Herpetofaunal Diversity of the Four Holes Swamp, South Carolina

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By Russell J. Hall

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Preface

This account of the amphibians and reptiles of a portion of the Four Holes Swamp, South Carolina, is based on information collected in 1976, almost 20 years ago. The unusually long time span between the survey and the publication poses the questions: What is the current relevance of the results of a study conducted so long ago; why is it important to publish these results now?

Investigations in response to recent concerns about declining amphibian populations and loss of biological diversity have included tracking changes in populations over time, and the development of census methods that provide repeatable estimates of population status were remarkably improved during the past two decades. However, results reported here, like most collected more than a decade ago, fall short of current standards for surveys. It is unlikely that any older survey provides the basis for detection of a 20 percent or even a 50 percent change in any population.

Until the 1980s, censuses were almost entirely based on laborious, time-consuming, and costly total-count or mark-and-recapture studies. These studies were so difficult that investigators were able to determine population changes over time only in few instances. Lucille Stickel's study of changes in box turtle populations over three decades stands out as one of only a few attempts to discover the effects of long-term environmental change on a population. By his exhaustive research on populations of reptiles, Henry Fitch was in some instances able to track the effects of relatively rapid environmental change on populations, but few investigators have been able to devote the necessary concerted effort to conduct such studies. Fitch was among the first to use large-scale trapping in population studies, and his success in trapping many kinds of reptiles and amphibians may have helped to accelerate the eventual use of trapping for other kinds of censuses.

Campbell and Christman reported in 1982 on surveys along the route of the proposed Cross-Florida Barge Canal. Although they used methods closer to those employed in the Four Holes Swamp study than to those in current practice, their study may have been a benchmark because the results were intended for the development of government policy. Their findings probably had little influence on the ultimate outcome of the debate over the canal but almost certainly highlighted the potential use of verifiable census information in political and regulatory forums.

Advances in methodology producing better, statistically more reliable census information led in 1990 to Corn and Bury's preliminary handbook of methods found useful in Pacific Northwest forests. Improved methods and methods applicable to a wider variety of taxa and habitats are expected with the 1994 publication of *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, a compilation of recent advances by most specialists currently working in the field.

Herpetological Diversity of the Four Holes Swamp, South Carolina, like similar surveys elsewhere, predates the development of survey methodology and contributes almost nothing to it. Nevertheless, the results of these studies can provide a basis for future assessments of the effects of environmental change. The discovery that a formerly abundant species became absent or rare in time or that a formerly undetected or rare species became abundant certainly warrants investigation of the possible role of environmental change. A drastic change in the relative abundance of species may be reason to suspect real changes in populations. Moreover, when the directions of change are predictable from knowledge of the biology of species or from changes recorded elsewhere, qualitative or even anecdotal information is useful and valuable.

Comprehensively surveying amphibian and reptile populations will continue to be difficult and, regardless of future advances, no new methodology promises to reveal the past status of populations. For that we must continue to rely on data such as were obtained in the Four Holes Swamp in 1976. Despite their imperfections, they will probably remain the best representations that will ever be available on the past statuses of most ecosystems.

Herpetofaunal Richness of the Four Holes Swamp, South Carolina

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Abstract. A survey of the amphibians and reptiles in a sanctuary in the Four Holes Swamp, South Carolina, in 1976 revealed 62 species. An additional 27 species may have been residents. Species diversity and abundance were greatest in upland areas around the swamp and lowest on the oak flats that are often regarded as the most valuable swamp habitats. A few species were restricted to cypress creeks. Springs on the bluffs that border the swamp favor several species, including some species that are more common in cooler regions. The results of the survey were evaluated based on 50-year trends in population sizes of amphibian and reptilian species at the Patuxent Wildlife Research Center in Maryland and on 40-year trends in population sizes of amphibian and reptilian species on the University of Kansas Fitch Natural History Reservation to predict the possible consequences of different kinds of management. On the Fitch Reservation, where natural landscape patterns are mixed woodlands and prairies, all kinds of active management were discouraged, and succession produced an almost unbroken forest. By the late 1980s, 21 of the 31 herpetofaunal resident species had disappeared or declined significantly. Changes at the Patuxent Wildlife Research Center, where management sought to maintain existing landscape patterns, included nearly equal losses and gains. As many as half of the amphibian and reptilian species of the Four Holes Swamp may decline or be extirpated if all habitats proceed to climax communities, and even management to maintain present habitats may affect as many as 10% of the species. But natural disturbances may help to maintain habitat diversity and species richness. Conservation goals for the Four Holes Swamp should be based on the role of the swamp in the broader landscape.

Key words: Amphibians, reptiles, herpetofauna, diversity, South Carolina.

Few biologists question the need to preserve and protect outstanding examples of biotic communities from destruction or degradation. The conservation of wildlife is almost always an important motivation for preserving natural areas. In fact, the identification of important natural areas and their role in the preservation of biological diversity have become central questions for conservationists (Hunter 1990; Salwasser 1990; Keystone Policy Dialogue 1991; Noss 1991; Pimm and Gittleman 1992).

Problems in the conservation of amphibians and reptiles have received far greater attention since the early 1980s when a single paper (Bury et al. 1980) broadly addressed the conservation of amphibian or reptilian faunas in the United

States. Until recently, few researchers holistically considered the communities of amphibians and reptiles of protected areas, although lists of species—sometimes annotated—are common (Gehlbach 1965; Manville 1968; Higgins et al. 1992). A symposium in 1977 (Scott 1982) synthesized contemporary work on communities of amphibians and reptiles. A keynote paper (Heatwole 1982) advocated studies of herpetofaunal assemblages and cited significant studies, and a bibliography (Scott and Campbell 1982) listed publications of community-level studies through the late 1970s. Another symposium proceedings (Szaro et al. 1988) included 26 papers about the conservation of amphibians and reptiles. A more recent summary (Scott and Seigel 1992) provided a broad range of general issues that relate to the conservation of amphibians and reptiles. Declines of amphibian populations, in particular, are cause for concern (Wyman 1990; Wake 1991; Vial and Saylor 1993). No reports have specifically addressed management of natural areas to conserve herpetofaunal diversity in North America.

The assemblage of living things in such areas as the Four Holes Swamp in South Carolina is sufficiently prominent to merit its protection. However, after lands are secured and protection begins, less thought may be given to future management and its possible consequences for biotic communities. The problem may become acute when a land manager is faced with a variety of alternative interventions or passive protection. Consequences of this problem in the conservation of amphibian and reptilian diversity are the focus of the following discussions.

This report provides a list of species of the amphibians and reptiles in the Four Holes Swamp with notes on the geographical relations, life histories, ecological distributions, and relative abundances that serve as a basis for future studies of the effects of environmental change. It also introduces some published and unpublished information on population trends of amphibians and reptiles in two protected areas for which long-term data are available. These areas were managed differently, and comparisons of outcomes may bear on questions about the appropriate degree of intervention for conservation lands and the optimal scale for the conservation of herpetofaunal diversity.

The Four Holes Swamp

History, Biota, and Habitats

The Francis Beidler Forest, a 1,398-ha National Audubon Society sanctuary in the Four Holes Swamp, Dorchester and Berkeley counties, South Carolina, was owned for most of its recent history by lumber companies. Despite cutting of timber nearby and some logging within the boundaries of the present sanctuary, most forest was never severely cut, and good stands of ancient forest remained. When the National Audubon Society acquired the property in the mid-1970s, it initiated the preservation and protection of unique natural values. Staff were hired to maintain the boundaries and to guard against inimical uses. Removal of timber was halted and trespass by hunters was minimized. A lake was purchased from a fishing club to control a point of ready access to the sanctuary. Potential sedimentation problems from upstream clearance and erosion were monitored.

Information about the swamp and its history, biota, and representative habitats is provided in the guidebook *The Francis Beidler Forest in the Four Holes Swamp* (Brunswig and Winton 1978) and in an earlier general description (Carr 1971). That information is not reproduced here except when necessary to explain references to habitats, descriptions of which follow Brunswig and Winton's (1978) terminology.

This description is of the Francis Beidler Forest in 1976. The 18 years that have elapsed are a minor interval in the life of a complex of ecosystems that may have remained mostly unchanged for hundreds of years. But in 1989, Hurricane Hugo hit the Four Holes Swamp and downed many of the largest and oldest trees and changed for decades or perhaps for centuries the character of the dominant vegetation. Long-term effects of the devastation are not fully known, but this record from 1976 may be useful in following and understanding its regeneration.

Distinctness of habitats and biotic communities results from physical and historical differences. Topography and the availability of water define the undisturbed communities of the swamp. Primary historical influences have been land uses, typically clearing followed by agriculture on the uplands and logging in bottomland areas unsuitable

for agriculture. A list of plants and the general description of the area and its vegetation was provided by Porcher (1981).

One major habitat type is pine uplands, which occur on the high ground that surrounds the swamp. They have good drainage and light sandy soil. Several species of pines, dominated by loblolly pine (*Pinus taeda*) comprise the primary vegetation, but pines tend to be succeeded in the absence of fire by xerophytic and mesophytic hardwoods, including prominently several species of oaks (e.g., *Quercus alba, Q. falcata, Q. nigra,* and *Q. schumardii*). Clearance for agriculture and controlled burning to retard succession and to favor commercially valuable species of pines over hardwoods have been common on the uplands.

A second major habitat type is on the bluffs that outline the swamp and are the transition between the uplands and the stream valley. The bluffs are steep in some places but more gradual and more extensive in other places. Numerous seeps and springs make the bluffs around the Four Holes Swamp particularly important for some kinds of amphibians and reptiles. Porcher (1981) described

Pine (*Pinus* spp.) upland adjacent to the Four Holes Swamp, South Carolina; a rapidly growing pine sapling is in the foreground, 1976.

the vegetation of the bluffs as mixed mesophytic forest. The forest canopy tends to be dominated by hardwoods, of which five species of oaks and beech (*Fagus grandifolia*) are most abundant.

Oak flats are areas of alluvial floodplain created by deposition of sediments. They are occasionally flooded but are above the level of frequent floods. Their dry, loose soils in close proximity to saturated soils make them particularly suitable for the growth of many kinds of plants. Moreover, subtle differences in elevation and access to water result in a great variety of different soil-moisture combinations, each more or less favorable to different species. Consequently, plant diversity and productivity on the oak flats are high. Wetter parts of the oak flats are sometimes referred to as *flatwoods swamp*. Porcher (1981), in describing the plant communities of this habitat, referred to moderate elevations as *hardwood bottoms* and to higher areas as *ridge bottoms*.

Cypress creeks are areas of swamp that are flooded much or nearly all of the time. They are dominated by baldcypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*), tree species adapted to tolerate prolonged periods with inundated roots and lower stems. Porcher (1981) referred to this community as the *swamp forest*.

Lakes are deep portions of stream channel in the swamp that permanently hold water. With large channels and almost imperceptible flow, they resemble lentic systems. Lakes differ from cypress creeks because they are deeper and not completely shaded by the forest canopy.

Some areas of the sanctuary, referred to as *cut-over swamp*, were clear-cut before acquisition. Logging involved diking and building raised roads that

Portion of oak flats with trunks of the hardwood canopy and dwarf palmetto (*Sabal minor*); Four Holes Swamp, South Carolina, 1976.

Cypress Creek when water is receding; trunks of baldcypresses (*Taxodium distichum*) and tupelos (*Nyssa aquatica*) and numerous cypress knees are evident; Four Holes Swamp, South Carolina, 1976.

disrupted and rechanneled waterways in areas subject to flooding. Early regeneration became rank thickets of water-tolerant, seral species such as sweetgum *(Liquidambar styraciflua)*, tuliptree (*Liriodendron tulipifera*), and various shrubs.

The physical and biotic environments comprise a complexity of diverse, intergraded, and intermixed components. Pine uplands often contain ditches and large puddles that provide habitats for aquatic animals. The bluffs are not straight borders that outline the swamp but wind along the edges of the swamp and, in places, extend into it. Oak flats and the cypress creeks are not simply divided into wet and dry areas but have many gradations between extremes.

Survey of Herpetofauna in 1976

The 1976 survey of the herpetofauna of the swamp began after the acquisition but before the opening to the public of the Francis Beidler Forest by the National Audubon Society. The survey was conducted for one week in late March and resumed in mid-May. From 19 May onward, S. Winton was employed by the Francis Beidler Forest as a biologist and was able to continue the survey part-time until 17 October. N. Brunswig, Superintendent of the sanctuary, and his assistant, D. Clayton, facilitated the survey and provided information they gathered during performing their other duties. In all, the survey totaled approximately 40 person-weeks or about three-fourths person-year. No significant work was done during November through February, when little activity of ectothermic animals is expected but when absences may account for the failure to record some species.

Sampling was greatest in two areas near the center of the sanctuary. The Neely Smith tract on the north side of the swamp comprises most major habitat types of the system. Certain species were

Singletary Lake in midsummer; Four Holes Swamp, South Carolina, 1976.

particularly abundant near springs and small streams that flowed from its bluffs to the swamp floodplain. The Goodson Hill is nearly opposite the Neely Smith tract on the south side of the swamp. It encompasses the present sanctuary headquarters and visitor center and serves as the starting point for the boardwalk. Other productive areas included the area around Mellard's Lake (also called Mallard Lake), which is the largest and most accessible of the sanctuary's lakes. Frequent sampling in an area of cutover swamp in the southeastern portion of the property also provided records of some species not found elsewhere.

The survey was not vigorously quantitative because precise data on abundance were not needed to accomplish the general objectives of a species inventory, learning of habitat associations, and acquiring information on the biology of abundant species. Some of these objectives required quantitative determinations, but such information could be obtained for only the most abundant and accessible species.

Captured animals were routinely marked by standard methods, including toe-clipping of amphibians and lizards. Lizards and adult-sized frogs were given unique individual marks, but recently transformed amphibians were marked with codes that represented the date of the first capture. Snakes were marked by removal of unique combinations of subcaudal scales (Blanchard and Finster 1933), and turtles were marked by notching marginal scutes with the method of Cagle (1939). Alligators were not handled because of their endangered status. One or a few specimens of most species were preserved, and the collections are now in the Charleston Museum.

Useful methods for surveying communities of amphibians and reptiles were summarized by

The shoreline of Mellard's Lake with overhanging tupelos (*Nyssa aquatica*) and baldcypresses (*Taxodium distichum*); Four Holes Swamp, South Carolina, 1976.

Campbell and Christman (1982b), and many of the methods they described were used in the survey in the Four Holes Swamp. Recently, Corn and Bury (1990) and Bury and Corn (1991) among others described sampling methodologies to obtain quantitative indices of the abundance of amphibians and reptiles, but neither the methods nor the levels of effort in the Four Holes Swamp were adequate for quantitative comparisons. Collection by hand and animals moving on the surface and turning of logs and other objects yielded the greatest number of records. Some species were collected by scraping debris with a dipnet from the bottom of standing or flowing water. Traplines with wire funnel traps and drift fences following the design of Fitch (1951, 1960) were used in two areas to capture some species not recorded otherwise and to obtain information about the timing and extent of moves by the animals. Commercial and custom-built turtle traps and a small funnel trap for capturing moving lizards on tree trunks were used without success. An aluminum pole with a rubber-padded, remotely operated tong was used to immobilize basking water snakes until they could be grasped by hand. Calling frogs and toads were captured at night with the aid of a headlamp.

Conventions in Expressing Results

Scientific names follow Banks et al. (1987) but were updated to reflect more recent changes in nomenclature, and appropriate references are given in species accounts. Snout-to-vent length (SVL) is the standard measure of the size of most amphibians and reptiles. It discounts the length of the tail, which may vary by sex or may be incomplete because of breakage. Sizes of turtles were

recorded in carapace length (CL) and those of tadpoles in total length (TL). Species recorded from the nearby Four Holes Swamp were recorded within a few kilometers of the sanctuary and are regarded as occurring in the swamp, even though their presence within the boundaries of the property of the National Audubon Society was not recorded. The identity of species not verified by actual specimens remains open until supported by a definitive taxonomic opinion. For example, the species first identified as the slender glass lizard, *Ophisaurus attenuatus*, may actually be the eastern glass lizard, *O. ventralis*, or even *O. compressus* or *O. mimicus*. Even when specimens are available, the identity may be in doubt; the apparent hybrid river cooter, *Pseudemys concinna*, specimen may ultimately fail to verify the occurrence of that species in the ecosystem. Finally, records of species are regarded as a crude indication of abundance, even though search methods favored finding some species and nearly obviated finding others. Most abundant species were recorded frequently and most only-rarely-recorded species are not abundant. Exceptions are noted in the species accounts.

Throughout this discussion the term *diversity* is used as if it were synonymous with species richness (Scott et al. 1987). Technically, and particularly among invertebrate zoologists, diversity takes into account not only the number of present species but also their relative abundance (Wilson and Bossert 1971). Species richness is only one indicator of biological diversity, but it is used here as if the terms were interchangeable.

Species Accounts

A list of the recorded species and the nature of the records is provided in Table 1. Basic biological information on life histories, relations, and distributions of species is not provided in the following accounts because it is readily available in general works such as that of Duellman and Trueb (1986).

Salamanders

Eight species of tailed amphibians representing four families were recorded (Table 1). Their life histories and habits are diverse. Ambystomatid and eastern salamandrid salamanders generally breed in ponds, whereas the sirenians and most plethodontids breed in flowing water. One plethodontid, *Plethodon glutinosus* complex, lays its eggs on land in moist forests.

Family Sirenidae

Lesser Siren (*Siren intermedia* Barnes, 1826). A single juvenile (40 mm SVL) was captured with a dipnet in Mellard's Lake.

Family Salamandridae

Eastern Newt (*Notopthalmus viridescens* (Rafinesque 1820)). Two larvae (19 and 22 mm SVL) were captured from ditches in the southeastern cutover area of the swamp in late March. They were near the size at transformation reported from the northern part of the range (Bishop 1941). Subadult efts were captured on the Neely Smith tract in March and on the Goodson Hill in September (18 mm SVL). The normally pond-dwelling adults were not recorded.

Family Ambystomatidae

Marbled Salamander (*Ambystoma opacum* (Gravenhorst, 1807)). Ten adults and 2 larvae were recorded on the Neely Smith tract between 25 March and 29 March. All were found in the lower portion of a large ravine where small, spring-fed streams meet the flat alluvial valley of the swamp. Four females were between 53 and 62 mm SVL and 3 males were between 57 and 64 mm SVL. The larvae were 29 and 31 mm SVL. Six more individuals were captured between 20 September and 12 October in funnel traps in an area of the Goodson Hill that is not subject to flooding. The size distribution of 2 males and one female were within the ranges of those caught in March, but 2 males of 45 and 46 mm SVL may have transformed that year. Failure to capture individuals in summer despite frequent efforts suggests that *A. opacum* remained congregated in breeding areas in March, moved upland to underground burrows in summer, and were migrating to breeding areas when captured on the surface in September and October.

Family Plethodontidae

Southern Dusky Salamander (*Desmognathus auriculatus* (Holbrook, 1838)). A single female (63 mm SVL) was collected in leaf litter in a largely flooded area of flatwoods swamp. Extensive

Table 1. Recorded amphibians and reptiles in the Four Holes Swamp, South Carolina, 1976.[a] A total of 62 species were recorded (24 amphibians, 38 reptiles); specimens of 7 species are lacking. Identities of six of these (*Rana clamitans*, *Terrapene carolina*, *Cnemidophorus sexlineatus*, *Farancia erytrogramma*, *Pituophis melanoleucus*, and *Alligator mississippiensis*)were not in doubt. The recorded *Ophisaurus* could be any one of four species.; 1,071 individuals were recorded (696 amphibians, 375 reptiles).

Species (number of records)	Specimen[b]	Photo	Fhs[c]	Nearby[d]
Amphibia:Caudata				
Ambystoma opacum (17)	X	X	X	
Desmognathus auriculatus (1)	X	X	X	
Eurycea cirrigera (8)	X	X	X	
Eurycea longicauda (127)	X	X	X	
Eurycea quadridigitata (51)	X	X	X	
Notopthalmus viridescens (4)	X	X	X	
Plethodon glutinosus complex (74)	X	X	X	
Siren intermedia (1)	X	X	X	
Amphibia:Anura				
Acris gryllus (3)	X		X	
Bufo quercicus (13)	X	X	X	
Bufo terrestris (236)	X	X	X	
Gastrophryne carolinensis (26)	X	X	X	
Hyla cinerea (14)	X	X	X	
Hyla squirella (25)	X	X	X	
Hyla versicolor (8)	X	X	X	
Hyla femoralis (2)	X	X	X	
Pseudacris crucifer (3)	X	X	X	
Pseudacris nigrita (25)	X		X	
Pseudacris ocularis (3)	X	X	X	
Pseudacris triseriata (1)	X	X	X	
Rana catesbeiana (11)	X	X	X	
Rana clamitans (1)	X	X		
Rana utricularia (17)	X	X	X	
Scaphiopus holbrookii (25)	X	X	X	
Reptilia:Testudines				
Chelydra serpentina (4)	X	X	X	
Clemmys guttata (6)	X	X	X	
Deirochelys reticularia (1)		X	X	
Kinosternon subrubrum (6)	X	X	X	
Pseudemys concinna (1)	X	X	X	
Pseudemys floridana (4)	X	X	X	
Sternotherus odoratus (4)	X	X	X	
Terrapene carolina (8)		X	X	
Trachemys scripta (11)	X	X	X	
Reptilia:Squamata:Sauria				
Anolis carolinensis (139)	X	X	X	
Cnemidophorus sexlineatus (2)		X		
Eumeces fasciatus (7)	X	X	X	
Eumeces inexpectatus (2)	X		X	
Eumeces laticeps (15)	X	X	X	
Ophisaurus sp. (1)				X
Sceloporus undulatus (5)	X	X	X	
Scincella lateralis (16)	X	X	X	
Reptilia:Squamata:Serpentes				
Agkistrodon contortrix (7)	X	X	X	

Table 1. *Continued.*

Species (number of records)	Specimen[b]	Photo	Fhs[c]	Nearby[d]
Agkistrodon piscivorus (9)	X	X	X	
Crotalus horridus (3)	X	X	X	
Coluber constrictor (6)	X	X	X	X
Diadophis punctatus (5)	X	X	X	
Elaphe guttata (2)		X		X
Elaphe obsoleta (25)	X	X	X	
Farancia abacura (1)	X		X	
Farancia erytrogramma (2)				X
Heterodon platirhinos (2)	X	X	X	
Heterodon simus (1)	X		X	
Lampropeltis getula (3)	X	X	X	
Nerodia erythrogaster (2)	X	X	X	
Nerodia fasciata (1)	X		X	
Nerodia taxispilota (51)	X	X	X	
Opheodrys aestivus (4)	X	X	X	
Pituophis melanoleucus (1)		X		
Storeria occipitomaculata (3)	X		X	
Thamnophis sauritus (1)	X		X	
Thamnophis sirtalis (1)	X	X	X	
Reptilia: Crocodilia				
Alligator mississippiensis (13)		X	X	

[a] Kinds of records are indicated; X-marks indicate that specimens and photographs were obtained and that the species was recorded in the sanctuary or in a nearby area.

[b] Specimens were deposited with the Francis Beidler Forest, National Audubon Society, Harleyville, South Carolina, and were later transferred to the Charleston Museum.

[c] Four Holes Swamp and adjacent uplands that comprise the Francis Beidler Forest Sanctuary.

[d] Species were recorded on adjoining properties and were therefore likely to occur on portions of the sanctuary.

searches in such areas failed to reveal additional specimens.

Southern Two-lined Salamander (*Eurycea cirrigera* (Green, 1830)). This species was formerly considered part of the wide-ranging species *Eurycea bislineata*, but Jacobs (1987) identified it as a distinct species. Eight *E. cirrigera* were recorded at small spring-fed streams on the Neely Smith tract, where they seemed to be much more closely associated with streams than either *E. longicauda* or *E. quadridigitata*. Two size classes may have been represented (28–33 mm and 38–42 mm SVL).

Long-tailed Salamander (*Eurycea longicauda* (Green, 1818)). This abundant species was especially sought because of the potential for learning more about its life history. Between late March and late September, 151 individuals were recorded. Most (133) were found near spring-fed streams on the Neely Smith tract, but individuals were near flowing water in all parts of the swamp. No larvae were found, but dissection of females revealed enlarged ovarian eggs in October, suggesting oviposition in winter or in early spring. The appearance of a new 30-mm-SVL size class in August suggested transformation in summer. Size-frequency histograms (Fig. 1) indicated the reaching of adult size of transformed individuals in 2 years and variability in the timing of life history events.

Dwarf Salamander (*Eurycea quadridigitata* (Holbrook, 1842)). The dwarf salamander was recorded less frequently than *E. longicauda* and seems to be restricted to the margins of flatwoods swamp. Two larvae (18 mm and 19 mm SVL) and three adults (32–35 mm SVL) were captured in late March in a cutover area in the northeastern part of the Neely Smith tract. A transformed adult was observed on 14 July on a tupelo trunk that was completely surrounded by water in the middle of Hill Creek. Seven adults were captured in August in flatwoods near the Goodson Hill, and

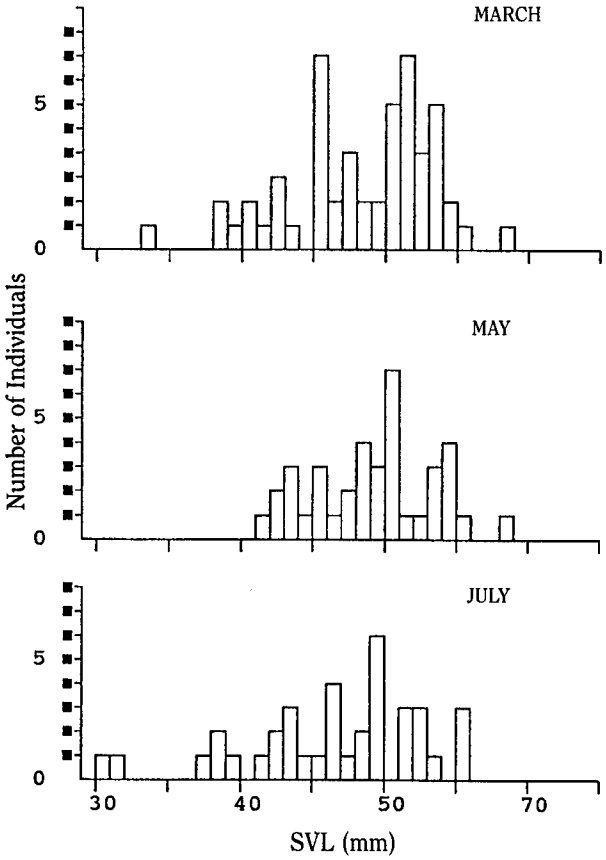

Fig. 1. Frequencies of differently sized long-tailed salamanders, *Eurycea longicauda*, recorded in different periods. Newly transformed young are evident in July and a single juvenile is present in March, but discrete size classes are not otherwise evident (data from present study).

4 more adults were captured in late September in the same area;these adults ranged in size from 28 to 33 mm SVL. The 2 males captured in September had well-developed cirri, suggesting the preparation by these individuals for the breeding season in winter.

Slimy Salamander (*Plethodon glutinosus* (Green, 1818) complex). Recent studies of variation in serum proteins (Highton et al. 1989) led to the proposal that animals formerly recognized as the widespread species *P. glutinosus* are a complex of many distinct species. Highton et al. (1989) classified slimy salamanders from the vicinity of the Four Holes Swamp as *P. variolatus*, the South Carolina coastal slimy salamander, although they could also be *P. chlorobryonis*, the Atlantic coast slimy salamander. The salamanders in Four Holes Swamp were particularly abundant in the moist forest of the Neely Smith tract but were found in several other areas. Altogether, 74 individuals were recorded between late March and mid-October; these animals were active even during the hottest parts of summer. The typical coloration consists of a slate-to-black background with white or silvery spots, but 15 (20%) lacked spotting or flecking. There was evidence of 3 size classes in size-frequency histograms from different periods (Fig. 2), suggesting that these salamanders may need at least 2 years to reach the size of maturity. The appearance of the smallest individuals in late March indicated hatching in winter or very early spring; newly-hatched young from New York averaged less than 10 mm SVL (Bishop 1941).

Frogs and Toads

Sixteen species of frogs and toads representing five families were recorded, nearly as many as Wright (1932) found in the Okefinokee Swamp, Georgia. Anurans in the eastern United States require standing water for breeding, and pools from seasonal floods may provide primary breeding habitat in the swamp floodplain. Nevertheless, the greatest concentrations of breeding anurans were observed in temporary upland pools in or adjacent to open fields.

Family Pelobatidae

Eastern Spadefoot (*Scaphiopus holbrookii* (Harlan, 1835)). Twenty-one adults (50 mm mean SVL, range 42–68) were captured at the Neely Smith tract in late March and were probably part of breeding congregations. Four juveniles were recorded in upland forest on the Goodson Hill between 30 August and 30 September. All were apparent young-of-the-year (range 20-24 mm SVL).

Family Bufonidae

Oak Toad (*Bufo quercicus* Holbrook 1840). A single oak toad was captured on the Neely Smith tract on 28 March, and all other individuals were captured on the Goodson Hill, in the same areas as the much more abundant *B. terrestris*. Evident adults (31, 38 mm SVL) were found in May and

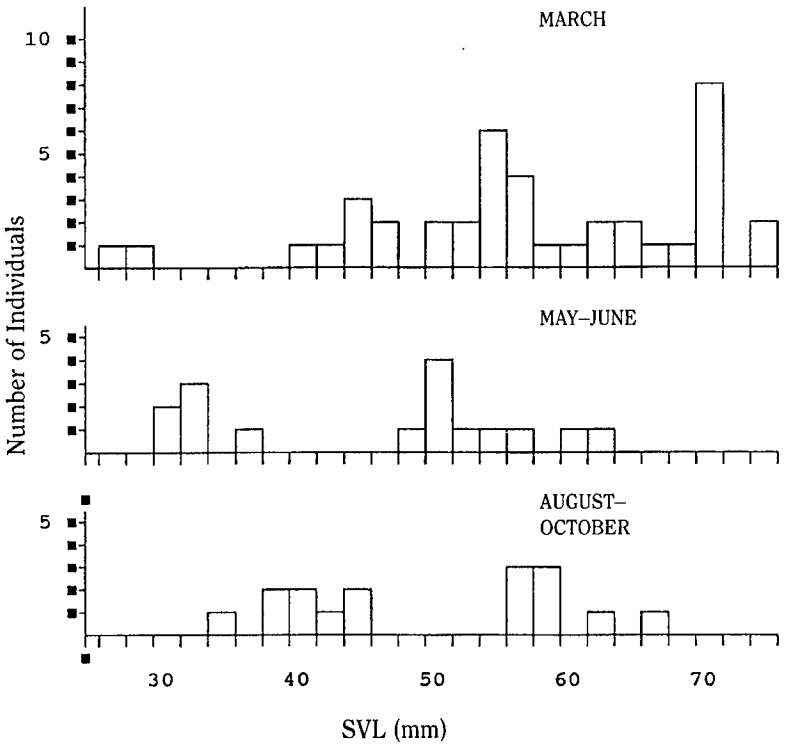

Fig. 2. Sizes of slimy salamanders, *Plethodon glutinosus* complex, recorded in different periods. Evident slow growth of young and the appearance of a possible subadult size class indicate that growth to adulthood may require two years. It is not known why very large adults were recorded only in March (data from present study).

September, and possible juveniles (25.4 mm mean SVL; range 20–26) were recorded from late August through early October. Both those considered young and those believed to be adults are larger than those measured by Wright (1932) in the Okefenokee Swamp, Georgia; he reported that transformation occurs at 16–18 mm SVL and that toads are adult in the 20–27.5 mm SVL range.

Southern Toad (*Bufo terrestris* (Bonnaterre, 1789)). The southern toad was abundant in all habitats of the Four Holes Swamp, and 236 individuals were recorded from late March into October. Ten adults (54 mm mean SVL; range 50–58) were collected on 29 March on the Neely Smith tract. They were in breeding condition; one female laid eggs in a holding bag. A large adult female (66 mm SVL) was captured at the base of a baldcypress tree in the channel of Hill Creek on 29 May. Numerous juveniles and a few adults were recorded from 19 August through early October in the Goodson Hill area, providing good information on the composition of the population in a single period and the growth of juveniles during an interval in late summer (Figs. 3 and 4).

Family Hylidae

Southern Cricket Frog (*Acris gryllus* (Le Conte, 1825)). This species was recorded once. Three individuals were obtained from a locality (Merkel Acres) immediately outside the boundary of the National Audubon Society property in late March.

Gray Treefrog (*Hyla chrysoscelis* Cope, 1880 and *Hyla versicolor* Le Conte, 1825). Gray treefrogs are a species complex that consists of two similar species that are distinguished by their numbers of chromosomes and the characteristics of their breeding calls (Johnson 1959). Although their ranges overlap, they apparently do not extensively interbreed. Some distribution maps indicate that the gray treefrogs in the Four Holes Swamp are probably *H. versicolor*, and the relatively large sizes of the adult specimens suggest *H. versicolor* rather than the smaller *H. chrysoscelis*. Gibbons and Semlitsch (1991) had a few individuals from the Savannah River site karyotyped and learned that they were *H. chrysoscelis* but were uncertain whether *H. versicolor* was also present. A single adult male (46 mm SVL) was captured in late March, and a subadult (28 mm SVL) was captured on 20 May.

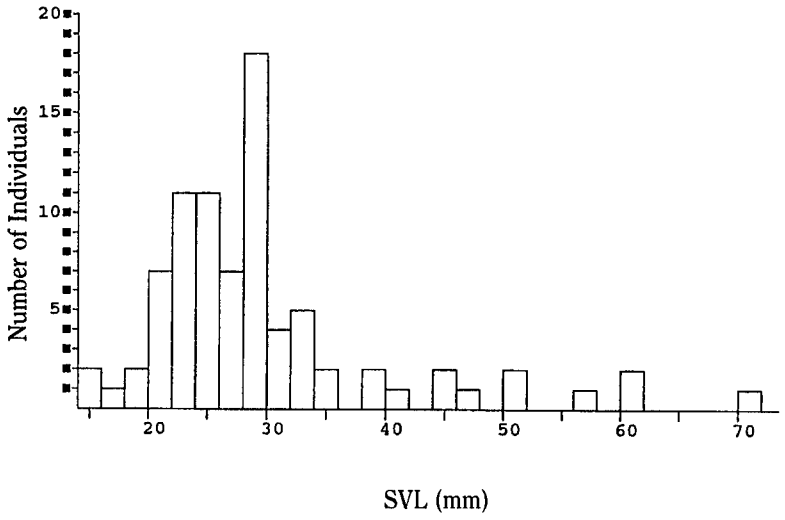

Fig. 3. Composition of the southern toad (*Bufo terrestris*) population during a two-week interval in August 1976. The great bulk (85%) of the population consists of subadult-sized individuals, >36 mm SVL, suggesting heavy annual mortality (data from present study).

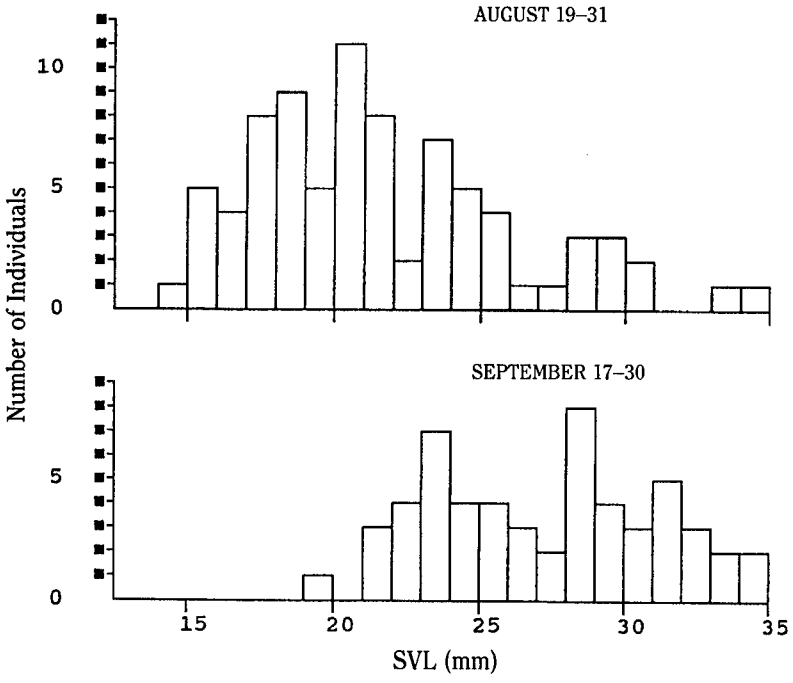

Fig. 4. Frequencies of different sizes of immature southern toads, *Bufo terrestris*, recorded in two intervals. Sizes are variable, but a pattern of overall growth is apparent (data from present study).

The species was heard calling at noon on a warm, cloudy 22 May. On 25 and 26 May, gray treefrogs were heard among choruses of several species of frogs, and several calling males were captured. Transformed young, presumably young-of-the-year (14 mm SVL), were found on 24 and 31 August.

Green Treefrog (*Hyla cinerea* (Schneider, 1799)). This species, like other treefrogs, is best known from breeding congregations. Nevertheless, individuals were occasionally encountered throughout the season, and the range of situations in which they were found suggests that *H. cinerea* is broadly adapted. Choruses were prominent among several amphibian species on the nights of 25 and 26 May, and several singing males were captured. There was evidence of three size classes among the nine other individuals. Large adults (43, 41, and 47 mm SVL) were found in March and October. Two apparent subadults (25 mm SVL) were found in March, and three others (33, 34, and 36 mm SVL) were found in late August and October. A juvenile (16 mm SVL) was captured on 30 September.

Pine Woods Treefrog (*Hyla femoralis* Bosc *in* Daudin, 1800). This species tends to be associated with pine forests elsewhere, but its breeding sites in the Four Holes Swamp were identical with breeding sites of apparent swamp-dwelling species. Pine woods treefrogs were calling with choruses of other species of frogs on the Goodson Hill on 25 and 26 May, and two individuals were captured to verify their identity. Additional adults were found on the Neely Smith tract on 13 July (36 mm SVL) and on the Goodson Hill on 6 October (27 mm SVL).

Squirrel Treefrog (*Hyla squirella* Bosc *in* Daudin, 1800). A single squirrel treefrog was captured on 26 March on the Neely Smith tract, but the species was much more in evidence when breeding individuals began to vocalize in late May. Squirrel treefrogs attracted at night to a mercury vapor light on the corner of a building were seen until late August. Sixteen adults were captured in summer (33.8 mm mean SVL; range 30–37); four juveniles were captured in late August through September (20.2 mm mean SVL; range 17–23).

Spring Peeper (*Pseudacris crucifer* (Wied-Neuwied, 1838)). The spring-peeper is among the earliest breeding frogs and probably begins breeding in the Four Holes Swamp in winter. These frogs were heard calling on the Neely Smith tract each night during 25–30 March, and three adults (28–32 mm SVL) were captured. A few individuals were heard calling with choruses of other frogs during and after heavy rains on 25 and 26 May, but the choruses were not large and calling was not intense. In other parts of the range, *P. crucifer* is seldom seen outside its breeding season, and it may be both abundant and widespread in the Four Holes Swamp.

Southern Chorus Frog (*Pseudacris nigrita* (Le Conte, 1825)). Chorus frogs are early breeders that are probably more abundant in the Four Holes Swamp than indicated by the few times they were recorded. Two adults (SVL 31 and 32 mm) were captured on 28 March. A collection of 23 larvae was taken from a ditch from a cutover area on the northeastern side of the swamp. Their sizes (26.2 mm mean SVL; range 21–30) and the presence of well-developed hind legs in late March suggest that they were close to transformation.

Little Grass Frog (*Pseudacris ocularis* (Bosc *in* Daudin *in* Sonnini and Latreille, 1801)). This species was recorded three times in the Four Holes Swamp, but it is inconspicuous and not easily detected when not calling. One individual was captured on 25 March and another on 5 October on the Neely Smith tract. The species was heard calling amid choruses of several different species of frogs on 25 May in a wet field in the Goodson Hill area. One calling individual was captured to verify its identity.

Chorus Frog (*Pseudacris triseriata* (Wied-Neuwied, 1838)). A single individual (33 mm SVL) was collected on a cross trail on the Goodson Hill on 7 October.

Family Microhylidae

Eastern Narrow-mouthed Frog (*Gastrophryne carolinensis* (Holbrook, 1836)). Individuals were found in upland areas bordering the Four Holes Swamp from late May through late September. Narrow-mouth frogs were heard calling with other species of frogs in the Goodson Hill area on 25 and 26 May. An adult female captured on 24 May was unusually plump and thought to be distended with eggs. Ten adults were captured from May through July (26.9 mm mean SVL, range 25–30). The first

juveniles were found on 18 August, and 16 were measured between 18 August and 30 September (16.1 mm mean SVL, range 13–22).

Family Ranidae

Bullfrog (*Rana catesbeiana* Shaw, 1802). Bullfrogs in the Four Holes Swamp are apparently restricted to disturbed, open areas. Eight tadpoles (57.1 mm mean TL, range 46–69) were collected on 27 March from a cutover area in the northeastern part of the swamp. A single adult male (191 mm SVL) was collected from a shallow pond along the entrance road to the Neely Smith tract on 3 June.

Green Frog (*Rana clamitans* Latreille *in* Sonnini and Latreille, 1801). A single adult was collected at night from a floating log in a deepwater portion of the Four Holes Swamp just above Mims Lake on 2 July. This species is usually conspicuous and seems to be rare in the swamp.

Southern Leopard Frog (*Rana utricularia* Harland, 1825). This generalized frog, part of the widespread *Rana pipiens* complex (Moore 1944, 1949; Pace 1974), was more abundant than initially expected in the specialized habitats of the Four Holes Swamp. Individuals were captured from a variety of areas in the swamp, but 13 of the recorded 17 were in funnel traps set for terrestrial species, suggesting frequent overland moves. Individuals seemed to be of either of two size classes. Seven adults (50.1 mm mean SVL, range 48–78) were present throughout the year and nine apparent juveniles were present in August and September (36.9 mm mean SVL, range 31–42).

Turtles

Turtles are conspicuous and abundant but difficult to capture in the Four Holes Swamp. Nine species representing three families were recorded.

Family Kinosternidae

Mud Turtle (*Kinosternon subrubrum* (Lacepede, 1788)). Six adult and subadult individuals (55–105 mm CL) were observed from late March to late September. All were captured on land.

Musk Turtle (*Sternotherus odoratus* (Latreille *in* Sonnini and Latreille, 1801)). Musk turtles were recorded in various parts of the Four Holes Swamp and included adult-sized individuals (66, 110 mm CL) and one juvenile (30 mm CL). Individuals were often seen climbing on tree trunks or branches that sometimes were far out over water. They were extremely wary and plunged into the water long before they could be approached closely by canoe.

Family Chelydridae

Snapping Turtle (*Chelydra serpentina* (Linnaeus, 1758)). Three snapping turtles were found and caught in June and July on roads in areas around the Four Holes Swamp, and another individual was seen swimming in shallow water near the Goodson Hill. A report that the alligator snapping turtle (*Macroclemys temminicki*) was found in the Four Holes Swamp is probably in error because that species is not known to occur on the Atlantic coastal plain.

Family Emydidae

Spotted Turtle (*Clemmys guttata* (Schneider, 1801)). Spotted turtles were recorded in several parts of the Four Holes Swamp, always in areas of shallow water. An adult male was captured on 22 May in a puddle on a dirt road on the Goodson Hill. On 10 June, an adult female was captured in the same puddle. Turtles were marked, and on 23 July the same female was again captured in the same puddle. Of the five measured individuals, three (100, 103, and 119 mm CL) were considered adults, one was considered a juvenile (32 mm CL) and one a subadult (70 mm CL).

Chicken Turtle (*Deirochelys reticularia* (Latreille *in* Sonnini and Latreille, 1801)). The general appearances of this species and *Pseudemys* and *Trachemys* are similar, but this was not seen with the other species in mature swamps. A single female (114 mm CL) was captured in a shallow cutover area of Hill Creek on 9 July.

River cooter (*Pseudemys concinna* (Le Conte, 1830)). This species was recorded only once, and the record is questionable. A small (31 mm CL) individual from Mellard's Lake was identified as *P. concinna* on the basis of carapace markings but had an unpatterned plastron, suggesting that it may have been a *P. concinna* × *P. floridana* hybrid. It was preserved as a specimen to permit further analysis, but failure to obtain more than a few cooters from the Four Holes Swamp made it

impossible to verify the identity of this individual and the occurrence of *P. concinna* in the swamp.

Cooter (*Pseudemys floridana* (Le Conte, 1830)). Cooters were caught from late May through late August near Mellard's Lake and a cutover area of Hill Creek. Four individuals (63 -128 mm CL) were measured.

Common Box Turtle (*Terrapene carolina* (Linnaeus, 1758)). Box turtles were captured mostly in open upland or at forest edges. Seven adults (114–148 mm CV) and one individual (84 mm CL) that was probably a subadult were measured. One was eating a mushroom and had become too engorged to swallow.

Common Slider (*Trachemys scripta* (Schoepf, 1792)). Turtles resembling *T. scripta* were often seen basking along the shoreline or on snags projecting from deep water, but only a small proportion of them—mostly juveniles—could be captured for positive identifications. Two adults were captured on land in late March, and two adult females were found excavating nest cavities far from water on 30 June and 5 July. Nest cavities were made in natural areas of loose earth or on dirt roads. Eight juveniles were captured from late March through June (35.1 mm mean CL, range 33–38). A juvenile was captured (45 mm CL) in a cutover area near Mellard's Lake on 26 July. Large adults exceeded 200 mm CL.

Lizards

The eight species of recorded lizards represent five families. They range from highly arboreal types such as the green anole (*Anolis carolinensis*) to the slender glass lizard (*Ophisaurus* sp.), which is terrestrial and snake-like in form and habits. Only one species, the green anole, can be regarded as truly abundant in the Four Holes Swamp, although the ground skink (*Scincella lateralis*) may be more abundant than evident. Five-lined skinks (*Eumeces* spp.) are conspicuous on large tree trunks in cypress creeks and may be locally abundant. Including the four cryptic species of *Ophisaurus*, only 11 species of lizards are regarded residents of South Carolina.

Family Anguidae

Slender Glass Lizard (*Ophisaurus attenuatus* (Cope, 1880)), Island Glass Lizard (*Ophisaurus compressus* (Cope, 1900)), Mimic Glass Lizard (*Ophisaurus mimicus* Palmer, 1987), and Eastern Glass Lizard (*Ophisaurus ventralis* (Linnaeus, 1766)). Any of four species of *Ophisaurus* may occur in the few areas of the Four Holes Swamp where grassy vegetation dominates. A medium-sized glass lizard was captured along a highway near the entrance road to the Goodson Hill area on 26 August. Its light background color and lined pattern resembled those of *O. attenuatus*. It was photographed but escaped from a collecting bag before its identity could be verified. Albert Sanders of the Charleston Museum, who is familiar with the herpetofauna of the area, stated that most *Ophisaurus* in South Carolina are *O. ventralis* and that young specimens of the two species are easily mistaken for one another. Gibbons and Semlitsch (1991) reported both species as occurring on the grounds of the Savannah River Ecology Laboratory but combined both species in a single account, suggesting that they could not reliably distinguish the species. Two additional species, *O. compressus* and *O. mimicus* (Palmer 1987), occur in coastal South Carolina, and it is possible that the specimen could have been either of these species.

Family Phrynosomatidae

Eastern Fence Lizard (*Sceloporus undulatus* (Latreille *in* Sonnini and Latreille, 1801)). Only five records were obtained, two from the Neely Smith tract in late March, one from the southwestern cutover area in July, and two from the shore of Mellard's Lake in October. All captured individuals were of adult or subadult size (48–72 mm SVL). This species is most often found in open forest or on forest edges and is not expected to be abundant in well-developed forest.

Family Polychridae

Green Anole (*Anolis carolinensis* Voigt, 1832). The green anole is present in all parts of the Four Holes Swamp, particularly in forest-edge habitats bordering either fields or open water. One individual was on a floating log in a deepwater channel, attempting to swallow a large luna moth (*Actias luna*). Special efforts were made to record large numbers of anoles to learn more about their life history in the area. In all, 139 records were obtained from all parts of the swamp; sampling was

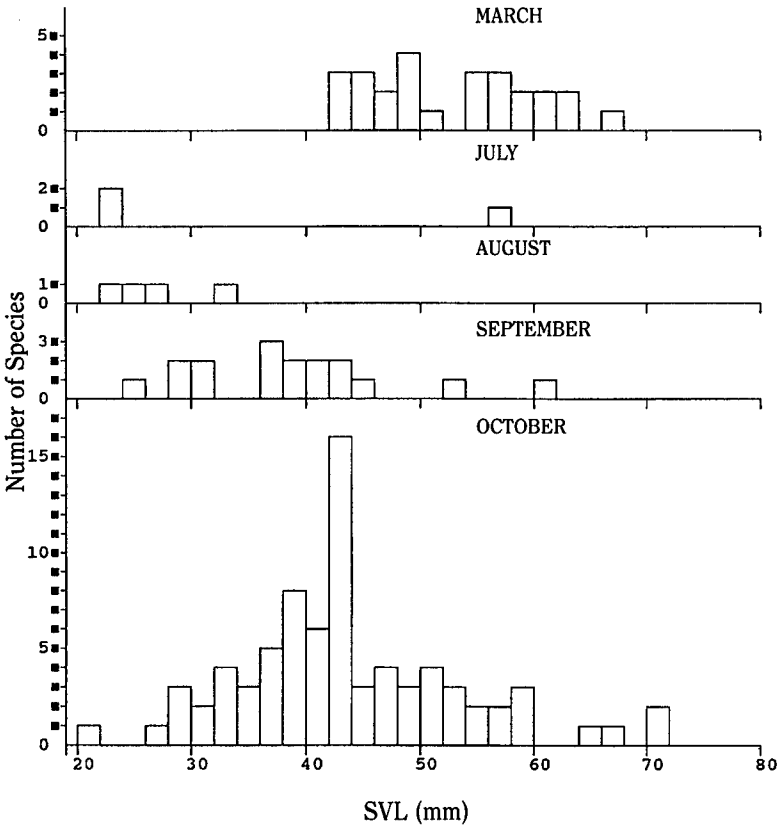

Fig. 5. Sizes and frequencies of green anoles, *Anolis carolinensis*, recorded in different months. The appearance of young in mid-summer is evident. Young seemingly grow to adult size in a single season. Large adults are more frequent early in the season than later, suggesting heavy annual mortality (data from present study).

concentrated in the vicinity of Mellard's Lake in October. Size distributions of animals in 5 months of sampling (Fig. 5) revealed the first appearance of young in July, an extended breeding season, and apparently rapid growth to adult size during the first year of life.

Family Scincidae

Genus *Eumeces*

Five-lined skinks are abundant in the swamp but difficult to capture on the trunks of huge trees where they are often found. The three species are similar in appearance and were once thought to be a single species (Taylor 1936). Little was learned about the ecological distribution of the three species because it is necessary to have individuals in hand for an examination of the minute scale characters that distinguish them.

Five-lined Skink (*Eumeces fasciatus* (Linnaeus, 1758)). Five-lined skinks were captured less frequently than broad-headed skinks (*E. laticeps*) but were found in many of the same areas. Adult females (65, 67 mm SVL) were captured in late March on the Neely Smith tract and in early August in the vicinity of Hill Creek.

Despite its apparent adult size, a 66-mm-SVL individual had a blue tail. A juvenile (31 mm SVL) was recorded from a cutover area near Mims Lake on 25 July, and 4 other juveniles (40-mm mean SVL, range 36–42) were recorded between late August and late September.

Southeastern Five-lined Skink (*Eumeces inexpectatus* Taylor, 1932). Two juvenile *E. inexpectatus* (45 mm SVL) were found beneath a log beside a tree-lined road between cultivated fields on the Goodson Hill on 28 March. Both had bright blue tails. This species is reported to use dry, open habitats (Fitch 1954), suggesting that it may be restricted to such sites around the margins of the swamp.

Broad-headed Skink (*Eumeces laticeps* (Schneider, 1801)). The broad-headed skink may be the most abundant species of *Eumeces* in the

swamp and probably accounts for many of the observed skinks on the trunks of large baldcypress and tupelo trees. Such trees are often surrounded by flowing water, and it is difficult to capture skinks that run far up tree trunks when approached. Nevertheless, 15 individuals were captured between late March and mid-October. Broadheaded skinks were found on the Neely Smith tract, at Mellard's Lake, near Hill Creek, on a cutover area, and on the Goodson Hill. Large adult males (108, 111, 122 mm SVL), smaller males (67–77 mm), and adult females (70, 75 mm) were recorded. Four juveniles (45–56 mm SVL) were recorded between 23 September and 12 October. All juveniles and one male (67 mm SVL) captured on 10 July had blue tails. Clark and Hall (1970) examined one possible function of blue tail-coloration in young skinks. Three individuals captured on 18 July and another on 17 August were in funnel traps set for snakes.

Ground Skink (*Scincella lateralis* (Say *in* James, 1823)). The ground skink occupies leaf litter and is probably far more abundant than evident in suitable habitats. Ground skinks were captured from March to October in forested areas of the Neely Smith tract and in the vicinity of the Goodson Hill. Adult-sized individuals were in the 38–50-mm-SVL range (mean SVL of 11 was 44 mm). The first juvenile (22 mm SVL) was seen on 23 August. Five juveniles were caught between late August and early October (27 mm mean SVL, range 22–32).

Family Teiidae

Six-lined Racerunner (*Cnemidophorus sexlineatus* (Linnaeus, 1766)). Only two records were obtained in the Four Holes Swamp, one from a bare-earth parking area near Mellard's Lake and the other from a road through a cutover swamp on the Westvaco property adjacent to the sanctuary. A general distribution of *C. sexlineatus* can be expected in the few disturbed areas around the swamp that provide suitable habitat.

Snakes

Twenty species of snakes representing two families were recorded. With the possible exception of the brown water snake (*Nerodia taxispilota*), no species is really abundant, and the apparent abundance of the brown water snake may result from an observation of seasonal aggregations. People associate southern swamps with snakes, and the concentrations of basking brown water snakes at certain times and the conspicuousness of cottonmouths (*Agkistrodon piscivorus*) at the water's edge may indeed give the impression of abundance. Nevertheless, snakes are far more abundant in other habitats, particularly in habitats with ample food supplies and suitable physiographic features. The estimated density of snakes was 1,322/ha or a biomass of 7.5 kg/ha on the Fitch Natural History Reservation in Kansas (Fitch 1982). Similar concentrations of snakes may occur elsewhere in the presence of abundant resources, but information from the Four Holes Swamp suggests no more than moderate numbers of a few—and rarity of most—species of snakes.

Family Colubridae

Racer (*Coluber constrictor* Linnaeus,1758). Of the six captured racers, five were in funnel traps. An 886-mm-SVL female was pursued and captured in a soybean field above Mallard Lake on 28 June. In August, males (1030, 955 mm SVL) were captured in funnel traps along drift fences on a raised road in cutover swamp in the Westvaco area, and the larger male was recaptured two weeks later. A female (974 mm SVL) and a male (1095 mm SVL) were trapped along a powerline on the Goodson Hill in mid-August and late September. Racers probably occur in most open areas around the borders of the Four Holes Swamp.

Ringneck Snake (*Diadophis punctatus* (Linnaeus, 1766)). Like other species of secretive small snakes, this species is probably more abundant than evident. All captures in the Four Holes Swamp were made on the Neely Smith tract. Two males (222, 260 mm SVL) were captured on 28 March, a male (264 mm SVL) and a juvenile (156 mm SVL) were captured on 24 May, and an adult female (273 mm SVL) was captured on 5 October.

Corn Snake (*Elaphe guttata* (Linnaeus, 1766)). A dead gravid female (881 mm SVL) was found on a road just southwest of the Four Holes Swamp on 23 May. Another female (975 mm SVL) was brought in and was said to have been captured from the swamp on 18 June.

Rat Snake (*Elaphe obsoleta* (Say *in* James, 1823)). Twenty-seven individuals were captured between 28 March and 7 September. They were found in all habitats in and around the swamp, and some swimming rat snakes were found in areas frequented by the brown water snake (*Nerodia taxispilota*). One snake was captured in a trap in an extensive area of cutover swamp. Twelve were adult males (1060 mm mean SVL, range 840–1,555), and 11 were females (1,107 mm mean SVL, range 700–1615). One individual (621 mm SVL) that was not identified to sex may have been a subadult. No juveniles were recorded. One snake captured on 28 March regurgitated a meal of unidentified bird eggs.

Mud Snake (*Farancia abacura* (Hoolbrook, 1836)). A single dead female (990 mm SVL) was found on the street of Dorchester, South Carolina, a few kilometers from the Four Holes Swamp on 9 July. The presence of this species in the Four Holes Swamp is probable.

Rainbow Snake (*Farancia erytrogramma* (Latreille *in* Sonnini and Latreille, 1801)). Two dead specimens were found on roads in the vicinity of the Audubon Sanctuary. On 3 June, one was found near the Four Holes Bridge, 5 km south of Dorchester, South Carolina. On 7 September, the other was found on U.S. Highway 178 between Harleyville, S.C., and the Four Holes Swamp. This species undoubtedly occurs in the Four Holes Swamp.

Eastern Hognose Snake (*Heterodon platirhinos* Latreille *in* Sonnini and Latreille, 1801). Only two records of *H. platirhinos* in the vicinity of the Four Holes Swamp near Mellard's Lake are available. One female (835 mm SVL) was found on 2 July. A dead, gravid female (650 mm SVL) was found on the road to the lake on 21 July.

Southern Hognose Snake (*Heterodon simus* (Linnaeus, 1766)). A single southern hognose snake was found on a sandy road in a commercial pine plantation near the entrance to Mellard's Lake on 2 June.

Common Kingsnake (*Lampropeltis getula* (Linnaeus, 1766)). Two common kingsnakes were captured in funnel traps on 14 July, one on the Goodson Hill near the visitor center and the other on a road in cutover swamp in the Westvaco area. Another individual was captured near a powerline in the Goodson Hill area. An apparently adult female (678-mm SVL) and an adult male (495 mm SVL) were measured.

Red-bellied Water Snake (*Nerodia erythrogaster* (Forster, 1771)). Two red-bellied water snakes were found on land near the shore of Mellard's Lake. One was a female (1,000 mm SVL). Both individuals had gray bellies with only faint reddish highlights along the edges. Another individual that was captured about 9 km from the Four Holes Swamp had a bright, orangish-red venter.

Southern Water Snake (*Nerodia fasciata* (Linnaeus, 1766)). The southern water snake is a close relative of the wide-ranging and generalized *N. sipedon*. Failure to find it more frequently in the Four Holes Swamp suggests that it is rare in the surveyed habitats. A single injured individual was captured from the shore of Mellard's Lake on 7 June.

Brown Water Snake (*Nerodia taxispilota* (Holbrook, 1838)). The brown water snake is characteristic of swamps on the southeastern coastal plain and is one of the most conspicuous inhabitants of the Four Holes Swamp in spring. Numerous basking brown water snakes can be seen on trees along the deeper watercourses on sunny days when riparian vegetation is still leafless. Special attention was given to recording as much information about the species as possible. Thirty-seven records were obtained by the end of May, 18 in June, 10 in July, 1 in August, and none thereafter despite a gradually increasing sampling effort through June and July. The snakes that were so abundant in spring were nearly invisible by the onset of summer, suggesting that their activity may be influenced by thermoregulatory needs. Eighteen females (648 mm mean SVL; range 475–1,013) and 23 males (630 mm mean SVL; range 405–752) were judged to be adults. Apparent subadults (238 mm SVL), were measured on 30 May and (305,330 mm SVL) on 2 July. A single large (1013 mm SVL) female handled on 31 May appeared gravid. Six individuals that regurgitated food when handled had eaten fish, three of which could be identified as redfin grass pickerels (*Esox americanus*; 100–150-mm size range). Some snakes were marked with quick-drying acrylic paints for identification without capture. Resightings at 1, 5, 7, and 8 days after release indicated a general fidelity to area but not the repeated use of basking sites.

Rough Green Snake (*Opheodrys aestivus* (Linnaeus, 1766)). Four individuals were found in the Four Holes Swamp or nearby. On 28 March, a dead male (422 mm SVL) was found on the road at the entrance to the Neely Smith tract on 25 August, and a dead male (402 mm SVL) was found on the road near the entrance road to the Goodson Hill on 4 October. A female (422 mm SVL) was captured on the bluffs at the Neely Smith tract and a male (390 mm SVL) was captured on a nearby hill in the swamp that was surrounded by water.

Pine Snake (*Pituophis melanoleucus* (Daudin, 1803)). A single male pine snake (1220 mm SVL) was captured approximately 8 km west of the Four Holes Swamp. Suitable upland habitat for this species surrounds much of the swamp, and the species may be there.

Red-bellied Snake (*Storeria occipitomaculata* (Storer, 1839)). The red-bellied snake is one of several species of small, terrestrial snakes that are abundant in suitable habitats but seldom seen because they are secretive. One red-bellied snake was caught on 2 July near a constructed pond on a tributary to the Four Holes Swamp, and one female (150 mm CVL) and one male (144 mm SVL) were captured in leaf litter on the Goodson Hill along the trail to Goodson Lake.

Eastern Ribbon Snake (*Thamnophis sauritus* (Linnaeus, 1766)). A single female (220 mm SVL) was captured in March on bluffs on the Neely Smith tract.

Common Garter Snake (*Thamnophis sirtalis* (Linnaeus, 1758)). The common garter snake is not abundant in the Four Holes Swamp. A single male (407 mm SVL) was captured on the access road to the Goodson Hill area on 3 September.

Family Viperidae

Timber Rattlesnake (*Crotalus horridus* Linnaeus, 1758). Rattlesnakes were observed only twice in the Four Holes Swamp and once in a nearby area, but they are probably present in low numbers all around the bluffs that surround the swamp. An adult female (1023 mm SVL; 12 rattles and button) was captured on bluffs on the Neely Smith tract on 26 March; she apparently was still in a hibernaculum beneath a large stump. Another large adult (estimated 1100 mm SVL; 11 rattles and button) was observed near the Goodson Hill on 16 July; she apparently was asleep in a shallow depression in the middle of a trail. A juvenile (365 mm SVL; button only) was found near the swamp on 1 September.

Copperhead (*Agkistrodon contortrix* (Linnaeus, 1766)). Copperheads are secretive and nocturnal, but enough information was collected to indicate that they probably occur on all the bluffs along the Four Holes Swamp. Intensive studies of the ecology of the species in Kansas (Fitch 1960) indicated that copperheads use wooded bluffs for shelter, maternity denning, and overwintering but move into open fields to feed on rodents. An adult male (651 mm SVL) was captured on the Neely Smith tract on 29 March, and several individuals (including 600-mm- and 655-mm-SVL females) were trapped or caught by hand in the Goodson Hill area in July. A subadult (320 mm SVL) was captured near a powerline on the Goodson Hill on 18 August. A dead male (860 mm CVL) was found on the road near the swamp on 23 September. Copperheads are often found in extensive grassy or brushy areas at the western extremes of their range but whether the snakes make regular moves into these areas near the Four Holes Swamp could not be determined.

Cottonmouth (*Agkistrodon piscivorus* (Lacepede, 1789)). Cottonmouths that were swimming in the water or resting on logs or along the shore were seen frequently. Usually coiled and apparently asleep, others were encountered along bluffs. Two cottonmouths were seen among several species of calling frogs in a shallow temporary pond in a powerline corridor across the Goodson Hill on the night of 24 May. Despite lengthy searching, we never encountered cottonmouths in unflooded flatwoods. Apparent adults captured on 26 March were a female (990 mm SVL) and a male (630 mm SVL), but many larger individuals were observed. Apparent subadults (261 mm SVL) on 26 March and (320 mm SVL) on 17 July had the characteristic yellow tail tip of young cottonmouths.

Crocodilians

Family Alligatoridae

American Alligator (*Alligator mississippiensis* (Daudin, 1803)). Alligators were moderately abundant in areas of permanent water in the Four Holes

Swamp but were more often seen in open, cutover areas than in densely shaded swamp. Alligators were recorded from 23 May through 9 September. They were commonly seen in the vicinity of Mellard's Lake, and on 25 July, eight were seen between Mellard's Lake and Mims Lake. Other sightings were made at Singletary Creek, in the Westvaco cutover area, and at Canoe Lake. No nest mounds were seen, and whether alligators breed there is not known.

Several species that were not recorded during the 1976 survey may, however, be present in the swamp.

Salamanders

Greater Siren (*Siren lacertina* Linnaeus, 1766). The greater siren may occur in parts of the Four Holes Swamp, but collecting efforts were not sufficient to determine whether this species is present.

Dwarf Waterdog (*Necturus punctatus* (Gibbs, 1850)). The range of the dwarf waterdog includes the South Carolina coastal plain and broadly overlaps the Four Holes Swamp. Failure to detect the species may have resulted from failure to adequately sample in aquatic habitats.

Amphiuma (*Amphiuma means* Garden *in* Smith, 1821). The amphiuma is another species that probably occurs in the Four Holes Swamp but cannot be detected except by specialized collecting methods not employed during surveys.

Mabee's Salamander (*Ambystoma mabeei* Bishop, 1928). The ecological requirements of Mabee's salamander are not well known. The Four Holes Swamp is well within the range of the species.

Spotted Salamander (*Ambystoma maculatum* (Shaw, 1802)). The spotted salamander is widely adapted to a variety of habitats in the eastern third of the United States, where it is often the most abundant species of *Ambystoma*. The spotted salamander breeds in early spring and is rarely seen outside the breeding season. Failure to detect this species may have been due to sampling too late to observe breeding adults or failure to sample in the kinds of ponds that may hold larvae.

Mole Salamander (*Ambystoma talpoideum* (Holbrook, 1838)). The mole salamander's range includes the Four Holes Swamp. Because its ecological range includes lowlands and valleys, the mole salamander may occur in the swamp.

Tiger Salamander (*Ambystoma tigrinum* (Green, 1825)). The tiger salamander is a wide-ranging species in suitable habitats in much of the eastern four-fifths of the United States. Natural ponds, farm ponds, or other pond-like habitats in the vicinity of the Four Holes Swamp may harbor this species.

Mud Salamander (*Pseudotriton montanus* Baird, 1849). The mud salamander was not recorded, and the probability of its occurrence in the Four Holes Swamp is unknown. It frequently coexists with *Desmognathus auriculatus*, a species recorded only once during the survey. Descriptions of its habitat preferences suggest that the mud salamander occurs in the leaf litter and debris around springs like those on the Neely Smith tract, but it was not recorded in extensive fieldwork there.

Many-lined Salamander (*Stereochilus marginatus* (Hallowell, 1856)). The many-lined salamander is essentially a pond-dwelling species that was not recorded. Suitable habitats almost certainly occur in the Four Holes Swamp and the surrounding areas, and this species should be sought.

Frogs

Brimley's Chorus Frog (*Pseudacris brimleyi* Brandt and Walker, 1933). Brimley's chorus frog should occur in the Four Holes Swamp but was not recorded, perhaps because sampling was not conducted during the early-spring breeding season.

Ornate Chorus Frog (*Pseudacris ornata* (Holbrook, 1836)). The ornate chorus frog breeds in ponds in the semi-open types of habitats dominated by pines. Such habitats occur on the uplands around the Four Holes Swamp and may support populations of this frog.

Gopher Frog (*Rana capito* Le Conte, 1855). The gopher frog is an elusive species wherever it occurs and may occur in the Four Holes Swamp. It inhabits crayfish burrows and possibly burrows of other animals and is rarely seen. Seemingly suitable habitats are abundant in the Four Holes Swamp, and it is probable that careful surveillance during the breeding season will reveal the gopher frog as a resident there.

River Frog (*Rana heckscheri* Wright, 1924). The river frog could be expected in the Four Holes Swamp, and a frog matching its description was found on the entrance road to the Neely Smith tract during the 1976 survey. But Albert Sanders of the Charleston Museum indicated it was an interesting and aberrant specimen of the common and widespread *R. catesbeiana*. The river frog is a probable, but undocumented inhabitant of the Four Holes Swamp.

Carpenter Frog (*Rana virgatipes* Cope, 1891). The carpenter frog is said to inhabit sphagnum bogs, and its range includes the Four Holes Swamp. Identification and survey of suitable habitats would be necessary to verify the occurrence of this species.

Testudines

Spiny Softshell (*Apalone spinifera* (Lesuer, 1827)). Softshell turtles seem to require sand or mud bars in quiet waters that are common in the Four Holes Swamp. The species is not readily collected in traps and is not commonly seen basking like many species of more typical turtles. The spiny softshell is a possible resident of the swamp.

Lizards

Glass Lizards genus (*Ophisaurus*)

The single collected glass lizard could not be definitively identified to species, and as many as four separate species may occur in the Four Holes Swamp.

Snakes

Worm Snake (*Carphophis amoenus* (Say, 1825)). The worm snake is a common secretive inhabitant of moist woods, but the species was not recorded in the Four Holes Swamp. Its presence in the swamp is possible.

Scarlet Snake (*Cemophora coccinea* (Blumenbach, 1788)). The scarlet snake probably occurs in the vicinity of the Four Holes Swamp but, being a burrower that inhabits dry uplands with loose soil, is not expected to be abundant in the hydric or mesic zones.

Mole Snake (*Lampropeltis calligaster* (Harland, 1827)). The mole snake is expected in the Four Holes Swamp, particularly where loose soil or an abundance of mammal burrows permit it to spend most of its time under the soil surface.

Scarlet Kingsnake (*Lampropeltis triangulum* (Lacepede, 1788)). The wide-ranging scarlet kingsnake is almost ubiquitous in a wide geographic range that extends over the eastern two-thirds of the United States. It was not found during the survey but should be sought in the Four Holes Swamps.

Coachwhip (*Masticophus flagellum* (Shaw, 1802)). The coachwhip, like the racer, is an active, mobile species that can be seen in a variety of habitats. It should be sought primarily in open, grassy areas around margins of the swamp.

Glossy Crayfish Snake (*Regina rigida* (Say, 1825)). The habitat preferences of this secretive species suggest that it should be in the swamps. A snake that escaped was tentatively identified as either this species or the black swamp snake. The glossy crayfish snake (*R. rigida*) has to be regarded as having a high probability of occurrence in the swamp.

Black Swamp Snake (*Seminatrix pygaea* (Cope, 1871)). The black swamp snake is said to inhabit cypress ponds that are surrounded by upland stands of pines. The species was not found during the survey and sampling in such habitats in the vicinity of the Four Holes Swamp was not conducted; this species may be present nearby.

Brown Snake (*Storeria dekayi* (Holbrook, 1839)). The brown snake is widely distributed throughout the East and seems to be able to adapt to a wide variety of habitats. Its preference for moist habitats, including damp woods and swampy areas, suggests that it could occur in the Four Holes Swamp. It commonly shares habitats with its relative the red-bellied snake (*S. occipitomaculata*), which was recorded.

Southeastern Crowned Snake (*Tantilla coronata* Baird and Girard, 1853). Snakes of the genus *Tantilla* are tiny, secretive, and rarely recorded. The southeastern crowned snake seems to be widely and generally distributed but rarely encountered. It is a probable inhabitant of the Four Holes Swamp.

Rough Earth Snake (*Virginia striatula* (Linnaeus, 1766)). The rough earth snake is a secretive species with a patchy distribution. It may be abundant in some locations and at extremely low

population densities in others. Its presence in the Four Holes Swamp is possible.

Smooth Earth Snake (*Virginia valeriae* Baird and Girard, 1853). The Four Holes Swamp is in the geographic range of the smooth earth snake that was, however, not found in the 1976 survey. The snake is one of several species of small snakes that inhabit the leaf litter or upper zones of the soil and are notoriously difficult to find.

The following are species with geographic or ecological ranges that are immediately outside Four Holes Swamp:

Salamanders

Dwarf Siren (*Pseudobranchus striatus* (Le Conte, 1824))
Ringed Salamander (*Ambystoma cingulatum* (Cope, 1868))

Frogs

Pig Frog (*Rana grylio* Stejneger, 1901)
Pickerel Frog (*Rana palustris* Le Conte, 1825)

Snakes

Eastern Diamondback Rattlesnake (*Crotalus adamanteus* Beauvois, 1799)
Eastern Coral Snake (*Micrurus fulvius* (Linnaeus, 1766))
Green Water Snake (*Nerodia floridana* (Goff, 1936))
Pine Woods Snake (*Rhadinea flavilata* (Cope, 1871))
Pigmy Rattlesnake (*Sistrurus miliarius* (Linnaeus, 1766))

Patuxent Wildlife Research Center

The Patuxent Wildlife Research Center (Patuxent) in Laurel, Maryland, is approximately 830 km north of the Four Holes Swamp. It has been protected since 1936. A description of the topography and vegetation of the core area of Patuxent was provided by Hotchkiss and Stewart (1947). This information was updated and information on biota gleaned from a variety of sources appears in Stickel's (1979) compilation. Hall (1988) provided an annotated bibliography of ecological studies published through 1987. Most of the original 1,053-ha area was submarginal farmland when acquired by a precursor of the U.S. Fish and Wildlife Service, but good stands of mostly second-growth timber remained in the alluvial floodplain of the Patuxent River, and forest regeneration had begun on the relatively xeric uplands. The area was originally dedicated to research into the benefits of enlightened farming practices to wildlife populations. Consequently, formerly farmed areas were kept in cultivation for a decade or longer. After the completion of the farming experiments, the fields were maintained by mowing on the rationale that this would produce a diverse assemblage of useful species for the mission of the center. Changes were made as buildings, pens, roads, powerlines, and large impoundments were built, but the basic pattern of forest and clearings remained (Hall 1988). Approximately one-third of Patuxent consists of alluvial floodplain and bluffs, one-third of xeric upland, and the remaining third of a broad terrace with the greatest amount of cultivation and development and evidence of intense human occupation for thousands of years. The diversity of Patuxent's biota is favored by its location at a latitude where the ranges of species characteristic of both the southeastern coastal plain and the northeastern uplands sometimes overlap.

Soon after the acquisition of Patuxent by the federal government, scientists began systematic surveys of plants and animals (Hall 1988). These surveys were discontinued in the 1950s, but some species were the focus of subsequent studies of the effects of pesticides. Studies of other species continued into the 1970s, and quantitative indices of abundance were maintained. Surveys and record-keeping have been sporadic, but periods of intense work revealed information about the herpetofauna and its changes. In all, 51 species—23 amphibians and 28 reptiles—have been documented (Stickel 1979); a single slider turtle (*Trachemys scripta* (Schoepff, 1792)) was thought to have been introduced, and the milk snake (*Lampropeltis triangulum* (Lacepede, 1788)) was believed to have been a transient. Hence, 49 species were regarded residents.

An annotated list of the herpetofauna of Patuxent (Stickel 1979) provided general information about population-size trends during 42 years (Table 2). Only one species, the six-lined racerunner

Table 2. Status of amphibians and reptiles of the Patuxent Wildlife Research Center, Maryland, 1937–1991, based on Stickel (1979).

Species	Status
Amphibia: Caudata	
Ambystoma maculatum	Believed declining
Ambystoma opacum	Believed declining
Desmognathus fuscus	Unknown; may be extirpated
Eurycea bislineata	Seemingly unchanged
Eurycea longicauda	Status unknown; only two records
Hemidactylium scutatum	Unknown; seems rare
Notopthalmus viridescens	Commonly recorded
Plethodon cinereus	Remains common
Pseudotriton montanus	Rare; status unknown
Pseudotriton ruber	Rare; status unknown
Amphibia: Anura	
Acris crepitans	Common in impoundments
Bufo americanus	Abundant
Bufo woodhousei	Abundant
Hyla cinerea	First recorded in 1989
Hyla versicolor	Common
Pseudacris crucifer	Abundant
Pseudacris triseriata	Common in 1940's; rare in 1970's
Rana catesbeiana	May have increased with impoundments
Rana clamitans	Common in variety of habitats
Rana palustris	Common in impoundments
Rana utricularia	Common but not abundant
Rana sylvatica	Seems to have declined since 1940's
Scaphiopus holbrookii	Not reported for many years
Reptilia: Testudinata	
Chelydra serpentina	Increased abundance with impoundments
Chrysemys picta	Increased abundance with impoundments
Clemmys guttata	Occasional; uses impoundments
Kinosternon subrubrum	Occasional
Pseudemys rubriventris	Apparent slow increase
Sternotherus odoratus	Occasional; no apparent change
Terrapene carolina	Documented decline in bottomland forest
Reptilia: Squamata: Sauria	
Cnemidophorus sexlineatus	Seemingly extirpated
Eumeces fasciatus	Uncommon; status unknown
Sceloporus undulatus	Occasionally seen in woods margins
Scincella lateralis	May be occasional; not often noticed
Reptilia: Sauria: Serpentes	
Carphophis amoenus	Seldom recorded; status unknown
Coluber constrictor	Seemingly unchanged
Diadophis punctatus	Seemingly unchanged
Elaphe obsoleta	Seemingly unchanged
Heterdodon platirhinos	Fairly common in upland oak forest
Lampropeltis calligaster	Has decreased since 1940's; now rare
Lampropeltis getula	Has decreased to occasional since 1940's
Lampropeltis triangulum	One record from power line cut
Nerodia septemvittata	Seemingly rare
Nerodia sipedon	Common; uses impoundments
Opheodrys aestivus	Very rarely recorded
Storeria dekayl	Rarely seen; probably not rare

Table 2. *Continued.*

Species	Status
Storeria occipitomaculata	Seemingly rare
Thamnophis sauritus	Occasional at margins of impoundments
Thamnophis sirtalis	Occasionally seen in open upland areas
Virginia valeriae	Unknown; rarely seen

(*Cnemidophorus sexlineatus* (Linnaeus, 1766)), was believed to have disappeared as a result of natural biological processes. It is a fugitive species (Hutchinson 1951) and occurred almost exclusively in gravel pits until they became overgrown with woody vegetation. Because a racerunner was recorded on a roadside at the boundary of the area in 1989, the presence of occasional dispersing racerunners cannot be ruled out. The dusky salamander (*Desmognathus fuscus* (Green, 1818)) may have been lost as a result of human activity; it was recorded at a single spring that was later converted into a reservoir for rearing facilities for endangered cranes (Gruidae). Other populations of *D. fuscus* elsewhere at Patuxent may persist. Good quantitative information is available on the population of eastern box turtles (*Terrapene carolina* (Linnaeus, 1758)) that occupy a bottomland forest. That population declined from a density of 10.6/ha in 1945 to less than 4.9/ha in 1985 (Stickel 1950, 1978; Patuxent Wildlife Research Center, unpublished data). Whether populations declined similarly in a mixture of forest and grassland communities is not known. Nine species are considered rare and have been recorded so infrequently that little can be inferred about their changes in abundance. Five species were the subject of a variety of studies on the effects of DDT in the 1940s and 1950s and are believed by the investigators to have declined since then. They are the mole salamanders (*Ambystoma maculatum* (Shae, 1802) and *A. opacum* (Gravenhorst, 1807)), the wood frog (*Rana sylvatica* Le Conte, 1825), and two snakes (*Lampropeltis calligaster* (Harlan, 1827) and *L. getula* (Linnaeus, 1766)). Another nine species—primarily frogs, turtles, and water snakes—are believed to have increased in abundance as the result of extensive wetlands created in the 1950s and 1960s. One species, the green treefrog, (*Hyla cinerea* (Schneider, 1799)), was first recorded in 1989; it is known from surrounding areas and may have been present long before it was noticed. The remaining 21 species seem to have maintained their populations at moderate to high levels throughout the 50-year history of the area. Because only one species was lost, one species was gained, and nearly equal numbers of species increased and decreased, the herpetofaunal diversity at Patuxent seems to have remained almost unchanged.

Stickel (1979) was concerned that formerly abundant species were declining despite habitat management to maintain species diversity. He cited as possible causes changes that eluded attempts to maintain habitat diversity. Formerly forested areas matured, and regenerating forest was replaced by increasingly dense forest. Beech increased in dominance because of selective browsing on other species by an overly large population of white-tailed deer (*Odocoileus virginiana*). Formerly grazed or cultivated areas that were maintained by mowing became densely sodded. The boundaries between these kinds of habitats became increasingly abrupt, and the edge became sharp with narrow or non-existent transition zones. Stickel (1979) referred to the change as an increasing polarization of habitats, lacking the dynamics characteristic of the normal cycle of habitat destruction and regeneration and the significant transitional areas that were present when the land was acquired.

Another factor may explain the declines in the density of certain species. Amphibians in the floodplain of the Patuxent River, particularly *Ambystoma* salamanders and the wood frog, (*Rana sylvatica* Le Conte 1825), rely on seasonally flooded pools for breeding. Increasing severity of floods from upstream deforestation and disruption of the normal periodicity of flooding by upriver impoundments can either prevent normal spring runoff from producing pools or inundate pools

when stored water is released. Stickel (1979) cited this problem and aperiodic floods from artificial hydrological regimes (Stickel 1978) were given as a possible cause of decline of box turtle populations at Patuxent.

Fitch Natural History Reservation

The Fitch Natural History Reservation of the University of Kansas (Fitch Reservation) is near the western limit of deciduous forests, 1,610 km west and 805 km north of the Four Holes Swamp. General descriptions, species lists, and bibliographies of studies on the reservation are provided by Fitch (1952, 1965a). The reservation is smaller and physiographically less diverse than Patuxent. The 239-ha area is on the bluffs above the Kansas River valley, and aquatic habitats are restricted to two small intermittent streams and an artificial pond. Management of the reservation was designed to protect the area from as many varieties of human interference as possible and began in 1949. Cutting, mowing, burning, grazing by livestock, and all other forms of habitat alteration were prohibited (Fitch 1965a). When established, the area was perhaps half deciduous woodland, which was mostly on the escarpments, and grassland on the flat valleys and plateaus. Protection created profound changes. By 1991, the forests on the scarps had matured and woody vegetation had encroached on and displaced all significant areas of prairie.

Detailed information on the vertebrate fauna of the reservation has been collected since 1949 (Fitch 1965a; Fitch, personal communication), and the ecology of many reptilian species has been investigated (Fitch 1954, 1958, 1960, 1965b, 1975). In all, 10 species of amphibians and 27 species of reptiles have been recorded. Two species, the eastern box turtle (*Terrapene carolina* (Linnaeus, 1758)) and the painted turtle (*Chrysemys picta* (Schneider, 1783)), were single individuals believed to have been intentionally released. Four other species, the tiger salamander (*Ambystoma tigrinum* (Green, 1825)), the plains spadefoot (*Scaphiopus bombifrons* Cope, 1863), the speckled kingsnake (*Lampropeltis getula* (Linnaeus, 1766)), and the Great Plains rat snake (*Elaphe guttata* (Linnaeus, 1766)) are believed to have been transients without permanent breeding populations. One other species, the lined snake (*Tropidoclonion lineatum* (Hallowell, 1856)), is known from an immediately adjacent mowed area but is regarded as not having occurred on the reservation since prior to 1948. The collared lizard (*Crotaphytus collaris* (Say *in* James, 1823)) was intentionally introduced in an isolated habitat and reproduced for several generations; it is here regarded as a one-time resident. The number of now or formerly resident species on the reservation is thus 31.

Changes in the herpetofauna of the Fitch Reservation (Table 3) have been tracked throughout its existence by H. S. Fitch. Changes were drastic and primarily attributable to ecological succession. Changes were also relatively rapid, despite a slowing of succession by loss of an overstory of American elm (*Ulmus americana*) to disease midway through the period. The characteristic grasslands began dwindling early as encroachment by woody vegetation caused islands of grassland to become smaller and more isolated. Other species preserved in isolated patches of prairie were eliminated when the patches were obliterated. With one possible exception, no species, not even those normally associated with deciduous forest, has increased in abundance.

The earliest species that disappeared were characteristic of open, rocky sites or grazed areas. The Great Plains skink, (*Eumeces obsoletus* (Baird and Girard, 1852)), the prairie skink (*E. septentrionalis* (Baird, 1859)), and the flat-headed snake (*Tantilla gracilis* Baird and Girard 1853) had disappeared by 1960. The bullsnake (*Pituophis catenifer* (Blainville, 1835)) also disappeared as a resident in this period but, with some other species of snakes, continued to migrate from areas outside the reservation to hilltop rocky ledges for hibernation. A small colony of the collared lizard (*Crotaphytus collaris* (Say *in* James, 1823)), introduced at an old quarry site, persisted through several generations but dwindled and disappeared as brush encroached on its habitat. The abundance of the six-lined racerunner (*Cnemidophorus sexlineatus* (Linnaeus, 1766)) declined throughout the 1940s and 1950s, and the last individuals were recorded in the 1960s. The Great Plains narrow-mouthed frog (*Gastrophryne*

Table 3. Status of amphibians and reptiles of the Fitch Natural History Reservation, Kansas; 1948–91.

Species	Status
Amphibia: Caudata	
Ambystoma tigrinum	Dispersers recorded into 1960's - extirpated
Amphibia: Anura	
Acris crepitans	Persistently abundant
Bufo americanus	Persistently present
Bufo woodhousei	Rare and probably has declined
Gastrophryne olivacea	Formerly abundant—extirpated
Hyla chrysoscelis	May have increased in forest and edge
Pseudacris triseriata	Less common than in the 1950's and 1960's
Rana blairi	Small numbers persist
Rana catesbeiana	Persists with drastic fluctuations
Scaphiopus bombifrons	Dispersers appeared in wet years—extirpated
Reptilia: Testudinata	
Chelydra serpentina	Persists in lower numbers than formerly
Chrysemys picta	Single record of individual probably released
Terrapene carolina	One record in 1960's; almost certainly released
Terrapene ornata	Common in 1940's extirpated in early 1970's
Reptilia: Squamata: Sauria	
Cnemidophorus sexlineatus	Abundant in 1940's and 1950's; extirpated since 1960's
Crotaphytus collaris	Introduced colony dwindled, extirpated in 1950's
Eumeces fasciatus	Formerly 81-227/HA; now confined to open sites
Eumeces obsoletus	Once abundant in open sites; extirpated in 1950's
Eumeces septentrionalis	Colonies in open areas—extirpated by 1960
Ophisaurus attenuatus	Peaked in 1960's; now less than 10% of peak
Scincella lateralis	Persists at low densities in grassland edge
Reptilia: Squamata: Serpentes	
Agkistrodon contortrix	Gradual decline to fraction of former numbers
Carphophis amoenus	Drastic decline in open woodland
Coluber constrictor	Abundant in 1950's; relatively scarce in 1990
Crotalus horridus	Abundant in 1940's; extirpated in 1960's
Diadophis punctatus	Declined to perhaps 5% of former abundance
Elaphe guttata	Found 1 KM West but never on Reservation
Elaphe obsoleta	Persists but declined more than 50%
Lampropeltis calligaster	Small numbers persist in grassland remnants
Lampropeltis getula	Known from only nearby areas
Lampropeltis triangulum	Persists throughout in low densities
Nerodia sipedon	Small persistent colony at pond
Pituophis catenifer	Moderately common in 1940's—extirpated
Storeria dekayi	Persists in low numbers in relatively open areas
Tantilla gracilis	Colony at old quarry extirpated in 1950's
Thamnophis sirtalis	Persistent but declining with habitat change
Tropidoclonion lineatum	Recorded from mowed area adjacent to Reservation
Virginia valeriae	Secretive; few well-spaced records to present

olivacea (Hallowell, 1857)) also disappeared in this period. The abundance of the ornate box turtle (*Terrapene ornata* (Agassiz, 1857)) began to decline with cessation of grazing, and the species was last recorded in the early 1970s. The slender glass lizard (*Ophisaurus attenuatus* (Cope, 1880)) increased in abundance as tall grass developed on formerly grazed areas and reached its maximum abundance in 1966; subsequently the population declined to less than 10% of its greatest size. The

species that disappeared from the Fitch Reservation have overwhelmingly been characteristic of the Great Plains and therefore were not present at Patuxent or in the Four Holes Swamp (Table 4).

The abundance of species with largely eastern distributions that commonly inhabit deciduous forest also declined, or the species disappeared with progressive maturation of woody vegetation. The timber rattlesnake (*Crotalus horridus* Linnaeus, 1758) was abundant in the 1940s, but its abundance declined through the 1950s, and the species disappeared in the 1960s. The copperhead

Table 4. Herpetofaunal species that occur in only one of the three protected areas: Patuxent Wildlife Research Center (Patuxent), Maryland; University of Kansas Fitch Natural History Reservation (Fitch Reservation); and Four Holes Swamp (Four Holes Swamp), South Carolina.

Patuxent (1937–1991)	Fitch Reservation (1948–1991)	Four Holes Swamp (1976)
Amphibia: Caudata		
Ambystoma maculatum	*Ambystoma tigrinum*[a]	*Desmognathus auriculatus*
Desmognathus fuscus[a]		*Eurycea cirrigera*
Eurycea bislineata		*Eurycea quadridigitata*
Hemidactylium scutatum		*Plethodon glutinosus* sp.
Plethodon cinereus		*Siren intermedia*
Pseudotriton montanus		
Pseudotriton ruber		
Amphibia: Anura		
Rana palustris	*Gastrophryne olivacea*[a]	*Acris gryllus*
Rana sylvatica	*Hyla chrysoscelis*	*Bufo quercicus*
	Rana blairi	*Bufo terrestris*
	Scaphiopus bombifrons[a]	*Gastrophryne carolinensis*
		Hyla femoralis
		Hyla squirella
		Pseudacris ocularis
		Pseudacris nigrita
Reptilia: Testudinata		
Chrysemys picta		*Pseudemys concinna*
Pseudemys rubriventris		*Pseudemys floridana*
		Trachemys scripta
		Deirochelys reticularia
Reptilia: Squamata: Sauria		
	Crotaphytus collaris[a]	*Anolis carolinensis*
	Eumeces obsoletus[a]	*Eumeces inexpectatus*
	Eumeces septentrionalis[a]	*Eumeces laticeps*
Reptilia: Squamata: Serpentes		
Regina septemvittata	*Pituophis catenifer*	*Agkistrodon piscivorus*
	Tantilla gracilis[a]	*Farancia abacura*[b]
	Tropidoclonion lineatum[b]	*Farancia erytrogramma*[b]
		Heterodon simus[b]
		Nerodia erythrogaster
		Nerodia fasciata
		Nerodia taxispilota
		Pituophis melanoleucus
Reptilia: Crocodilia		
		Alligator mississippiensis

[a] Extirpated.
[b] Known from adjacent area.

(*Agkistrodon contortrix* (Linnaeus, 1766)) declined to a fraction of its former abundance as its primary prey, the prairie vole (*Microtus ochrogaster*), declined with the shrinkage of grassland. The worm snake (*Carphophis amoenus* (Say, 1825)) declined in abundance with forest development but persists where forest regeneration has been least rapid. Clark (1970) studied a population of worm snakes adjacent to the Fitch Reservation. The snakes were abundant in a grazed forest, suggesting that forest cover alone may not be the most important limiting factor of the distribution and abundance of the snake. The ringneck snake (*Diadophis punctatus* (Linnaeus, 1766)) declined to 5% or less of its former abundance, whereas the abundance of the black rat snake (*Elaphe obsoleta* (Say *in* James, 1823)) declined by only about 50%. The five-lined skink (*Eumeces fasciatus* (Linnaeus, 1758)) that once had a density of 82–230/ha in grazed woodland became rare and localized in open areas. A single eastern species, Cope's gray treefrog (*Hyla chrysoscelis* Cope, 1880), may have increased its abundance since protection began.

Several generalist species also declined in abundance or maintained only small populations (Table 3). Of the 31 resident species on the Fitch Reservation in 1949, 9 disappeared, only 9 seem to have maintained their former population sizes, and the abundances declined of 12 and increased of only 1. The biological diversity declined because 29% of the resident species were lost and the distribution and abundance of another 39% of the resident species diminished.

Changes in the population sizes of amphibians and reptiles of the Fitch Reservation hardly differ from those of mammals and resident and migratory birds. General declines are the rule, and no vertebrate species or species group is more abundant now than in 1948. One possibility is that intensive study such as that on the Fitch Reservation in the 1960s and 1970s caused various stresses on studied populations and the consequent decline in the abundances these of species. This is unlikely, however, because studies were not evenly distributed among species or areas and investigators had begun concentrating on more abundant populations elsewhere by the mid-1960s.

Some of the published and unpublished data (Table 5) on snakes of the Fitch Reservation permit an application of the Shannon-Wiener diversity index (Wilson and Bossert 1971) to changes in the

Table 5. Densities and biomasses of snakes on the Fitch Natural History Reservation, Kansas, in two periods. Figures from the 1950's are based on published information (Fitch 1982), and figures from 1991 are estimates and projections based on unpublished data collected by Henry S. Fitch.

Species	Density (/HA)		Biomass (KG/HA)	
	1950–60	1991	1950–60	1991
Agkistrodon contortrix	7.400	0.700	0.800	0.080
Coluber constrictor	4.700	2.000	0.600	0.300
Diadophis punctatus	1,266.000	60.000	5.060	0.200
Elaphe obsoleta	0.900	0.400	0.230	0.100
Thamnophis sirtalis	3.700	2.000	0.250	0.100
Carphophis vermis	22.900	20.000	0.150	0.100
Crotalus horridus	0.300	0	0.160	0
Lampropeltis calligaster	0.320	0.300	0.050	0.040
Lampropeltis triangulum	0.140	0.100	0.010	0.001
Nerodia sipedon	0.240	0.200	0.050	0.040
Pituophis catenifer	0.130	0	0.080	0
Storeria dekayi	15.700	10.000	0.070	0.040
Total	1,322.000	96.000	7.500	1.000
H_0 Shannon-Wiener Diversity Index	0.254	0.892		
H_0 without data for *D. punctatus*	1.551	1.661		

fauna during 1950–91. During the period, the total density of snakes decreased by a factor of 10 and the biomass decreased by a factor of more than 7, but the diversity index in 1991 is nearly 4 times that in the 1950s. The numbers of individuals and biomass are dominated by a single species, the ringneck snake (*Diadophis punctatus* (Linnaeus, 1766)), which doubtlessly has great influence on the diversity index. Even when this species is removed from the analysis, the index still shows slightly greater diversity of the diminished fauna of 1991 than of the abundant fauna of the 1950s. The Shannon-Wiener diversity index measures uncertainty, and in this instance does not provide needed information on the status of natural areas, their wildlife populations, or our success in conserving them.

Discussion

Adequacy of the 1976 Survey

The lists of species that were not recorded in the Four Holes Swamp during the 1976 survey suggests that additional effort and different kinds of surveys would reveal more species. Fifteen of the 62 found species were recorded just once and often by chance occurrences. Once-recorded species may be rare in the swamp and its surroundings, may be of normally low abundance anywhere else in their range, may be wanderers usually found in habitats not represented in the swamp, or may be secretive and seldom encountered despite good abundance. Thirty-nine species were first recorded in March, 19 more species were recorded toward the end of July, and 4 new species were found by the end of October. Two new species were recorded toward the end of the survey during the first 2 weeks of October. Two more weeks of sampling may have revealed more species, and many months of sampling may have revealed even more species.

Sampling in some habitats was inadequate because of a lack of suitable techniques. Better techniques to sample aquatic habitats probably would have resulted in the discovery of more species, for example, of aquatic salamanders. More effective capturing techniques would have revealed more about the distribution and abundance of turtles. Trapping with funnel traps was effective in two habitats, and species not otherwise recorded were captured. More extensive trapping and trapping in more habitats may have revealed the presence of more species.

The beginning of the survey in late March may have precluded recording additional species of amphibians that breed in the winter or in early spring. Species of chorus frogs (*Pseudacris*) and mole salamanders (*Ambystoma*) for example, may have finished breeding by the time the survey began. Nevertheless, the failure to discover tadpoles or larvae suggests these species may not breed in the Four Holes Swamp.

Some unrecorded species are most abundant around ponds or ditches in more or less open upland. Such areas occur near the swamp but sampling in these areas was not comprehensive. Good habitats in temporary pools of the swamp may have formerly existed but may have been disrupted by increased runoff and more violent fluctuations in water levels from upstream deforestation. Their loss may have been accompanied by a reduction or loss of species and may account for the failure to record some of the expected species.

Some of the expected species may not occur in the Four Holes Swamp despite its apparent suitability for them. One of the results of habitat fragmentation is the absence of widespread species from rich faunas, and these holes in expected occurrences may be common in groups like amphibians and reptiles with low vagility (Cutler 1991).

Species Diversity

Species richness, one aspect of diversity, offers information about the diversity of the amphibian and reptilian fauna of the Four Holes Swamp. The discovery of 62 species in an area of less than 1,600 ha in less than one year exceeds the number of species of amphibians and reptiles ever recorded in the state of Colorado. Only 50 species of amphibians and reptiles were recorded in the 1,900 ha Patuxent Wildlife Research Center, Maryland, during more than 50 years. Only 35 species have been recorded on the 239-ha Fitch Natural History Reservation in Kansas in more than 40 years of intensive study. The presence of 95 species of amphibians and reptiles has been confirmed on the nearby Savannah River Site (Gibbons and Semlitsch 1991), but the area is nearly 55 times as large as the Four Holes Swamp, has a great variety of

habitats, and has been intensively studied for 30 years.

The diversity of amphibians, reptiles, and other biota in the Four Holes Swamp is a result of several favorable characteristics. Diverse topography is responsible for the close proximity of xeric uplands, seasonally flooded lowlands, and transition zones along the bluffs. Permanent water in streams and pools provides a variety of conditions that favor species with specialized habitat requirements. Topographic variety and land use created diverse vegetation. Cleared uplands, a pine subclimax, cutover swamp, and a range of successional stages in forest regeneration provide habitat types in different configurations and many zones of transition that provide habitats for various species. The Four Holes Swamp is part of a drainage basin with aquatic and riparian habitats that, although fragmented by development along rivers, provides routes for travel and expansion. Through such corridors, populations of amphibians and reptiles in the Four Holes Swamp may receive immigrants and exchange genetic material with larger populations of the coastal plain. The Four Holes Swamp is large enough to provide ample habitats of several types. Saunders et al. (1991) summarized an extensive body of literature on the effects of fragmentation of ecosystems. Generally, the larger an area of unbroken habitat is, the more species of wildlife can be expected to inhabit it (Whitcomb et al. 1976).

Diversity is also favored by climate. Amphibians and reptiles are more abundant and varied in lower latitudes. The climate of the South Carolina coastal plain is sufficiently mild that some subtropical groups of amphibians and reptiles can occur there, but it is temperate enough that species characteristic of cooler climates occur there also. The temperate genus *Plethodon* and the tropical genus *Anolis*, which overlap in the Four Holes Swamp, have largely exclusive distributions. The mix of species may be much less diverse if the assemblage had fewer typically northern and northeastern species groups. Mature forests, coldwater springs, and topographic breaks moderate the effects of extreme heat, cold, drought, and scouring floods on the biota.

The diversity of protected herpetofauna could be increased by addition of surrounding lands to the Audubon holdings, either by inclusion of a greater portion of the Four Holes Swamp or by acquisition of nearby habitat types not protected by the sanctuary.

Ecological Distribution of Species

The records of some species are particularly complete, and a reasonably good picture of the ecological distribution of these species in the Four Holes Swamp is possible. For example, the long-tailed salamander (*Eurycea longicauda*) was captured in all major habitats except in pine uplands, and the number of recorded individuals may reflect the relative abundance of the species in each kind of habitat. But little was learned about the distribution of the two species of *Farancia*, which were found only on roads at a distance from the permanent water bodies that are the normal habitats of these species. Other species, *Anolis carolinensis* for example, were so common and widespread that only handled individuals were routinely recorded.

The number of species and number of recorded individuals in each of the major habitat types give some indication of the herpetofaunal diversity supported by each (Table 6). Proceeding from most rich in species to least rich, the habitats are pine uplands (35 species), bluffs (28 species), cypress creeks (24 species), oak flats (20 species), and cutover swamp (16 species). The number of recorded individuals follows the same pattern; 422 were recorded in uplands and 316 on bluffs, 61 on the oak flats, and 56 in cutover swamp. By a different breakdown, 47% of the species and 70% of the individuals were recorded on the uplands and bluffs; 32% of the species and 24% of the individuals were obtained from the wet creeks, lakes, and cutover swamps; and only 20% of the species records and 6% of the capture records were obtained from the oak flats. This is unexpected because the oak flats are regarded as the heart of the swamp system, comprise the greatest area, and probably have the greatest plant species diversity. The survey efforts were greater in the oak flats than in any other kind of habitat and far out of proportion to their productivity in records. The data from the surveys suggest that the edges of the swamp, the upland-swamp transition, and the land-water transition along the lakes and larger creeks are most favored by the animals, and the extensive areas of bottomland hardwoods were least favored.

Table 6. Ecological distribution of recorded species in the Four Holes Swamp, South Carolina, 1976.

Species (number of records)	Habitat type				
	Pine uplands	Bluffs	Oak flats	Cypress creeks	Cutover swamp
Amphibia: Calidata					
Ambystoma opacum (17)	8	9			
Desmognathus auriculatus (1)			1		
Eurycea cirrigera (8)		8			
Eurycea longicauda (129)		108	10	9	2
Eurycea quadridigitata (51)		36	11	1	3
Notopthalmus viridescens (2)	1	1			
Plethodon glutinosus complex (74)		67	5	2	
Scaphiopus holbrookii (25)	25				
Siren intermedia (1)				1	
Amphibia: Anura					
Acris gryllus (3)					3
Bufo quercicus (13)	12	1			
Bufo terrestris (236)	226	9		1	
Gastrophryne carolinensis (26)	23		2	1	
Hyla cinerea (11)	3		5	3	
Hyla femoralis (2)		1	1		
Hyla squirella (25)	16	6	3		
Hyla versicolor (8)	6		2		
Pseudacris crucifer (3)	1	2			
Pseudacris nigrita (25)			2		23+
Pseudacris ocularis(3)	1*	2	?		
Pseudacris triseriata (1)	?	1	?		
Rana catesbeiana (11)	1				10+
Rana clamitans (1)				1	
Rana utricularia (17)	13	2	1		1
Reptilia: Testudines					
Chelydra serpentina (3)	3			1	
Clemmys guttata (6)			3	3	
Deirochelys reticularia (1)					1
Kinosternon subrubrum (6)	4			2	
Pseudemys concinna (1)				1	
Pseudemys floridana (4)				3	1
Sternotherus odoratus (4)		1	2	1	
Terrapene carolina (8)	6	2			
Trachemys scripta (11)		2*		8	1
Reptilia: Squamata: Sauria					
Anolis carolinensis (139)	36	24	5	74	
Cnemidophorus sexlineatus (2)	2				
Eumeces fasciatus (7)	3	1		2	1
Eumeces inexpectatus (2)	2				
Eumeces laticeps (16)		5		8	3
Ophisaurus sp. (1)	1				
Sceloporus undulatus (5)	2			2	1
Scincella lateralis (16)		16			
Reptilia: Squamata: Serpentes					
Agkistrodon contortrix (7)	5	2			
Agkistrodon piscivorus (9)			2	7	?
Coluber constrictor (6)	3				3
Crotalus horridus (3)	2	1			
Diadophis punctatus (5)		5			

Table 6. *Continued.*

Species (number of records)	Habitat type				
	Pine uplands	Bluffs	Oak flats	Cypress creeks	Cutover swamp
Elaphe guttata (2)	2	?			
Elaphe obsoleta (25)	3	2	1	18	1
Farancia abacura (1)	1			X#	?
Farancia erytrogramma (2)	2			X#	?
Heterodon platirhinos (2)	2				
Heterodon simus (1)	1				
Lampropeltis getula (3)	1	1			1
Nerodia erythrogaster (2)			2		
Nerodia fasciata (1)			?	1	?
Nerodia taxispilota (51)				51	
Opheodrys aestivus (4)	2	1	1		
Pituophis melanoleucus (1)	1				
Storeria occipitomaculata (3)	2	1			
Thamnophis sauritus (1)		1			
Thamnophis sirtalis (1)	1				
Reptilia: Crocodilia					
Alligator mississippiensis (13)			1	12	
Total number of species	36	28	20	24	16
Total number of records	422	316	61	213	56

* Choruses of breeding frogs were observed in upland pools; turtles were laying eggs.
+ These records were of tadpoles.
# Normal ecological range of these species; recorded individuals were seemingly on overland migrations.

The distribution of species in characteristic southeastern habitats is available from results of surveys for assessments of the Cross-Florida Barge Canal (Campbell and Christman 1982a, 1982b). The numbers of species and individuals of amphibians and reptiles were greater in xeric than in hydric or mesic habitats in a broad range of habitat types. In the Pacific Northwest, Welsh and Lind (1988) found 25 species of amphibians and reptiles that were more diverse and more abundant in old growth forest than in younger stands. Analysis of the effects of logging on salamander populations in the northeast (Petranka et al. 1993) showed significant and long-lasting declines in salamander populations from clear-cutting. These few examples suggest complex relations between habitat types and the number of species of amphibians and reptiles that occupy them.

Prominent Species

Certain organisms may function as keystone species in particular biotic communities (Noss, 1990). Plants that significantly modify the physical environment or animals that have important influences on other biota are regarded as keystones. For example, if baldcypress and tupelo, the two dominant tree species in cypress creeks, were removed, the physical characteristics of these habitats would be changed significantly, probably making them unsuitable for species such as the brown water snake (*Nerodia taxispilota*). Their removal could be seen as precipitating the collapse of the entire biotic community.

The keystone-species idea sometimes led to untenable extremes in which biotic communities are seen as superorganisms that depend on every component to function normally (Solbrig 1991). Conversely, the term is sometimes used in the same way as the older appellation of *indicator species* (Trauger and Hall 1992). Noss (1990) restricts the keystone-species concept, limits the meaning of indicator species to those indicating perturbations, and furthermore recognizes three additional categories of species that attracted special attention

from conservationists. He calls these additional categories *umbrella species, flagships,* and *vulnerable species.*

I designated some species in the Four Holes Swamp as *prominent* species. This terminology may include keystones, indicators, and the other categories but avoids distinctions among them. Species are included because they are (1) particularly abundant in the Four Holes Swamp—for example, the great number of southern toads in the swamp is an important component; (2) represented strongly in all the habitats of the swamp—the green anole is a good example of a frequently encountered species in almost all habitats; (3) characteristic of some of the swamp's unique habitats—the brown water snake is a dominant member of the species in the narrow ecological zone of the cypress creeks; and (4) an influence on the ecology of the area that is not in proportion to their abundance. The American alligator exemplifies species that despite their limited ecological distribution and only moderate abundance may exert strong influences in local biotic communities.

The species abundance in the Four Holes Swamp is relative. Alligators are never as abundant as toads, and a few large rat snakes may have a greater biomass than hundreds of ringneck snakes. None of the species or groups of species fully meets Noss' (1990) categories. The cottonmouth (*Agkistrodon piscivorus*) and the American alligator (*Alligator mississippiensis*) may qualify as flagship species, and local populations of the brown water snake and some amphibians may be vulnerable to deforestation or disruption of water flows, but no species seems to be a true keystone. Nevertheless, these species are important, if not deterministic, influences on the ecological characteristics of the swamp.

Geographic Affinities of Species

Five (8%) of the 62 recorded species in the Four Holes Swamps (Table 7; Fig. 6) occur in suitable habitats across much of the United States. The largest number of species (25 or 40%) are widely distributed in the eastern United States.

Table 7. Prominent species of amphibians and reptiles in the Four Holes Swamp, South Carolina, 1976. Species are included because of (1) absolute abundance, (2) representation in a variety of habitats, (3) dominance in characteristic swamp habitats, or (4) influence on the overall ecology of the swamp.

Species or Group	(1) Abundance	(2) Representation	(3) Characteristic	(4) Influence
Long-tailed salamander (*Eurycea longicauda*)	X	X		
Treefrogs (Genus *Hyla*)	X	X		
Southern toad (*Bufo terrestris*)	X	X		
Basking turtles (*Pseudemys; Trachemys*)	X		X	
Green anole (*Anolis carolinensis*)	X	X		
Skinks (Genus *Eumeces*)		X	X	
Brown water snake (*Nerodia taxispilota*)	X		X	
Rat snake (*Elaphe obsoleta*)	X	X		
Cottonmouth (*Agkistrodon piscivorus*)	X		X	
American alligator (*Alligator mississippiensis*)			X	X

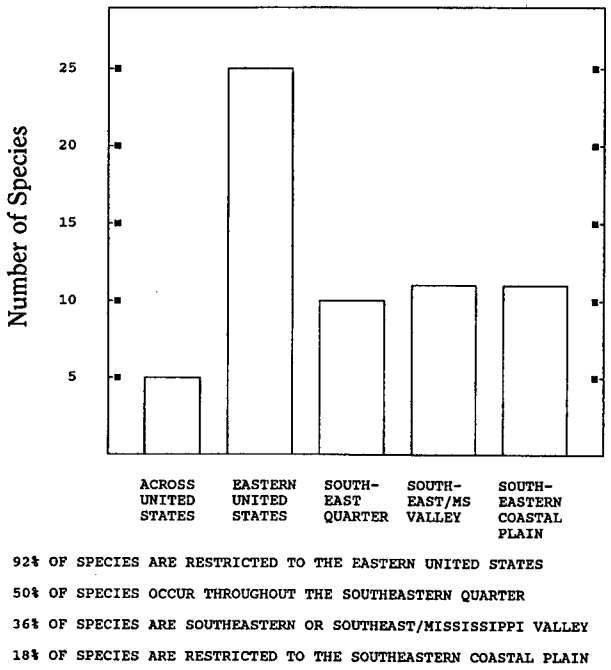

Fig. 6. Geographic affinities of recorded species in 1976. Classification from Table 8, based on published range maps (Conant and Collins 1991; Behler 1979).

The remaining 32 are essentially southern species, but each can be grouped into one of three basic distribution patterns. Ten species (16%) occur across the Southeast in a variety of upland and lowland habitats throughout the region. Eleven species (18%) have distributions that include mesic habitats of the southeastern Atlantic coastal plain and the coastal plain of the Gulf of Mexico and ascend into the midcontinental region in lowlands of the Mississippi River system. The remaining 11 species (18%) are restricted to the coastal plain of the Southeast, including peninsular Florida in most instances. Thus, the amphibians and reptiles of the Four Holes Swamp are primarily (92%) eastern, heavily (50%) southeastern, significantly (36%) restricted to moist southern areas, and somewhat less (18%) characteristic of the southeastern coastal region.

Another indication of the geographic diversity of the species of amphibians and reptiles of the Four Holes Swamp is that 19 (31%) of the 62 recorded species also occur in Canada and 20 (32%) species occur also in Mexico. Accounting for the 5 species that occur in both Canada and Mexico, 34 (55%) of the recorded species are widely enough distributed that they occur in either Canada or Mexico.

The uniqueness of the amphibian and reptilian fauna of the Four Holes Swamp may be questioned. Half its species are very widely distributed, occupying significant portions of North America, and the other half consists of species that are southern but in no sense narrowly distributed. No species is wholly restricted to the Four Holes Swamp or even to the South Carolina coastal plain. Can any kind of uniqueness be claimed by a fauna that consists largely of common and widely distributed species?

The answer is complex. All the prominent species in the Four Holes Swamp occur elsewhere but may be less abundant or successful in most other places. Species vary morphologically, genetically, and ecologically in different parts of their ranges, and local variations in genetics and ecology are important in maintaining the overall fitness of populations. Furthermore, animal populations tend to be formed by environments through the process of adaptation. An amphibian or reptilian inhabitant of the Four Holes Swamp may have the opportunity to interact with at least 60 other species of amphibians and reptiles and with many physical and biotic components of the environment. For example, the common garter snake (*Thamnophis sirtalis*) is abundant and fills many niches as the only snake species in northern Canada (Fitch 1965b), but it seems to be rare and to have a minor role in the ecosystem of the Four Holes Swamp. Its ecologic characteristics probably differ importantly in the two places. Because this argument can be made for one of the least unique species in the fauna, it can also be made for many or most other species.

Conservation of Biological Diversity

There is little agreement on optimal methods of managing natural areas to conserve biological diversity. Part of the problem results from different perspectives. One manages an area far differently if the goal is the maintenance of an endangered-species population (and thus a contribution to global biological diversity) than if the goal is the maintenance of a maximum variety of viable wild populations (thus maximization of local biological

diversity). People may disagree about the best ways to achieve goals, even when they agreed on the general goals, because the consequences of actions cannot be predicted with confidence. Predicting the effects of alternative management on the Four Holes Swamp is difficult. However, some insight may be gained from examining two areas that have been managed differently to maintain or enhance wildlife. The size, age, basic vertebrate diversity, management philosophies, and histories of the two areas differ from those of the Four Holes Swamp. Nevertheless, it is possible within limits to apply to the Four Holes Swamp the outcomes of treatments elsewhere.

The emphasis on amphibian and reptilian faunas in this analysis has consequences that must be recognized, and the choice of these taxa as exemplars of biological diversity offers some advantages and some serious disadvantages. Amphibians and reptiles are resident species that are less mobile than animals of some other groups. Consequently, the presence of populations in an area indicates more about the suitability of that area than, for example, the transient presence of migratory or highly vagile species. Thus, resident species may be good indicators of local biological diversity. But amphibians and reptiles are poikilotherms that may be heliotherms at least seasonally and may rely more than other faunal groups on the penetration of sunlight to the ground. Certain amphibians and reptiles also tend to rely on low vegetation for shelter, concealment, or forage sites. Any conclusion about favorable conditions for amphibian and reptilian diversity is affected by these facts and may produce a bias toward open canopied, structurally diverse communities that are less suitable for a diversity of certain other groups of vertebrates such as neotropical migrant forest birds (Robbins et al. 1989). Some of the ways in which the unique characteristics of amphibians and reptiles affect their biology and relation to the environment are discussed by Pough (1980).

The herpetofaunas at the Patuxent Wildlife Research Center, Maryland, and on the Fitch Natural History Reservation, Kansas, have had long-term protection, and good information is available on their statuses. As in the Four Holes Swamp, at or soon after the establishment of Patuxent and the Fitch Reservation, information was collected on the amphibian and reptilian faunas, and variably good information is available on subsequent trends in populations. No survey has been conducted of the amphibians and reptiles of the Four Holes Swamp since 1976, but predictions of probable outcomes may be possible from findings in the other areas and from composition and known habitat associations of its fauna.

Comparison of the Herpetofaunas of the Four Holes Swamp, Patuxent Research Center, and Fitch Natural History Reservation

Species Common to Two or More of the Areas

Of the 62 recorded species in the Four Holes Swamp, 30 (48%) were recorded at Patuxent and 12 (19%) on the Fitch Reservation. Eleven of the recorded species on the reservation occur at Patuxent. Hence, 33 recorded species (53%) at the Four Holes Swamp also occur in one or both of the other areas. The number of species that occur in all three areas is greater if it includes closely related species in adjacent geographic ranges that, except in a few areas of sympatry, are distinguished primarily on the basis of geography. These include dusky salamanders (*Desmognathus fuscus* and *D. auriculatus*), two-lined salamanders (*Eurycea bislineata* and *E. cirrigera*), leopard frogs (*Rana utricularia* and *R. blairi*), gray treefrogs (*Hyla versicolor* and *H. chrysoscelis*), toads (*Bufo americanus* and *B. terrestris*), bull and pine snakes (*Pituophis catenifer* and *P. melanoleucus*), and watersnakes (*Nerodia sipedon* and *N. fasciata*). Assuming that these pairs of close relatives play essentially similar roles in their respective ecosystems and are ecological equivalents, 34 (55%) species that occur in the Four Holes Swamp also occur or have ecological equivalents at Patuxent, 20 (32%) occur or have ecological equivalents on the Fitch Reservation, and 38 (61%) occur or have ecological equivalents in at least one of these two areas.

Geographic Affinities

Most species that occur in the swamp, at Patuxent, and on the reservation are either widespread across much of temperate North America or widely distributed in the eastern United States. They include 37 (75%) recorded species at Patuxent

and 23 (74%) recorded species on the Fitch Reservation. In contrast, only 31 (50%) of the recorded species at the Four Holes Swamp have such broad distributions. The remaining recorded species at the swamp are restricted to the Southeast. The projected outcomes of different management apply more strongly to species that occur not only in the swamps but at Patuxent or on the reservation than to regional species because little information relates to species that are restricted to the Southeast. Lack of information on this important component may result in unexpected effects of environmental change.

Differences in the Faunas

Some differences in the faunas of the three areas can be attributed to known factors (Zug 1993). Amphibians are richer in the East than in the Midwest. They comprise 47% of the recorded herpetofauna of Patuxent, only 26% of that of the Fitch Reservation, and 39% of that of the Four Holes Swamp. Reptiles are richer in the South than in the North; the 38 recorded species at the Four Holes Swamp exceed the 26 recorded species at Patuxent and the 23 resident species on the Fitch Reservation. Topographic diversity is also an important contributor to the richness of animal species, and the number of species on the Fitch Reservation would be greater if it had the variety of wetland habitats present on the other areas and less without the constructed pond.

The effect of topographic diversity on species richness is reflected in the percentage of the recorded species in an area of the total number of species the geographic range of which includes the area. Whereas the recorded species at Patuxent are 84% of all species with geographic ranges that include Patuxent, the recorded species at the Four Holes Swamp are only 69% and on the Fitch Reservation only 54% of the species with geographic ranges that include these areas.

Predicted Effects of Management on the Four Holes Swamp

The persistence of 61% of the herpetofauna of the Four Holes Swamp may be projected from an analysis of the persistence of the same species at the Patuxent Wildlife Research Center and on the Fitch Reservation during the past 40–50 years. The projected persistence of the amphibian and reptilian species at the swamp that do not occur at either of the other two locations may be projected from an analysis of records of the ecological distribution of these species in the survey in 1976. Altogether, projecting the persistence of 43 species in the Four Holes Swamp under alternative management should be possible with the available information (Table 8).

If managers of the Four Holes Swamp maintain the existing openings in the largely forested preserve and continue present uses of surrounding uplands, results such as those at Patuxent may be expected. The single lost species at Patuxent, *Cnemidophorus sexlineatus*, occurs in a few areas of bare earth in the Four Holes Swamp and may be lost there also. The abundances of *Terrapene carolina*, *Ambystoma opacum*, *Scaphiopus holbrookii*, *Coluber constrictor*, and *Lampropeltis getula* may be expected to decline, but these species will probably not become rare. The expected overall declines in biological diversity may be slight.

If policies were effective in protecting the Four Holes Swamp, including the surrounding uplands, to the same degree that the Fitch Reservation has been protected, one may expect the loss of 5 species that are shared with or are close relatives of those lost from the Fitch Reservation. An additional 10 species may be expected to decline to relatively small populations as on the Fitch Reservation. If only these species were affected, loss of diversity would be limited to loss of 8% of the resident species and to a reduction of distribution and abundance of an additional 16%. Given what is known of habitat requirements by some other species (Table 9), however, conservative estimates indicate that six more species would be lost or seriously reduced for an overall effect on populations of 39% of the recorded species. As many as 53% of the species may be affected if all species recorded as having significant use of pine uplands or cutover swamp were diminished in some way. Openings in the forest canopy of the Four Holes Swamp from treefall during Hurricane Hugo and openings in the forest canopy over several large lakes may mitigate or at least delay the total loss of some species, but losses over the long term are expected nevertheless.

Whether management of the herpetofauna following that at Patuxent or that on the Fitch

Table 8. Geographic ranges of recorded species in the Four Holes Swamp, South Carolina, 1976. Ranges of different species differ in many details and were classified based on general distributional patterns.

Species	Geographic range
Amphibia: Caudata	
Ambystoma opacum	Eastern U.S., except peninsular Florida
Desmognathus auriculatus	Southeast coastal plain, except south Florida
Eurycea longicauda	Eastern U.S., except peninsular Florida
Eurycea quadridigitata	Southeast/Mississippi Valley
Eurycea cirrigera	Southeast except peninsular Florida
Notopthalmus viridescens	Eastern U.S.
Plethodon glutinosus complex	Eastern U.S., except south Florida
Siren intermedia	Southeast/Mississippi Valley
Amphibia: Anura	
Acris gryllus	Southeastern U.S.
Bufo quercicus	Southeast coastal plain
Bufo terrestris	Southeast coastal plain
Gastrophryne carolinensis	Southeastern U.S.
Hyla cinerea	Southeast/Mississippi Valley
Hyla femoralis	Southeast coastal plain
Hyla squirella	Southeast coastal plain
Hyla versicolor	Eastern U.S., except south Florida
Pseudacris crucifer	Eastern U.S., except south Florida
Pseudacris nigrita	Southeast coastal plain
Pseudacris ocularis	Southeast coastal plain
Pseudacris triseriata	Eastern and central U.S.
Rana catesbeiana	Eastern U.S.
Rana clamitans	Eastern U.S.
Rana utricularia	Southeastern U.S.
Scaphiopus holbrookii	Eastern U.S.
Reptilia: Testudines	
Chelydra serpentina	Eastern U.S.
Clemmys guttata	Eastern U.S. (northeast and coastal plain)
Deirochelys reticularia	Southeast/Mississippi Valley
Kinosternon subrubrum	Southeast/Mississippi Valley
Pseudemys concinna	Southeast/Mississippi Valley, except south Florida
Pseudemys floridana	Southeast/Mississippi Valley
Sternotherus odoratus	Eastern U.S.
Terrapene carolina	Eastern U.S.
Trachemys scripta	Eastern U.S., except peninsular Florida
Reptilia: Squamata: Sauria	
Anolis carolinensis	Southeastern U.S.
Cnemidophorus sexlineatus	Eastern and central U.S.
Eumeces fasciatus	Eastern U.S., except peninsular Florida
Eumeces inexpectatus	Southeastern U.S.
Eumeces laticeps	Southeastern U.S., except south Florida
Ophisaurus sp.	Eastern and central U.S.
Sceloporus undulatus	Southeastern and southcentral U.S.
Scincella lateralis	Southeastern U.S.
Reptilia: Squamata: Serpentes	
Agkistrodon contortrix	Eastern U.S., except peninsular Florida
Agkistrodon piscivorus	Southeast/Mississippi Valley
Coluber constrictor	Across North America
Crotalus horridus	Eastern U.S., except peninsular Florida
Diadophis punctatus	Across North America

Table 8. *Continued.*

Species	Geographic range
Elaphe guttata	Southeastern U.S.
Elaphe obsoleta	Eastern U.S.
Farancia abacura	Southeast/Mississippi Valley
Farancia erytrogramma	Southeast coastal plain, except south Florida
Heterodon platirhinos	Eastern U.S.
Heterodon simus	Southeast coastal plain
Lampropeltis getula	Across southern North America
Nerodia erythrogaster	Eastern U.S., except south Florida
Nerodia fasciata	Southeast/Mississippi Valley
Nerodia taxispilota	Southeast coastal plain
Opheodrys aestivus	Southeastern U.S.
Pituophis melanoleucus	Across North America (as species complex)
Storeria occipitomaculata	Eastern U.S., except South Florida
Thamnophis sauritus	Eastern U.S.
Thamnophis sirtalis	Across North America
Reptilia: Crocodilia	
Alligator mississippiensis	Southeast/Mississippi Valley

Table 9. Possible effects on herpetofauna occupying the Four Holes Swamp; based on observations in other natural areas and habitat information. Blank spaces indicate that no prediction was possible.

Species	Observed change at Patuxent	Observed change at Fitch Reservation	Predicted from habitat requirements
Amphibia: Caudata			
Ambystoma opacum	decline		
Desmognathus auriculatus	no change[a]		
Eurycea cirrigera	no change		
Eurycea longicauda	unknown		
Notopthalmus viridescens	no change		decline
Amphibia: Anura			
Acris gryllus	no change[a]	no change[a]	
Bufo terrestris	no change[a]	no change[a]	
Gastrophryne carolinensis		decline[a]	
Hyla cinerea		unknown	
Hyla versicolor	no change	no change[a]	
Pseudacris ocularis			decline
Pseudacris crucifer	no change		
Pseudacris triseriata	decline	decline	
Rana catesbeiana	no change	no change	
Rana clamitans	no change		
Rana utricularia	no change	no change[a]	
Scaphiopus holbrookii	decline	decline[a]	
Reptilia: Testudinata			
Chelydra serpentina	no change	no change	
Clemmys guttata	no change		
Kinosternon subrubrum	unknown		
Sternotherus odoratus	no change		
Reptilia: Squamata: Sauria			
Cnemidophorus sexlineatus	decline	decline	decline
Eumeces fasciatus	unknown	decline	

Table 9. *Continued.*

Species	Observed change at Patuxent	Observed change at Fitch Reservation	Predicted from habitat requirements
Eumeces inexpectatus			decline
Ophisaurus sp.		decline	
Sceloporus undulatus	unknown		
Scincella lateralis	no change	decline	
Reptilia: Squamata: Serpentes			
Agkistrodon contortrix		decline	
Coluber constricotr	decline	decline	
Crotalus horridus		decline	
Diadophis punctatus	no change	decline	
Elaphe guttata		decline	
Elaphe obsoleta	no change	decline	
Heterodon platirhinos	unknown		
Lampropeltis getula	decline		
Nerodia fasciata	no change[a]	no change[a]	
Opheodrys aestivus	unknown		
Pituophis melanoleucus		decline[a]	
Storeria occipitomaculata	unknown		
Thamnophis sauritus	no change		
Thamnophis sirtalis	no change	decline	
Reptilia: Crocodilia			
Alligator mississippiensis			decline

[a] Information based on a closely related species.

Reservation is employed, some loss of biological diversity seems inevitable (Table 8). To maintain or enhance the diversity of lower vertebrates in the Four Holes Swamp may require innovative management. Attention should also be devoted to the possible effects of increased runoff, water control regimes, and influences on groundwater supplies from the destruction or degradation of the vernal pools and springs in the swamp that may be required for reproduction by some species.

Conservation of Herpetofaunal Diversity in the Four Holes Swamp

Biological diversity exists on local, regional, and national or global levels and is sometimes referred to as α, ß, and δ diversity (Hunter 1990; Trauger and Hall 1992). For example, results of this analysis may lead to the conclusion that managers of the Four Holes Swamp should create more disturbed uplands because amphibians and reptiles are more abundant in them. But this study only revealed that the edges of the swamp are richer in amphibians and reptiles than the center. A more reasonable conclusion may be that in focusing on a portion of a landscape that included a swamp, the study revealed the value of the swamp as a component of the larger landscape. In the terminology of Pimm and Gittleman (1992), all parts of the swamp system can be regarded as contributing to ß-diversity, diversity across space, although its parts differ in α-diversity, the absolute diversity in each.

The goal of a natural area such as the Francis Beidler Forest in the Four Holes Swamp should be the preservation of biological diversity on as many levels as possible and the minimization of conflicts. Finally, as Hurricane Hugo illustrated, absolute stability in ecological systems is not as natural as many may suppose. Storms, floods, drought, and—particularly on the uplands—fires are common sources of disturbance that operate in the absence of human intervention (Rotenberry et al. 1993). Most ecosystems are dynamic, and most are resilient to moderate levels of disturbance. Continuing

to protect and manage the area so that the unique and relatively undisturbed habitats are preserved is a safe course that protects regional biological diversity and produces benefits on the local and national levels.

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