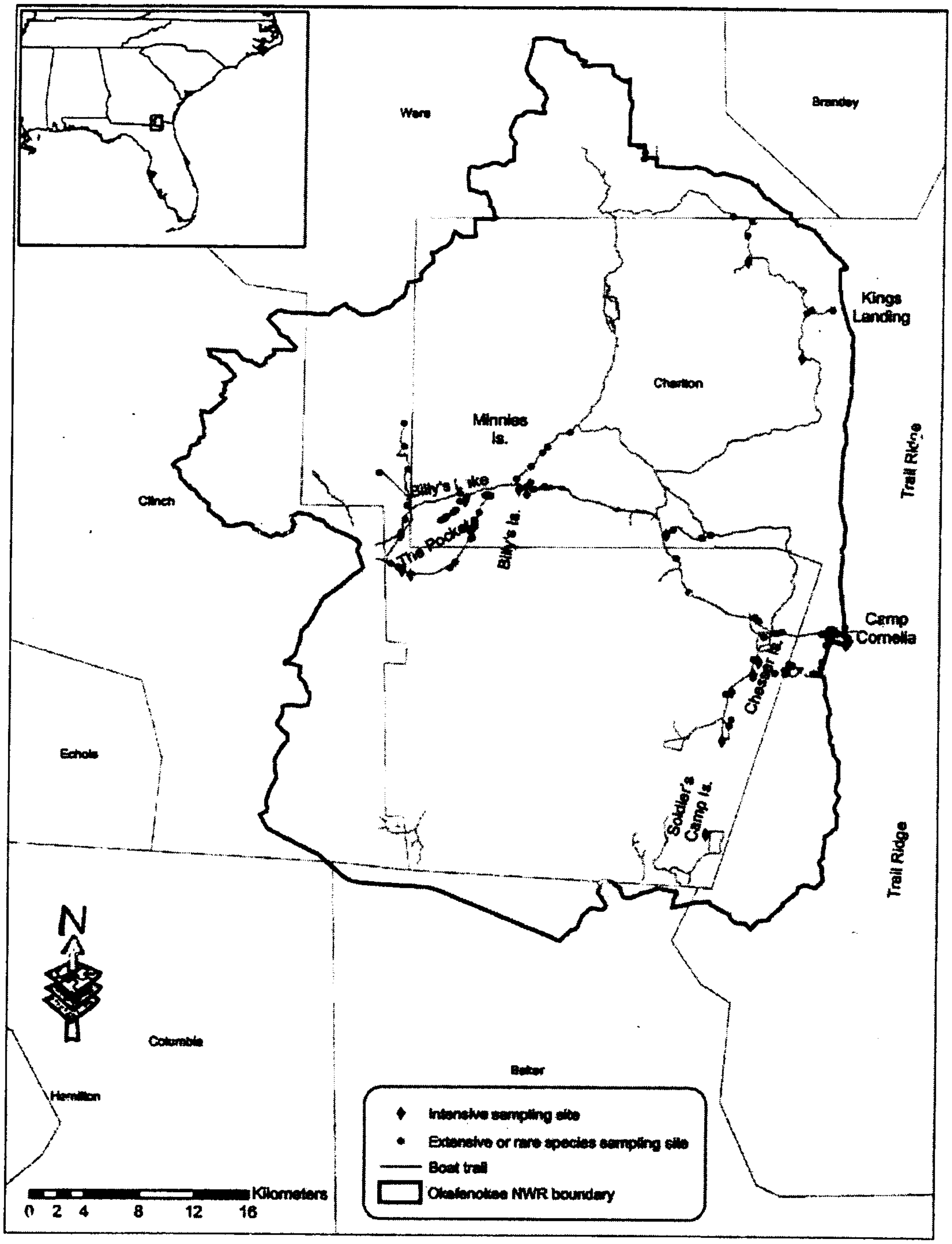

FIG. 1.—Amphibian survey sites at the Okefenokee National Wildlife Refuge, Georgia. Sampling took place from August 2000 through June 2002

et al., 1994), whereas, if no water were present, we conducted timed litter/cover searches (Scott, 1994). Each of the two methods was employed for a minimum of 1 person-h at each site. For 3-d surveys at inundated sites we set aquatic traps [floating funnel traps (*see* description below), commercial minnow and crayfish traps (Casazza *et al.*, 2000; Johnson and Barichivich, 2004)] and automated frog call data loggers (Barichivich, 2003) to detect calling anurans. At terrestrial sites, we deployed funnel traps and conducted timed searches for amphibians. Funnel traps were double-ended and constructed from aluminum window screen (0.90 m long and 0.33 m diameter) with 5 cm openings (Enge, 1997). During all surveys we recorded any opportunistically encountered amphibians. All amphibians were identified to the lowest possible taxonomic level and were categorized by life stage (eggs, larva, subadult and adult) (Wright, 1932; Conant and Collins, 1991).

Initially, the 1-and 3-d survey sites were selected by traveling along boat trails or roads and stopping to sample at fixed time intervals (*e.g.*, 20 min of paddling) or fixed distances. However, beginning in September 2001, we used a Geographic Information System to generate a series of grid cells for different habitats along access ways such as roads and boat trails. We then selected random sampling points from within these cells, which could be used for either 1-or 3-d surveys, depending on accessibility. In the interest of efficiency, all sampling points were within 0.5 km of boat trails or roads but were a minimum of 50 m from the trail/road edge.

We sampled 16 permanent "intensive" monitoring sites within the Refuge seasonally (spring = March–April; summer = June–July; fall = September–October; winter = December–January) for 1 y (Fig. 1). Four of the sites were located in forested wetland habitat, four in wet prairies, two at lakes, two at ponds, two at shrub wetlands and two in pine flatwoods. The sampling effort included three visits per site for 5 d each season. Both active (litter search and dip-netting) and passive sampling techniques (PVC refugia, funnel traps, crayfish traps, minnow traps, cover boards and automated frog call data loggers) for detecting amphibians were used. Polyvinylchloride (PVC) pipes, which serve as artificial refugia for treefrogs (Boughton, 1997), were placed at all sites 1 mo prior to initiating sampling. At forested sites (pine flatwoods, forested wetlands, shrub wetlands, ponds and lakes), 15 pipes (5 cm diameter × 0.6 m long, capped at the bottom) were mounted on trees at approximately 2 m above ground. Fifteen additional pipes (5 cm diameter × 0.9 m long) were placed in the ground with approximately 0.6 m of pipe above ground. At non-forested sites (wet prairies), all 30 pipes were placed in the ground. Amphibians captured in the pipes were identified to species, measured, marked and released at the point of capture. Treefrogs were individually marked by clipping a unique series of toes (Ferner, 1979). Cover boards (Fellers and Drost, 1994) were made from 0.6 m by 0.6 m (0.6 cm thick) hardboard and were placed at sites a month before the first sampling event. Details of the sampling effort within each habitat type are presented in Table 1.

At intensive monitoring sites we used the suite of sampling techniques described above to generate species lists. Life stage also was recorded for all individuals encountered (eggs, larva, subadult and adult) (Wright, 1932; Conant and Collins, 1991). During the sampling efforts we also collected data on selected environmental variables (covariates), which we thought would influence amphibian distribution. The covariates collected at each site included: habitat type, weather, air and water temperature and presence or absence of standing water. By conducting multiple visits to each intensive site within a season we were able to estimate the detection probabilities for a given species within a sampling period. We used PRESENCE software (MacKenzie *et al.*, 2002, 2003, 2004) to estimate detection probabilities and site occupancy for selected species over time. In this paper, we present the detection probabilities and estimates of site occupancy for four species for which we had

TABLE 1.—Sampling effort at 16 intensive amphibian monitoring sites at the Okefenokee National Wildlife Refuge. Numbers represent quantities of traps per site, with the exception of litter searches and dip netting, which were time-constrained sampling methods (*see* footnote). Frog loggers were deployed (one per site) for four consecutive nights at all sites except in the pine flatwoods, which were terrestrial. Sites were visited three times over a five-day period each season/quarter and the methods outlined below were used at each visit. See text for details of individual sampling methods

	Habitat type					
Sampling method	Forested wetland	Lake	Pine flatwoods	Pond	Prairie	Shrub wetland
PVC Pipes	30	30	30	30	30	30
Cover boards	30	0	30	15	0	30
Funnel traps	10	0	10	10	0	10
Crayfish traps	5	5	0	0	5	0
Minnow traps	5	5	0	5	5	0
Litter search[1]	1 ph[2]	0	1 ph	1 ph	0	0
Dip-netting[1]	1 ph	0	0	1 ph	1 ph	0
Frog logger	4 nights	4 nights	0	4 nights	4 nights	4 nights

[1] Litter searches were conducted when there was no standing water present, whereas, dip-net sampling was employed when water was present. Both dip-net and litter searches were concentrated within a 50 m^2 area at each site

[2] Person-hour

reasonable sample sizes, the Pinewoods Treefrog (*Hyla femoralis*), Pig Frog (*Rana grylio*), Southern Leopard Frog (*R. sphenocephala*) and Carpenter Frog (*R. virgatipes*). Data from all capture methods and for all life stages were combined for these analyses.

Major collections of amphibians from the Okefenokee region are housed at Cornell University (CUMV), Florida Museum of Natural History (FMNH; Florida State Museum), National Museum of Natural History (NMNH), Georgia Museum of Natural History (GMNH) and University of Michigan Museum of Zoology (UMMZ). In addition to published surveys (Wright, 1932 and Laerm *et al.*, 1980), we searched museum databases from these collections to determine the historic distribution of amphibians at the Refuge.

RESULTS

Rare amphibian surveys were conducted at 32 sites on the Refuge (Fig. 1). One Gopher Frog was captured by funnel trap at a Gopher Tortoise burrow on the east side of the Refuge in July 2001. However, we did not detect breeding activity in this species on the Refuge during our study. We were not able to confirm the presence of either the Flatwoods Salamander or Striped Newt at ephemeral ponds on the Refuge.

We documented the presence of 19 of the 37 amphibian species previously known from the region (Table 2). The locality data for museum specimens revealed that 28 of the 37 species reported by Laerm *et al.* (1980) were collected from within Okefenokee Swamp; of these, 18 were anurans and 10 were caudates. Of the amphibians recorded in our study, the highest species richness occurred at wet prairies (15 species) and forested wetland (14 species) sites (Table 3). Pinewoods Treefrogs and Southern Cricket Frogs were found in nearly every habitat type on the Refuge. Pig Frogs were common in all aquatic habitats.

Not all sampling techniques employed in the study were effective at detecting amphibians. As many species were encountered incidentally as were detected with the next most successful technique, dip-netting (Fig. 2). Incidental observations, dip-netting, crayfish traps

TABLE 2.—Amphibians historically known from the Okefenokee Swamp region of south Georgia and northeast Florida (Wright, 1932; Laerm *et al.*, 1980). Nineteen species were confirmed with surveys on the Okefenokee National Wildlife Refuge from August 2000 though June 2002

Species	Historic surveys (within swamp)	This survey (within refuge)
Anurans		
Acris gryllus, Southern Cricket Frog	x	x
Bufo quercicus, Oak Toad	x	x
Bufo terrestris, Southern Toad	x	x
Gastrophryne carolinensis, Eastern Narrow-mouthed Toad	x	x
Hyla chrysoscelis, Cope's Gray Treefrog	x	
Hyla cinerea, Green Treefrog	x	x
Hyla femoralis, Pinewoods Treefrog	x	x
Hyla gratiosa, Barking Treefrog	x	
Hyla squirella, Squirrel Treefrog	x	x
Pseudacris crucifer, Spring Peeper	x	x
Pseudacris nigrita, Southern Chorus Frog	x	
Pseudacris ocularis, Little Grass Frog	x	x
Pseudacris ornata, Ornate Chorus Frog	x	
Rana capito, Gopher Frog	x	x
Rana catesbeiana, Bullfrog	x	
Rana clamitans, Bronze Frog	x	x
Rana grylio, Pig Frog	x	x
Rana heckscheri, River Frog	x	x
Rana sphenocephala, Southern Leopard Frog	x	x
Rana virgatipes, Carpenter Frog	x	x
Scaphiopus holbrooki, Eastern Spadefoot	x	
Caudates		
Ambystoma cingulatum, Flatwoods Salamander	x	
Ambystoma opacum, Marbled Salamander	x	
Ambystoma talpoideum, Mole Salamander	x	
Ambystoma tigrinum, Tiger Salamander	x	
Amphiuma means, Two-toed Amphiuma	x	x
Desmognathus auriculatus, Southern Dusky Salamander	x	
Eurycea cirrigera, Southern Two-lined Salamander	x	
Eurycea quadridigitata, Dwarf Salamander	x	x
Notophthalmus perstriatus, Striped Newt	x	
Notophthalmus viridescens, Eastern Newt	x	
Plethodon grobmani, Southeastern Slimy Salamander	x	
Pseudobranchus striatus, Northern Dwarf Siren	x	x
Pseudotriton montanus, Mud Salamander	x	
Siren intermedia, Lesser Siren	x	
Siren lacertina, Greater Siren	x	x
Stereochilus marginatus, Many-lined Salamander	x	

and funnel traps yielded captures of species not detected by any other means. Eleven of the 15 anurans were detected using automated frog loggers, and this was the only technique by which we detected Carpenter Frogs at prairie sites. PVC pipe sampling yielded 440 captures of 261 individual treefrogs (68.5% recapture rate). Pinewoods Treefrogs were the most frequent occupants of the pipes (88.9% of all captures), followed by Green Treefrogs

TABLE 3.—Distribution of amphibians among different habitat types at Okefenokee National Wildlife Refuge from August 2000 through June 2002. Habitat types included manmade canals (C), ditches (D), forested wetlands (FW), lakes (L), ponds (P), pine flatwoods (PFW), wet prairies (PR) and shrub wetlands (SHW)

	Habitat							
Species	C	D	FW	L	P	PFW	PR	SHW
Acris gryllus			x	x	x	x	x	x
Amphiuma means	x		x	x			x	
Bufo quercicus		x				x		
Bufo terrestris		x	x	x		x	x	
Eurycea quadridigitata			x		x		x	
Gastrophryne carolinensis		x	x	x		x		
Hyla cinerea			x	x	x		x	x
Hyla femoralis		x	x	x	x	x	x	x
Hyla squirella		x			x	x	x	
Pseudacris crucifer	x							
Pseudacris ocularis		x	x		x		x	x
Pseudobranchus striatus			x				x	
Rana capito						x		
Rana clamitans		x	x	x	x		x	
Rana grylio			x	x	x		x	
Rana heckscheri	x			x	x		x	
Rana sphenocephala	x		x	x	x		x	
Rana virgatipes			x	x			x	
Siren lacertina			x	x			x	

(*Hyla cinerea*; 10.3%), Squirrel Treefrogs (*H. squirella*; 0.4%) and unidentified hylids (0.4%). The highest capture rates occurred during the spring and fall sampling (10% and 13%, respectively); the capture rate during the summer sampling period was 6%. Litter searches, minnow traps and cover boards were not particularly effective at detecting amphibians in this ecosystem.

The various sampling techniques used in this study yielded different results for the various life stages of amphibians. Incidental sightings and litter searches, which were the most productive in terms of numbers of individuals observed, yielded predominantly adult anurans (Table 4). Crayfish traps were the most effective method for capturing adult caudates (primarily the aquatic salamander *Amphiuma means*). Most of the anurans caught in crayfish and minnow traps were larvae. Dip-net captures were primarily larval anurans and although only a few caudates were captured by this method, most were larvae.

Detection probabilities and site occupancy estimates for the four select anuran species at intensive monitoring sites are presented in Table 5. Pinewoods Treefrogs had high detection probabilities that were fairly consistent across seasons (0.85 to ca. 0.89). The detection probability for Pig Frogs was highest in summer (0.92), slightly less in spring (0.74) and lowest in fall and winter (0.44 and 0.03, respectively). Detection probabilities for Southern Leopard Frogs were highest in spring and summer (0.78 and 0.73, respectively). The Carpenter Frog was only detected in spring and summer and the detection probability was highest in spring (0.64).

Site occupancy estimates for Pinewoods Treefrogs ranged from 0.75 in spring to 0.94 in the summer and winter surveys (Table 5). This species was most often detected in PVC pipes and we suspect the lower site occupancy estimates in spring and fall are a reflection of the

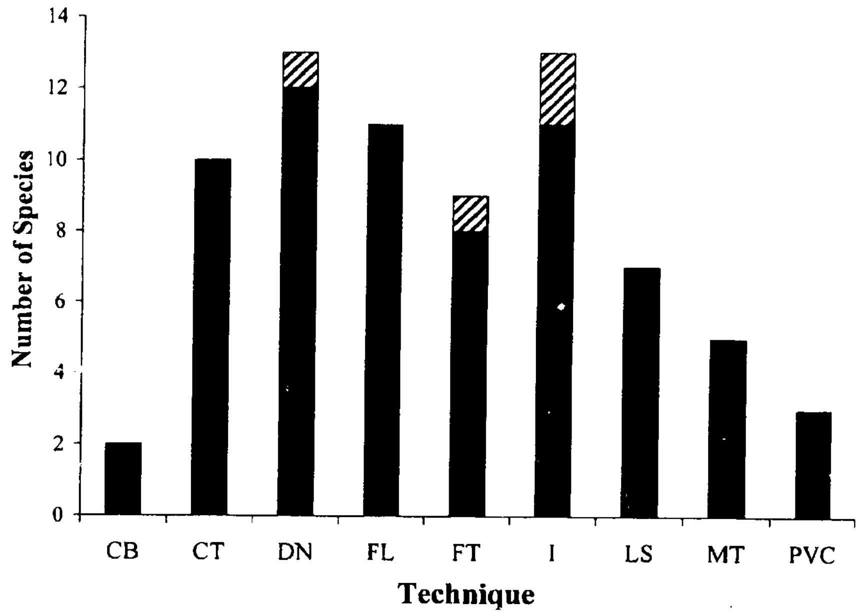

FIG. 2.—Number of amphibian species detected with various sampling techniques at Okefenokee National Wildlife Refuge, Georgia. I = incidental observations, LS = litter search, DN = dip-net, CT = crayfish trap, MT = minnow trap, FT = funnel trap, FL = frog logger, PVC = PVC pipe, CB = cover board. Hatched lines indicate the number of species detected only by this technique. Data were collected from August 2000 through June 2002

frogs seeking a different type of shelter during these seasons. The highest site occupancy estimate for Carpenter Frogs was in spring (0.26, Table 5). The site occupancy estimate for Pig Frogs was ca. 0.50 in spring and summer and was much lower in fall (0.20, Table 5). Site occupancy estimates for Pig frogs in winter and Southern Leopard Frogs in fall were high (0.69 and 0.96, respectively); however, the low detection probabilities at these sampling events (0.03 and 0.16, respectively) indicated that more than three site visits per season would be necessary to reliably estimate site occupancy for this species.

DISCUSSION

Before the development of a monitoring program, thorough species inventories are necessary to establish presence, distributional patterns and general impressions of abundance (Dodd *et al.*, *in press*). Unfortunately, knowledge of the current distribution and status of most amphibian species is lacking on nearly all federal lands in the southeastern U.S. The Okefenokee Swamp presents unique challenges to establishing an amphibian monitoring program and even to conducting preliminary inventories. The swamp is not only extensive, but many habitats are inaccessible due to vegetation structure, variability in water level and restrictions on human activities in federally designated wilderness areas. Traditional approaches such as stratified random sampling prove difficult to employ given the limited number of access points into the swamp, as well as the stochastic nature of the swamp's hydrology. Repeat site visits at standardized intervals within remote regions of Okefenokee NWR may not be possible given logistical access constraints, thus compromising the ability to use statistical programs such as PRESENCE which require

TABLE 4.—Life stages of amphibians captured with different sampling techniques at Okefenokee National Wildlife Refuge from August 2000 through June 2002. *See* text for details on sampling methodologies. NA = not an applicable technique for this taxa or life stage

				Life stage (% of total captures)			
Technique	Taxa	No. species	No. individuals	Eggs	Larvae	Subadult	Adult
Coverboards	Anura	2	11	0.0	0.0	27.3	72.7
	Caudata	0	0	0.0	0.0	0.0	0.0
Crayfish trap	Anura	8	41	0.0	58.5	4.9	36.6
	Caudata	2	30	0.0	0.0	3.3	9.7
Dip-net	Anura	9	595	0.5	62.0	4.9	32.6
	Caudata	3	7	0.0	71.4	0.0	28.6
Frog logger	Anura	11	NA	NA	NA	NA	100.0
	Caudata	NA	NA	NA	NA	NA	NA
Funnel trap	Anura	6	53	0.0	0.0	22.6	77.4
	Caudata	3	7	0.0	14.3	0.0	85.7
Incidental	Anura	13	700	0.1	0.0	23.0	76.9
	Caudata	0	0	0.0	0.0	0.0	0.0
Litter search	Anura	7	310	0.0	0.0	35.5	64.5
	Caudata	0	0	NA	NA	0.0	0.0
Minnow traps	Anura	5	21	0.0	76.2	9.5	14.3
	Caudata	0	0	0.0	0.0	0.0	0.0
PVC pipe	Anura	3	261	0.0	0.0	20.0	80.0
	Caudata	NA	NA	NA	NA	NA	NA

multiple site visits during the period of amphibian activity which in the Okefenokee is year-round. However, automated monitoring systems such as frog loggers and passive sampling methods such as PVC pipes could be used to minimize the need for return trips.

We observed 19 of the 37 amphibian species historically known from the region during nearly two years of field surveys at Okefenokee NWR. This difference may be the result of our efforts being restricted to surveys on the Refuge, whereas earlier surveys (Wright, 1932; Laerm *et al.*, 1980) included a broader region (Okefenokee Swamp, Folkston and Fargo, Georgia and St. Mary's, Florida). In addition, our data were collected over a 2-y period, while the historic data were collected over more than 70 y (1921–1993), which suggests that a total species list collected over a long period of time is inaccurate, given natural processes of extinction and recolonization or that our study design was inadequate to detect all species present and perhaps rare species in particular. However, several of the species previously reported from the Swamp and not detected in our study were those associated with longleaf pine uplands and isolated wetlands, including the Striped Newt, Barking Treefrog (*Hyla gratiosa*) and Eastern Spadefoot (*Scaphiopus holbrooki*). The Refuge contains very little upland habitat and nearly all of the longleaf pine ecosystem that historically occurred adjacent to the Refuge has been converted to slash pine plantation (*see* Dodd and LaClaire, 1995). Many of the amphibian species associated with this habitat may no longer occur in the region.

It is noteworthy that we observed only four of 10 species of salamanders that had previously been reported from the Swamp; of the four species observed, only one, the Dwarf Salamander *Eurycea quadridigitata* is terrestrial. It is likely that our effort was insufficient to detect rare species like the Flatwoods Salamander or Striped Newt. Drift fence sampling (Campbell and Christman, 1982), over multiple years, in both terrestrial and wetland breeding habitat, would have increased the chances of detecting these species. However, it would have greatly increased the sampling effort. Regarding other species of salamanders,

TABLE 5.—Overall estimate of proportion of sites occupied by four species of amphibians at Okefenokee National Wildlife Refuge from 2001–2002. Seasons were defined as: spring = March–April; summer = June–July; fall = September–October; winter = December–January. Ψ is an estimate of the proportion of sites occupied; SE is the bootstrap estimate of the standard error for proportion of sites occupied; and P is the detection probability. The detection probabilities presented are for all sampling methods combined and for all age/life stages. * = species not detected

Species	Season	Ψ	SE	P
H. femoralis	Spring	0.7500	0.1083	0.8889
	Summer	0.9375	0.0605	0.8889
	Fall	0.8000	0.1033	0.8889
	Winter	0.9375	0.0646	0.8552
R. grylio	Spring	0.5069	0.1270	0.7397
	Summer	0.5000	0.1250	0.9167
	Fall	0.2000	0.1033	0.4444
	Winter	0.6868	10.3151	0.0324
R. sphenocephala	Spring	0.1875	0.0976	0.7778
	Summer	0.3125	0.1159	0.7333
	Fall	0.9583	0.7493	0.1623
	Winter*			
R. virgatipes	Spring	0.2607	0.1140	0.6393
	Summer	0.1636	0.1263	0.3820
	Fall*			
	Winter*			

however, we invested ca. 109 person-h searching beneath cover objects in forested wetlands and should have encountered conspicuous species such as Southeastern Slimy Salamander (*Plethodon grobmani*) and the Southern Dusky Salamander (*Desmognathus auriculatus*) if they were present in even moderate abundance. The Southeastern Slimy Salamander was collected from Billy's and Minnie's Island in the 1970s and 1980s (GMNH 15206–15208). We surveyed these areas extensively and failed to detect this species. The Southern Dusky Salamander was collected from a number of localities in the Swamp including Kings Landing and Camp Cornelia (Fig. 1) in the late 1960s (GMNH 18034 and GMNH 17976–17983). This species has declined from unknown causes throughout its former range (Dodd, 1998). A Mud Salamander (*Pseudotriton montanus*) was collected from Kings Canal in 1967 (GMNH 13133) and a specimen of the Southern Red Salamander (*P. ruber*) was reportedly collected from Billy's Island (Fig. 1) in 1912 (CUMV 2049), although Laerm *et al.* (1980) did not include this species in their list of vertebrates of the Swamp. It also seems surprising that we did not encounter Eastern Newts (*Notophthalmus viridescens*) in dip-nets or minnow traps at wetlands, as this species can often be collected with such methods. The absence of these species from our sample is not easily explained. However, rainfall was below average over the study period from August 2000 to June 2002 (191.80 cm recorded, as compared to 244.73 cm average; Southeast Regional Climate Center), which may have been a factor limiting our ability to detect these species.

Flatwoods salamanders were collected from Chesser Island in Charlton County in 1922 (CUMV 2933 and 2936), and there are two records from the Swamp in Ware County from 1972 (GMNH 8747–8748). Surveys in the mid-1990s failed to detect this species (Jensen, 1995). During our surveys the timing of fall and winter rains was not ideal for Flatwoods Salamander breeding events (Palis, 1997). However, several of the ponds on Chesser Island, The Pocket and Soldier's Camp Island (Fig. 1) appear potentially suitable as breeding sites for this species, although most of the upland pine forests have been heavily disturbed by forestry practices and/or fire suppression. The presence of Striped Newts on the Refuge was last verified in 1995 at a pond on Trail Ridge near the Refuge headquarters (Dodd and LaClaire, 1995); however, the status of that population in recent years in unknown. The pond is now transected by two service roads. Although the uplands within the Refuge are managed with prescribed burns, there is very little of the xeric habitat required by this species (Johnson, 2003) within the Refuge, and the adjacent private lands have been converted to slash pine plantations. We recommend more intensive targeted searches for these two species over multiple years in order to determine whether they are still present on the Refuge.

Sampling techniques that were most successful (in terms of numbers of species detected) in our study included dip-netting, crayfish traps and funnel traps. Automated frog loggers were particularly useful for detecting anurans and we recommend this technique for use in other areas with difficult access like Okefenokee Swamp. Cover boards, minnow traps and litter searches did not yield observations of species not detected by other techniques and, hence, were not effective means of sampling amphibians in this wetland system. Interestingly, incidental observations of amphibians yielded nearly as many species as dip-netting and trapping.

Our estimates of detection probabilities and site occupancy for the Pinewoods Treefrog, Pig Frog, Southern Leopard Frog and Carpenter Frog at the 16 intensive monitoring sites indicate that, in general, the best time to sample for these species is spring or summer. Our results also indicate that in order to detect trends in amphibian populations, particularly in less common species such as the Carpenter Frog, every effort should be made to sample as many sites as frequently as possible. With more intensive, longer-term sampling at a greater number of sites, PRESENCE Software could be used to model factors that would be expected to affect occupancy estimates such as habitat type, co-occurrence with predators and drought. Over the long term, these models might have utility in monitoring changes in amphibian species richness. In any case, the incorporation of estimates of detection probabilities into the reporting of survey results allows a clearer understanding of the effectiveness of a sampling program and the potential rarity of species. This assumes, of course, that appropriate sampling techniques are used at the right times and habitats in order to detect presence.

Given the low numbers of observations of salamanders in this study and despite logistical constraints, further inventory and monitoring at the Refuge is needed. Select amphibian species and associated habitats may be targeted for a monitoring program, rather than attempting to monitor all amphibians in all habitats throughout the swamp. Further, although the Refuge encompasses more than three quarters of the Swamp basin, silvicultural activities and changes in the natural fire regime within the Refuge and on adjacent lands could be influencing amphibian populations. Thus, the long-term impacts of land use practices on the swamp's amphibians also need to be examined.

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LITERATURE CITED

ALFORD, R. A. AND S. J. RICHARDS. 1999. Global amphibian declines: a problem in applied ecology. *Ann. Rev. Ecol. Syst.*, **30**:133–165.

BARICHIVICH, W. J. 2003. Appendix IV: guidelines for building and operating remote field recorders, p. 87–96. *In:* Monitoring Amphibians in Great Smoky Mountains National Park. U.S. Geological Survey Circular No. 1258.

CAMPBELL, H. W. AND S. P. CHRISTMAN. 1982. Field techniques for herpetofaunal community analysis, p. 193–200. *In:* N. J. Scott, Jr. (ed.). Herpetological communities. U.S. Fish and Wildlife Service Research Report No. 13.

CASAZZA, M. L., G. D. WYLIE AND C. J. GREGORY. 2000. A funnel trap modification for surface collection of aquatic amphibians and reptiles. *Herpetol. Rev.*, **31**:91–92.

DASZAK, P., L. BERGER, A. A. CUNNINGHAM, A. D. HYATT, E. D. GREEN AND R. SPEARE. 1999. Emerging infectious diseases and amphibian population declines. *Emerg. Infect. Dis.*, **5**:735–748.

DODD, C. K., JR. 1995. The rare newt of Trail Ridge. *Rep. & Amp. Mag.*, **(July/Aug)**:36–37, 39–45.

———. 1998. *Desmognathus auriculatus* at Devil's Millhopper State Geological Site, Alachua County, Florida. *Flor. Sci.*, **61**:38–45.

——— AND L. V. LACLAIRE. 1995. Biogeography and status of the striped newt (*Notophthalmus perstriatus*) in Georgia, USA. *Herpetol. Nat. His.*, **3**:37–46.

———, J. LOMAN, D. COGĂLNICEANU AND M. PUKY. In press. Monitoring amphibian populations. *In:* H. H. Heatwole and J. L. Wilkenson (eds.). Conservation and decline of amphibians. Amphibian Biology, Vol. 9A. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.

ENGE, K. M. 1997. A standardized protocol for drift fence surveys. Florida Game and Freshwater Fish Commission, Technical Report No. 14. Tallahassee, Florida. p. 68.

GIBBONS, J. W. 2002. Afterword, p. 479–486. *In:* A. H. Wright (ed.). Life-histories of the frogs of Okefinokee Swamp, Georgia. Comstock Publishing Associates, Ithaca, New York. [2002 reissue of the 1932 original edition]

HALL, R. J. AND C. A. LANGTIMM. 2001. The U.S. National Amphibian Research and Monitoring Initiative and the role of protected areas. *The George Wright Forum*, **18**:14–25.

HARPER, F. 1932. A voice from the pines. *Nat. His.*, **33**:280–288.

HOULAHAN, J. E., C. S. FINDLAY, B. R. SCHMIDT, A. H. MEYER AND S. L. KUZMIN. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**:752–755.

JENSEN, J. B. 1995. Survey of potential habitat on Okefenokee National Wildlife Refuge for *Ambystoma cingulatum*, *Rana capito*, and *Notophthalmus perstriatus*. Unpublished report to the U.S. Fish and Wildlife Service, Order No. 4310-5-0092.

JOHNSON, S. A. 2003. Orientation and migration distances of a pond-breeding salamander (*Notophthalmus perstriatus*, Salamandridae). *Alytes*, **21**:3–22.

——— AND W. J. BARICHIVICH. 2004. A simple technique for trapping *Siren lacertina*, *Amphiuma means*, and other aquatic vertebrates. *J. Fresh. Ecol.*, **19**:263–269.

LAERM, J., B. J. FREEMAN, L. J. VITT, J. M. MEYERS AND L. LOGAN. 1980. Vertebrates of the Okefenokee Swamp. *Brimleyana*, **4**:47–73.

LOFTIN, C. S. 1998. Assessing patterns and processes of landscape change in Okefenokee Swamp, Georgia. Ph.D. Dissertation, University of Florida, Gainesville, Florida. 835 p.

MACKENZIE, D. I., J. D. NICHOLS, G. B. LACHMAN, S. DROEGE, J. A. ROYLE AND C. A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**: 2248–2255.

———, J. D. NICHOLS, J. E. HINES, M. G. KNUTSON AND A. B. FRANKLIN. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**:2200–2207.

———, L. L. BAILEY AND J. D. NICHOLS. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *J. Ani. Ecol.*, **73**:546–555.

McQUEEN, A. S. AND H. MIZELL. 1926. History of the Okefenokee Swamp. Privately Published, Folkston, Georgia. 218 p.

PALIS, J. G. 1997. Distribution, habitat, and status of the flatwoods salamander (*Ambystoma cingulatum*) in Florida, USA. *Herpetol. Nat. His.*, **5**:53–65.

SCOTT, N. J., JR. 1994. Complete species inventories, p. 78–84. *In:* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek and M. S. Foster (eds.). Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington.

SHAFFER, H. B., R. A. ALFORD, B. D. WOODWARD, S. J. RICHARDS, R. G. ALTIG AND C. GASCON. 1994. Quantitative sampling of amphibian larvae, p. 130–141. *In:* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek and M. S. Foster (eds.). Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington.

TROWELL, C. AND R. T. IZLAR. 1984. Jackson's folly: the Suwannee Canal Company in the Okefenokee swamp. *J. For. His.*, **28**:187–195.

WRIGHT, A. H. 1926. The vertebrate life of Okefinokee Swamp in relation to the Atlantic Coastal Plain. *Ecology*, **7**:77–95.

———. 1932. Life-histories of the frogs of Okefinokee Swamp, Georgia. The Cayuga Press, Ithaca, New York. 497 p.

——— AND A. A. WRIGHT. 1932. The habitats and composition of the vegetation of Okefinokee Swamp, Georgia. *Ecol. Monogr.*, **2**:109–232.

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