Amphibians and Reptiles of Longleaf Pine Communities

Craig Guyer
Department of Zoology and Wildlife Science, Auburn University

Mark A. Bailey
Alabama Natural Heritage Program

ABSTRACT

The herpetofauna associated with longleaf pine forests is unusually diverse and includes two general groups that use this habitat during some portion of their life history: 1) species whose distributional limits are not associated with longleaf (residents) and 2) species whose limits are included within or closely associated with that of longleaf pine (specialists). This fauna comprises a total of 34 amphibian and 38 reptilian species, about one third of which are specialists.

Because amphibians and reptiles are secretive and difficult to observe, their importance is often underappreciated. Ecologically, these organisms perform a wide variety of roles, including serving as regulators of prey population density, food sources for a variety of predators, seed dispersal agents for some understory plants, and creators of nesting and hiding sites. Biogeographically, the specialists form a cohesive unit that shares an historical association with desert regions of the southwest U.S. and Mexico.

The current literature on amphibians and reptiles of longleaf pine habitats is dominated by anecdotal notes; few long-term studies have been performed. If these organisms are to be preserved into the future, much effort will be required to document regional, seasonal, and yearly variation in population biology. Relatively few amphibian and reptilian species are federally listed as threatened or endangered. However, about 35% of the species inhabiting longleaf pine forests (56% of the specialists) are listed by at least one conservation agency as being of special concern. Foremost among reasons for the decline of these populations are habitat loss and fragmentation. Other important threats include fire suppression, introduced predators, alteration of breeding sites, and certain site preparation practices on managed timber lands. Management practices needed to maintain amphibians and reptiles in longleaf pine forests include prescribed burning (to encourage appropriate understory plants, vegetation structure, and associated arthropods), maintenance of fallen trees and logs (used as nesting and hiding sites), and conservation of drainage patterns at amphibian breeding sites.

INTRODUCTION

In this paper we examine the diversity and natural history of amphibians and reptiles that occupy longleaf pine forests of the southeastern Coastal Plain, highlighting their ecological importance and conservation needs. Our objectives are to: 1) characterize the herpetofauna associated with longleaf pine forests, 2) make general comparisons between this fauna and those of other pine forests found at similar latitudes, 3) describe the diverse ecological roles played by amphibians and reptiles in the longleaf pine community, 4) discuss the evolutionary origins of these organisms, and 5) indicate conservation concerns for amphibians and reptiles of longleaf pine forests as well as recommending management strategies for maintaining this portion of the fauna.

Amphibians and reptiles are tetrapods (vertebrates possessing land limbs as part of their evolutionary history) that are traditionally placed in separate classes. For many people, these are vile creatures to be avoided, if not eliminated. Thus, any consideration of amphibians and reptiles confronts a serious image problem perpetuated by folklore. An additional part of this image problem is the fact that, because amphibians and reptiles are principally ectothermic, biologists tend to group them with fishes as "lower" vertebrates. One im-

Proceedings of the Tall Timbers Fire Ecology Conference, No. 18, The Longleaf Pine Ecosystem: ecology, restoration and management, edited by Sharon M. Hermann, Tall Timbers Research Station, Tallahassee, FL, 1993

plication of this classification scheme is that many biologists consider these creatures to be shackled with ectothermy. However, recent energetic considerations document that a distinctive benefit of ectothermy, relative to endothermy, is efficient conversion of food energy to biomass, either by producing more offspring or growing to a larger body size (mass and/or length). For this reason, amphibians and reptiles tend to predominate in terrestrial vertebrate communities, both in population density and in biomass (Pough 1983). Additionally, amphibians and reptiles require less total food intake (e.g. some snakes may require as few as 6 meals per year [Greene 1986]) and, therefore, are more likely than endotherms to survive periods of poor food production.

The fact that amphibians and reptiles often reach fantastic densities has important ecological implications. For example, density and diversity of frog prey are correlated with the diversity of vertebrate predators (Arnold 1972, Greene 1988). Additionally, as predators, amphibians and reptiles may regulate the abundance of insects and other prey (Pacala and Roughgarden 1984, Schoener and Spiller 1987). This predatory action may, in turn, alter the species assemblage within a habitat (Morin 1981, Fauth and Resetarits 1991). Thus, amphibians and reptiles are important regulators within natural communities (Chew 1974) and are worthy of special consideration.

SPECIES RICHNESS

Longleaf pine-grassland (often wiregrass) vegetation once dominated large parts of the southeastern United States (Simberloff, this volume), ranging generally along the Coastal Plain from South Carolina, south and then west through parts of Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas. The region delimited by the distribution of longleaf pine encompasses all or part of the geographic distributions of 73 species of amphibians and 95 species of reptiles (taxa listed in Appendix I; distributional data from Conant and Collins 1991). Thus, many herpetofaunal species are distributed within the range of longleaf pine, each potentially having had part of its evolutionary history associated with this type of forest. These species have disparate degrees of overlap with the habitat (Fig. 1), but most overlap relatively little. However, there is an apparent non-random group of species whose patterns of distribution exhibit a high degree of overlap with longleaf pine and which, therefore, appear to specialize on this habitat (Fig. 1). Because the initial list included many species that are not known to use longleaf pine, even though their geographical distributions overlap, we generated a second list of species known or expected (from field guide accounts and other sources) to maintain viable populations in

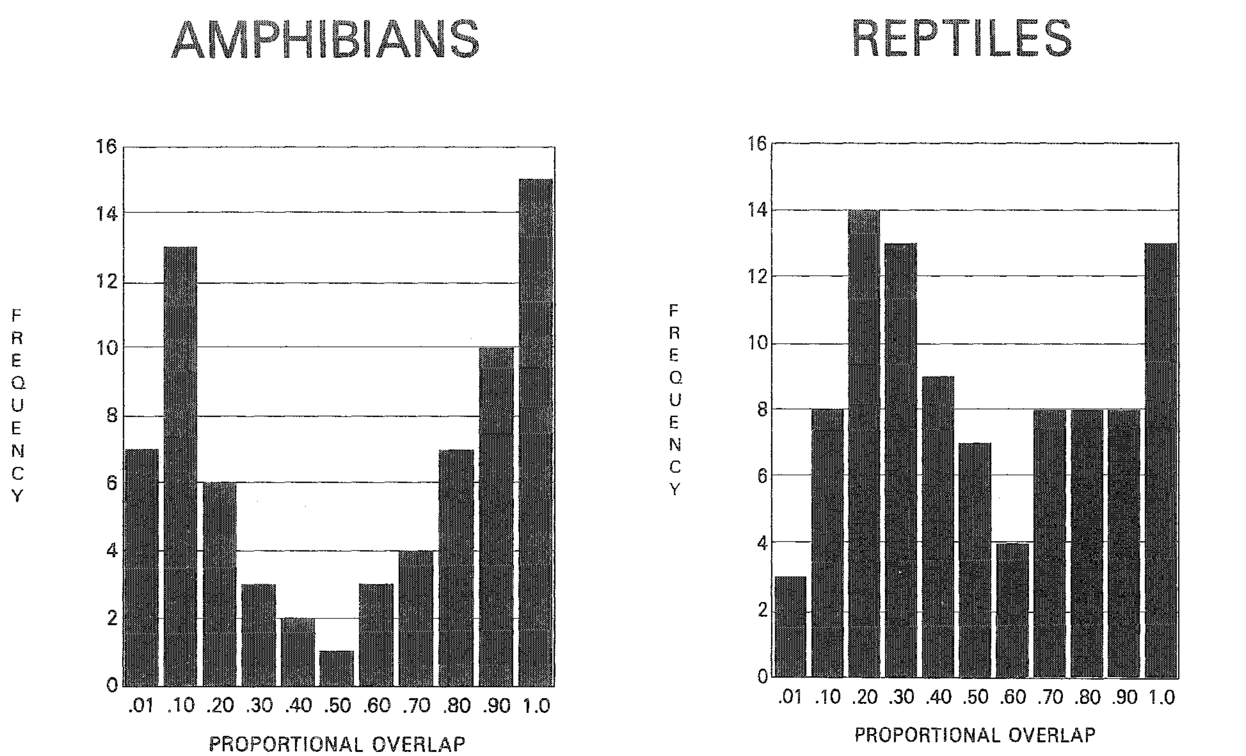

Figure 1. Frequency distribution of categories of proportional overlap between amphibians and reptiles and longleaf pine. Data are from an unrestricted list (see text) and are given in appendix I.

longleaf pine forests. One might expect that the frequency distribution of these species would be biased towards longleaf specialists (those terrestrial forms with a high proportion of their distribution within the geographic boundaries of longleaf pine). The distribution of overlap of species from this more restricted list (Fig. 2; Appendix I) and longleaf pine is indistinguishable from the more inclusive list (Fig. 1). This is because some groups (e.g. river turtles like *Pseudemys* and *Graptemys*) are restricted within the geographic range of longleaf pine and, yet, do not maintain populations within the forest type; other groups, (e.g. *Coluber* and *Ambystoma*) inhabit many forest types besides longleaf pine. Thus, many species that maintain viable populations in longleaf pine habitats apparently have their distributional limits set by some other factor than the presence of longleaf pine itself. Those species, therefore, are distributed independently of longleaf pine. Campbell and Christman (1982) reached a similar conclusion while characterizing the herpetofauna of Florida sandhills. A second group of species occupies longleaf pine forests and has distributional limits that are closely associated with longleaf pine. Because those species are distributed in a fashion that is dependent on longleaf pine, we categorized them as specialists of this forest type. An 80% overlap of the distributional range of a species with longleaf pine was used as an arbitrary cutoff for classifying specialists. Note, however, that our definition does not imply that specialists are found only in longleaf pine forest.

We found three other pine forest associations that are located at approximately the same latitude as longleaf pine and for which amphibian and reptilian species lists could be generated. These are pinyon pine-juniper of the southwestern United States (distribution from Lanner 1981; herpetofauna from Stebbins 1985), pine-oak woodlands of Mexico (distribution and herpetofauna from McCranie and Wilson 1987), and *Pinus halapensis* forest of the Mediterranean (distribution from Mirov 1967; herpetofauna from Arnold and Burton 1978). Each of these covers approximately the same area as longleaf pine. Herpetofaunal diversity of these forests is about half that found in longleaf pine forests (Table 1). This difference in diversity results from increased numbers of frogs, salamanders, and turtles in longleaf pine forests; lizards and snakes have approximately equal numbers of species among the four forests. A similar pattern is maintained when the taxa are restricted to species suspected of maintaining viable popu-

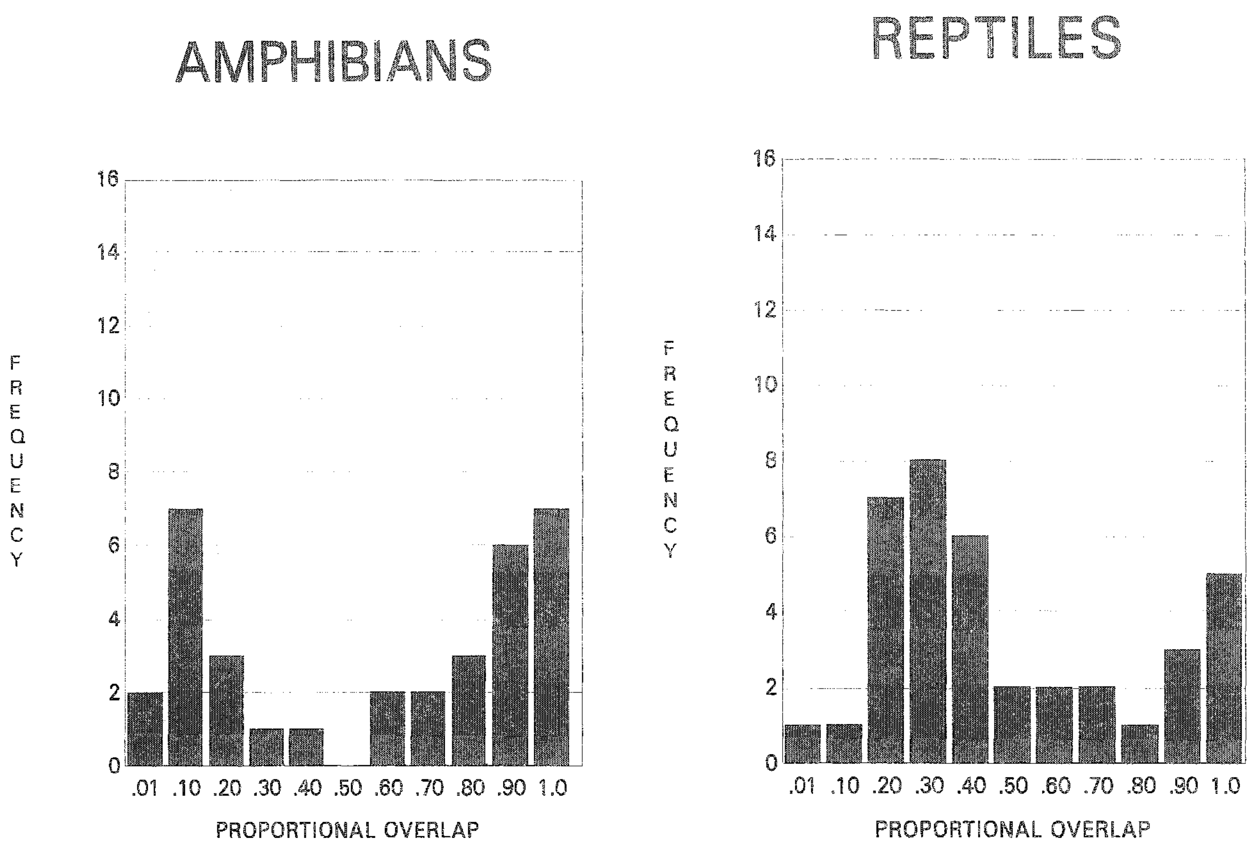

Figure 2. Frequency distribution of categories of proportional overlap between amphibians and reptiles and longleaf pine. Data are from a restricted list (see text) and are given in appendix I.

lations in each forest type (Table 2; described as non-peripheral taxa by McCranie and Wilson 1987) and to specialist taxa of each forest type (Table 3). In the latter case, the increased species richness found in longleaf pine relative to other forests is associated with increased diversity of frogs and salamanders but not turtles, lizards, or snakes. Taken together, the above analyses suggest that the herpetofauna associated with longleaf pine forests is unusually diverse. Additionally, this fauna is characterized by a greater degree of specialization than in other pine forests.

Table 1. Distribution of amphibian and reptilian species among four forests. Unrestricted list.

	Longleaf Pine	European Pine	Pinyon Pine	Mexican Pine-Oak
Anura	35	16	14	17
Caudata	38	12	1	3
Testudines	30	5	1	3
Squamata	64	52	51	63
Crocodilia	1	0	0	0
Total	168	85	67	86

Table 2. Distribution of amphibian and reptilian species among four forests. Restricted list.

	Longleaf Pine	European Pine	Pinyon Pine	Mexican Pine-Oak
Anura	26	3	4	10
Caudata	8	3	1	1
Testudines	3	3	0	0
Squamata	35	38	30	31
Total	72	47	35	42

Table 3. Distribution of amphibian and reptilian species among four forests. Specialists list.

	Longleaf Pine	European Pine	Pinyon Pine	Mexican Pine-Oak
Anura	8	--	0	2
Caudata	2	--	0	1
Testudines	1	--	0	0
Squamata	7	--	0	5
Total	18	--	0	8

ECOLOGICAL GUILDS

The diversity of the herpetofauna of longleaf pine forest is further expressed in the variety of ecological roles performed by these vertebrates. We recognized four major foraging guilds of vertebrates occupying longleaf pine forest; these are folivore/herbivore, detritivore/filter feeder, invertebrate predator, and vertebrate predator. Because most amphibians have aquatic larvae, this stage was considered separately from adults. Four major habitat guilds were also recognized: arboreal, terrestrial, fossorial, and aquatic.

Most amphibians and reptiles of longleaf pine are predators of arthropods or vertebrates. However, the other major foraging guilds are exhibited by one or more members of the herpetofaunal assemblage (Table 4).

Additionally, amphibians and reptiles inhabiting longleaf pine occur in all of the major habitat guilds (Table 4). While many forms are found on the soil surface or leaf litter, an unusual number of species are fossorial or semifossorial, taking advantage of the relatively sandy soils preferred by longleaf pine. The latter group includes species that spend the majority of their lives underground (e.g. *Scaphiopus* and *Rhineura*) as well as those that burrow for shorter periods but still have anatomical features useful for burrowing (e.g. *Bufo* and *Heterodon*).

Table 4. Distribution of longleaf amphibians and reptiles in foraging and habitat guilds.

Foraging Guild	Amphibians		Reptiles
	Larvae	Adults	
Folivore/Frugivore	0	0	3
Detritivore/Filter	26	0	0
Invertebrate Predator	2	34	15
Vertebrate Predator	6	0	20

Habitat Guild	Amphibians		Reptiles
	Larvae	Adults	
Arboreal	0	7	5
Surface	1	12	21
Fossorial	0	13	11
Aquatic	33	2	1

Only two genera of reptiles occupying longleaf pine habitats consume terrestrial vegetation (*Gopherus* and *Terrapene*), but these two are known to eat fruit and seeds of understory herbs and shrubs and may be important dispersal agents for these plants (Kaczor and Hartnett 1990). Thus, they may impact current and future structure, although this has not been studied in detail. Additionally, the gopher tortoise creates a lengthy burrow that serves as hiding, nesting, and overwintering sites for a variety of obligate and facultative associates (Jackson and Milstrey 1989). Because of its wide-ranging impact on the longleaf environment, the gopher tortoise is considered to be a keystone species within the community.

BIOGEOGRAPHY

The southeastern Coastal Plain is a geologically young landscape, raising the question of where the diverse and specialized herpetofauna of longleaf pine habitats originated. Two general approaches have been used to infer historical origins of faunas. One approach is to examine the distribution of congeners in an effort to identify the center of origin for a genus (or other higher taxonomic group; Pielou 1979). Typically, the center of diversity is assumed to be the center of origin with outlying taxa being derived from this center. A second approach is to examine the phylogenetic relationships of monophyletic lineages from an area of interest to determine whether or not taxa from this area share a consistent pattern of sister-taxon relationships with another area or areas (Platnick and Nelson 1978). If well-corroborated phylogenies are available, the second method is preferable because it represents a search for general pattern rather than a series of ad hoc, independent hypotheses (Humphries and Parenti 1986).

Phylogenetic relationships have been analyzed for only a few taxa of amphibians and reptiles of longleaf pine habitats. Despite this dearth of information, we examined the biogeography of the longleaf herpetofauna by searching for three types of information. Where possible, phylogenies were collected for groups found within this forest type. If such data were not available, then narrative statements were collected that hypothesized the closest living relative of forms found in longleaf pine. Finally, if the previous two bits of information were lacking, centers of diversity of genera with species thought to be longleaf pine specialists were examined and assumed to be the origin of forms currently found in longleaf pine forests. These data demonstrate a consistent pattern of relationships between taxa found in longleaf pine and those found in arid regions of the southwestern United States and Mexico (Table 5). This pattern can be interpreted as indicating a fragmentation of a once-widespread biota or the presence of a dispersal route used by several taxa (Savage 1982) traveling between the southeastern Coastal Plain and southwestern desert habitats. The former explanation conforms to Rosen's (1978) hypothesis of a Cannonball seaway separating eastern and western portions of North America; the latter conforms to a hypothesis of concordant dispersal across this barrier during the Pleistocene (Martin and Harrell 1957). The biogeographic pattern observed for amphibian and reptilian taxa that are longleaf pine

Table 5. Biogeographic affinities of amphibians and reptiles specializing on longleaf pine forests.

Taxon	Area of Closest Living Relative	Method of Inference	Source
Notophthalmus perstriatus	S. Texas and N. Mexico	Phylogenetics	Reilly 1990
Ambystoma cingulatum	Ozarks	Phylogenetics	Shaffer et al. 1991
Rana capito	SW desert and N. Mexico	Phylogenetics	Hillis and Davis 1986
Gopherus polyphemus	Chihuahua desert Mexico	Phylogenetics	Lamb et al. 1989
Rhadinaea flavilata	Mexico	Evol. System.	Myers 1974
Crotalus adamanteus	SW desert	Evol. System.	Klauber 1972

specialists differs from that exhibited by incidentals (those species that overlap the range of longleaf pine but do not live in pine forests) or residents (Table 6). This finding indicates that patterns other than the one observed for specialist taxa are possible and that the pattern observed for specialists does not result merely from the fact that the longleaf biota had to come from some source unit and the southwestern desert biota was the only possible source. This comparative information indicates that the assemblage of amphibians and reptiles most strongly associated with longleaf pine forests is a cohesive evolutionary unit in that its members share a common biogeographic history.

CONSERVATION

The amphibians and reptiles occupying longleaf pine habitats are integral parts of a functioning forest; their maintenance should be part of management and conservation efforts. Ideally, such efforts should be based on well-documented information about population ecology. At a minimum, this information should include data regarding yearly and geographic variation in demography (births and deaths). However, such data are rare for any vertebrate species, let alone a group of animals from the same forest type.

To characterize the literature available on amphibians and reptiles of longleaf pine forests, we surveyed papers published from 1978 to 1991. We examined studies that provided information on the following topics that we believe are important for conservation purposes: diet, movement, reproduction, habitat, competition, predators, diseases and parasites, life history, morphology, and management. Papers were classified as being notes if they dealt with anecdotal information or major papers if they dealt with substantial data. Major papers were further subdivided into those that indicated yearly and/or regional variation versus those that provided no such information.

Not surprisingly, the literature on the natural history of the herpetofauna of longleaf pine forests consists predominantly of anecdotal information (Tables 7 and 8). Among the topics that we surveyed, most information was in the form of new diet items, new predators, or unusual reproduction (e.g. record clutch size). Major studies with no regional or yearly variation consisted principally of papers documenting seasonal patterns of reproduction (timing of courtship and/or clutch deposition). Most of the major studies examined patterns of survival and reproduction that we classified as life history.

Taxonomically, the literature is dominated by studies of *Hyla* and *Ambystoma*, among amphibians, and *Gopherus*, *Eumeces*, and *Anolis*, among reptiles (Table 8). The emphasis on these five genera stems from two sources. First, the information on *Gopherus* can be traced largely to the efforts of the Gopher Tortoise Council to increase knowledge of the status and ecology of this keystone species. Second, efforts of herpetologists at the Savannah River Ecology Lab (SREL) are responsible for the proliferation of papers regarding the other

Table 6. Biogeographic affinities of selected non-specialist inhabitants of longleaf pine forests.

Taxon	Area of Closest Living Relative	Method of Inference	Source
Scaphiopus holbrooki	SW desert	Phylogenetics	Sattler 1980
Anolis carolinensis	Cuba	Evol. System.	Williams 1969
Sceloporus undulatus	SW desert	Evol. System.	Larsen and Tanner, 1975
Sistrurus miliarius	Great Plains	Evol. System.	Klauber, 1972
Micrurus fulvius	Costa Rica	Phylogenetics	Slowinski pers. comm.
Agkistrodon contortrix	S.E. U.S./Mexico	Evol. System.	VanDevender and Conant, 1990
Terrapene carolina	Veracruz, Mexico	Phylogenetics	Rosen, 1978

Table 7. Distribution of recent (1978 to 1991) published data (by topic) on amphibians and reptiles of longleaf pine forests.

TOPIC	NOTES		MAJOR PAPERS	
	AMPHIBIANS	REPTILES	AMPHIBIANS	REPTILES
Predation	1	37	3	2
Food	3	9	3	3
Movement	3	1	5	2
Reproduction	2	22	10	13
Habitat	2	0	1	2
Competition	0	0	9	2
Disease/Parasites	0	6	2	4
Management	1	0	0	2
Life History	2	5	15	19
Morphology	2	5	7	0

Table 8. Distribution of recent (1978 to1991) published data (by genus) on amphibians and reptiles of longleaf pine forests.

AMPHIBIANS			REPTILES		
Taxon	Notes	Major Papers	Taxon	Notes	Major Papers
Ambystoma	6	28	Gopherus	7	9
Hyla	4	10	Anolis	7	8
Others (9 genera)	6	17	Eumeces	5	12
			Others (19 genera)	56	20

well-studied genera. This indicates the importance of sites where long-term monitoring and ecological research are appreciated and encouraged. The establishment of similar field stations will allow documentation of how patterns described at the SREL change from site to site within the southeastern Coastal Plain.

The major problem faced in conservation of the herpetofauna of longleaf pine forests, as well as the rest of the fauna and flora of this habitat, was succinctly argued by Means and Grow (1985); this habitat was the primary building site for past agricultural and urban development. Therefore, longleaf pine was severely impacted long before any conservation lobby could be effected. Current examples of old-growth longleaf pine are restricted to private holdings, each of a few hundred acres, located principally in southern Georgia. Because most of this forest type has been lost and the remaining forest is severely dissected, lists of species of special concern have burgeoned (Noss 1988). Additionally, conservation and management strategies for these species often have been implemented from scant data that may not reflect forest processes likely to have been experienced in the evolutionary history of native amphibians and reptiles (Means and Grow 1985). This observation establishes the value of conserving and studying the few remaining old-growth reserves because these areas are our last hope for recovering the natural history of organisms in this forest type.

A cursory examination of the conservation status of longleaf amphibians and reptiles indicates that an alarming percentage of the specialist fauna is imperiled. We gathered data regarding the current status of the herpetofauna by examining Natural Heritage Program species tracking lists for the states of Alabama, Florida, Georgia, Louisiana, Mississippi, South Carolina, North Carolina, and Texas. In examining these lists, we defined a species as being of conservation concern if it was listed as being rare (having at least an S3 Heritage rank or C2 of the federal regime). Of the species maintaining viable populations in longleaf pine forests, 6 of 34 (18%) amphibian and 18 of 38 (47%) reptilian species were listed by one or more state heritage programs as being of conservation concern (Appendix I). For specialist taxa, 3 of 10 (30%) amphibian and 7 of 8 (88%) reptilian species were listed by at least one heritage program as being of conservation concern. The majority of these species were listed in nearly all states within the historical range of these taxa, indicating that they were considered threatened throughout their range and not just in some portion of the range. The observation that over half of the specialist taxa are rare enough to be listed by state heritage programs reflects the severe loss of their ancestral habitat (Means and Grow 1985, Noss 1988). This pattern of forest specialists being more severely affected than widespread "weedy" taxa is consistent with effects of fragmentation observed at a variety of sites (Simberloff, this volume).

It is obvious that the major factors impacting the native amphibian and reptilian fauna are loss and fragmentation of habitat (Means and Grow 1985, Noss 1988, Simberloff, this volume). Within this reduced and fragmented environment some other general areas of conservation concern have been documented. One is the impact of new predators and/or increased population densities of native predators due to the loss of top predators (e.g. *Felis concolor*). Carr (1982) noted a dramatic increase in nest predation for amphibians and reptiles due to increased activity of armadillos (*Dasypus novemcinctus*), a predator that has expanded its range to include the southeastern Coastal Plain. Increased predation by raccoons (*Procyon lotor*; Landers et al. 1980) may also result from loss of top predators (Simberloff, this volume). Additionally, feral pets and farm animals are known to impact amphibians and reptiles of the Coastal Plain, again principally by consuming eggs and young (Causey and Cude 1978, Dobie 1986). Introduced fire ants have been hypothesized by Mount (1981) as impacting a variety of vertebrates, especially those that nest on or near the ground.

In addition to these predatory sources, humans can have direct or indirect impacts on mortality of longleaf amphibians and reptiles. Because adult tortoises have few natural predators and have unusually long life spans (Landers et al., 1982), predation by humans on large adults may have an especially rapid deleterious effect on the population dynamics of this keystone species. A suspected indirect effect of humans is mortality resulting from vehicle traffic (Landers and Buckner 1981). This effect may increase on small fragmented sites if animals attempt to migrate in search of better sites. In the case of gopher tortoises, these mortality sources may be exacerbated by the transfer of disease to isolated populations (Dodd and Seigel 1991). A final source of human-induced mortality for amphibians and reptiles of longleaf pine is the continued organization of rattlesnake roundups in some areas, most notably, Opp, Alabama and Whigham, Georgia. This activity remains an important source of mortality for the herpetofauna near these sites because gasoline continues to be used to drive rattlesnakes from the burrows (Williams 1990) and because of the demonstrable deleterious effect of this practice on burrow commensals (Speake and Mount 1973).

A second general factor of conservation concern for amphibians and reptiles in longleaf pine forests is the effect of certain forest management practices. The invasion of hardwood tree species and the resulting development of a closed canopy when fire is suppressed has obvious deleterious effects on the native longleaf herpetofauna, especially the specialist forms that trace their evolutionary history to arid, open environments. The reintroduction of fire as a management tool in longleaf pine forests is known to result in little direct mortality to the herpetofauna. In fact, of 38 amphibian and reptilian species studied by Means and Campbell (1981), only the eastern glass lizard (*Ophisaurus ventralis*) appeared to incur significant direct mortality from fire. Instead, fire is known to create a structural response in vegetation that is advantageous to longleaf amphibians and reptiles (Means and Campbell 1981, Campbell and Christman 1982). Forestry practices designed to produce single-species, even-aged, dense stands of timber (often replacing the native longleaf pine) are implicated in declining species diversity, especially of specialist forms (Means and Grow 1985, Noss 1988). However, data regarding these effects are scant and management interpretations often equivocal. For example, Lohoefener and Lohmeier (1981) recommended against windrows based on their restriction of movements in gopher tortoises. Landers and Speake (1980) reported that windrows were beneficial as foraging and cover sites for indigo snakes. In general, mechanical site preparation would appear to destroy and/or remove appropriate food, cover, and nest sites, so great care and planning must accompany its use if deleterious effects on amphibians and reptiles are to be minimized.

MANAGEMENT

The fact that amphibians and reptiles that specialize on longleaf pine forests cannot be maintained elsewhere (because of their restricted distributions) indicates an urgent need for studies documenting the ecological requirements of the longleaf herpetofauna so that the remaining habitat can be managed properly. Examination of the published literature indicates that management information is likely to come not from publications, but rather from the collective expertise of herpetologists with lengthy experience in this region.

As indicated in our introduction, the ability of ectothermic vertebrates to convert food energy into biomass permits dense populations of amphibians and reptiles in their native habitats. The implication for land managers is that many amphibians and reptiles should be relatively easy to manage, given that they need relatively low levels of food intake for maintenance. For many human-impacted sites, amphibians and reptiles have great potential for recovery as long as appropriate feeding and reproductive sites are maintained. Because many of these animals do not need to wander far for food resources, viable populations should be sustainable on the small fragments of longleaf pine that remain.

A number of general management practices should be considered for enhancing longleaf pine habitats for the herpetofauna. As indicated above, one is prescribed fire. Fire timing and frequency should be applied in a fashion that mimics natural fire occurrences (Mushinsky 1985). Summer fires are preferred over winter ones because they produce appropriate food (Cox et al. 1987) and cover (Means and Campbell 1981), especially for gopher tortoises. Fire frequency is known to vary considerably among habitats (Auffenberg and Franz 1982), making the development of specific guidelines difficult. For winter burned sites, Landers and Speake (1980) recommended fire every 2-4 years based on data regarding gopher tortoises and indigo snakes (*Drymarchon corais*). Periods as long as 7-10 years have been recommended for summer burns (Cox et al. 1987). Some flexibility is desirable in administering fire because natural fire regimes were inherently variable in nature (Myers 1990). Maintenance of patches with varying time since last burn may be important for providing appropriate habitat for the assemblage of amphibians and reptiles inhabiting longleaf pine forest because not all species prefer the same habitat conditions (Campbell and Christman 1982).

A second general management consideration is the physical diversity of the ground cover. Retention of downed trees, stumps, and snags as part of the habitat is highly desirable, based on a consideration of the natural history of amphibians and reptiles. These sites are known to serve as cover and/or nest sites (e.g. *Plethodon glutinosus*, *Eumeces inexpectatus*, and *Cemophora coccinea*, Mount [1975]; *Drymarchon corais*, Smith [1987]). Additionally, downed trees create appropriate regeneration sites for understory vegetation (Hermann, this volume), thereby improving the habitat for the herpetofauna.

A third management consideration is the conservation of temporary wetlands, especially sinkhole ponds and seasonally flooded flatwoods depressions. These areas are vital reproductive sites for most of the amphibian species in longleaf pine forests (Bailey 1990, Dodd and Charest 1988). Because amphibian species richness decreases in the presence of predatory fishes (Wilbur 1984), care must be taken to ensure that these areas remain fish-free. Additionally, because species richness is positively correlated with hydroperiod in these temporary sites (Pechmann et al. 1989), care must be taken to insure that drainage patterns are not altered at these sites. Draining caused by ditching has known deleterious effects on the species richness and abundance of metamorphosing juvenile amphibians (Pechmann et al. 1989). Additionally, siltation is suspected to affect some amphibians (Nickerson and Mays 1973). Therefore, plowed fire lanes or road beds may impact these sites, often for great distances. In places where temporary wetlands have been severely impacted or eliminated, the creation of artificial pond sites may be a viable management consideration (Pechmann et al. 1989).

A final management consideration is the effect of mechanical and chemical site preparation. As mentioned above, data regarding the impact of such techniques on amphibians and reptiles can be equivocal. However, mechanical techniques collapse gopher tortoise burrows (Tanner and Terry 1981; but see Diemer and Moler 1982) and alter understory vegetation, especially wiregrass (Outcalt and Lewis 1990). Because many of the specialized longleaf herpetofauna are affected directly or indirectly by the presence of native ground cover (Means and Grow 1985), mechanical site preparation in natural longleaf stands should be minimized. Bryan (1991) found no deleterious effects on the population structure or activity of gopher tortoises in the DeSoto National Forest, Mississippi, when efforts were made to minimize the effects of mechanical site preparation around each tortoise burrow. Virtually nothing is known of the effects of chemical site preparation on amphibians and reptiles (Cox et al. 1987), although some herbicides have known deleterious effects on tadpoles (Dial and Dial 1987). This indicates that chemicals should be avoided, especially near amphibian reproduction sites.

If appropriate components of longleaf habitats (e.g. downed logs, natural temporary wetland sites), are maintained, tremendous production of offspring can occur. For example, Pechmann et al. (1989) documented the production of over 75,000 juvenile amphibians in a single year at a one hectare pond in South Carolina. These are the organisms that provide food for other amphibian and reptilian specialists in longleaf pine forests (Moler and Franz 1988) and should allow rapid replacement of populations impacted by previous management activities.

ACKNOWLEDGMENTS

We thank J. Larry Landers for inviting us to participate in the symposium and Sharon M. Hermann for her attention to editorial details. George W. Folkerts and Paul E. Moler are thanked for suggestions that improved the manuscript, especially relative to the accuracy of information in the appendix. Any errors that remain, however, are our own.

APPENDIX I

List of amphibians and reptiles overlapping the range of longleaf pine. Overlap data represent the proportion of a species distributional range that overlaps the distribution of longleaf pine. Habitat use categories indicate species that were considered to be residents (R) or specialists (S) of longleaf pine forests (see text for definitions). Conservation status indicates states where species are listed as being of conservation concern (see text for explanation). Guilds represent foraging (invertebrate [I], vertebrate [V], filter/detritivore [D], or plant [P]) and habitat uses (arboreal [A], surface [S], aquatic [W], or fossorial [F]). Categorizations for the two major types of guilds are separated by a dash. For amphibians, categorizations of adults and larvae are listed in sequence.

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
Amphibia				
Ambystomatidae				
Ambystoma cingulatum	1.00	RS	AL,FL,GA,MS,SC	IV-FW
A. mabeei	1.00	R		IV-FW
A. maculatum	<.01			
A. opacum	.10			
A. talpoideum	.70	R	TX	IV-FW
A. texanum	.20			
A. tigrinum	.20	R	AL,FL,LA,MS,NC,SC	IV-FW
Amphiumidae				
Amphiuma means	.90			
A. pholeter	1.00			
A. tridactylum	.40			
Plethodontidae				
Desmognathus aeneus	.50			
D. apalachicolae	1.00			
D. auriculatus	.90			
D. fuscus	.20			
D. monticola	.10			
Eurycea cirrigera	.70			
E. longicauda	.30			
E. quadridigitata	1.00	R	NC	II-SW
Gyrinophilus porphyriticus	.10			
Haideotriton wallacei	1.00			
Hemidactylium scutatum	<.01			
Phaeognathus hubrichti	1.00			
Plethodon cinereus	.20			
P. glutinosus "complex"	.30	R		II-SS
P. serratus	<.01			
P. websteri	1.00			
Pseudotriton montanus	.60			
P. ruber	.10			

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
Stereochilus marginatus	1.00			
Proteidae				
Necturus alabamensis	.90			
N. beyeri	.80			
N. lewisi	.90			
N. punctatus	1.00			
Salamandridae				
Notophthalmus perstriatus	1.00	RS	FL,GA	IV-WW
N. viridescens	.10	R		IV-WW
Sirenidae				
Pseudobranchus striatus	.80			
Siren intermedia	.30			
S. lacertina	.80			
Anura				
Bufonidae				
Bufo americanus	<.01	R		ID-FW
B. quercicus	.90	RS		ID-FW
B. terrestris	.90	R		ID-FW
B. valliceps	.20	R		ID-FW
B. woodhousii	.10	R		ID-FW
Hylidae				
Acris crepitans	.10	R		ID-SW
Acris gryllus	.80	R		ID-SW
Hyla andersonii	.70	R		ID-AW
Hyla avivoca	.70			
H. chrysoscelis/versicolor	.20	R		ID-AW
H. cinerea	.80	R		ID-AW
H. femoralis	.90	R		ID-AW
H. gratiosa	.90	RS		ID-AW
H. squirella	.90	RS		ID-AW
Pseudacris brachyphona	.10	R		ID-SW
P. brimleyi	1.00	RS		ID-SW
P. crucifer	.10	R		ID-AW
P. nigrita	.80	RS		ID-SW
P. ocularis	.90	RS		ID-SW
P. ornata	1.00	RS		ID-FW
P. triseriata	<.01	R		ID-SW
Microhylidae				
Gastrophryne carolinensis	.60	R		ID-SW

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
G. olivacea	.10	R		ID-SW
Ranidae				
Rana areolata	.10	R		ID-FW
R. capito	1.00	RS	AL,FL,GA,LA,MS,NC	ID-FW
R. catesbeiana	.10			
R. clamitans	<.01			
R. grylio	.90			
R. heckscheri	1.00			
R. okaloosae	1.00			
R. palustris	.10			
R. utricularia	.60	R		ID-SW
R. sylvatica	<.01			
R. virgatipes	.80			
Pelobatidae				
Scaphiopus holbrooki	.40	R		ID-FW
Crocodilia				
Alligatoridae				
Alligator mississippiensis	.70			
Sauria				
Amphisbaenidae				
Rhineura floridana	1.00			
Anguidae				
Ophisaurus attenuatus	.40	R	GA	I-S
O. compressus	.90			
O. mimicus	1.00	RS	GA,NC	I-S
O. ventralis	.80			
Phrynosomatidae				
Sceloporus undulatus	.20	R		I-A
S. woodi	1.00			
Polychridae				
Anolis carolinensis	.50	R		I-A
Scincidae				
Eumeces anthracinus	.10			
E. egregius	.90	RS	GA	I-F
E. fasciatus	.30	R		I-S
E. inexpectatus	.60	R		I-S
E. laticeps	.40	R		I-A
Neoseps reynoldsi	1.00			
Scincella lateralis	.40	R		I-S

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
Teiidae				
Cnemidophorus sexlineatus	.30	R		I-S
Serpentes				
Colubridae				
Carphophis amoenus	.20	R		I-F
Cemophora coccinea	.40	R	TX	V-F
Coluber constrictor	.20	R	MS,LA	V-S
Diadophis punctatus	.20			
Drymarchon corais	.80	R	AL,FL,GA,MS	V-S
Elaphe guttata	.30	R		V-A
E. obsoleta	.20	R		V-A
Farancia abacura	.70			
F. erytrogramma	.90			
Heterodon platyrhinos	.30	R		V-F
H. simus	1.00	RS	GA,MS	V-F
Lampropeltis calligaster	.30	R	FL,LA,MS	V-F
L. getula	.20	R	FL,MS	V-S
L. triangulum	.20	R	GA,SC	V-S
Masticophis flagellum	.20	R		V-S
Nerodia clarkii	.80			
N. cyclopion	.50			
N. erythrogaster	.40			
N. fasciata	.60			
N. floridana	.80			
N. rhombifer	.30			
N. sipedon	.10			
N. taxispilota	.90			
Opheodrys aestivus	.30			
Pituophis melanoleucus	.10	R	AL,FL,GA,LA,MS,NC	V-F
Regina alleni	.70			
R. grahami	.20			
R. rigida	.80			
R. septemvittata	.20			
Rhadinaea flavilata	1.00	RS	GA,LA,MS	V-S
Seminatrix pygaea	.90			
Stilosoma extenuatum	1.00	RS	FL	V-F
Storeria dekayi	.20			
S. occipitomaculata	.20			
Tantilla coronata	.40	R		I-F

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
T. gracilis	.10			
T. relicta	1.00	RS		I-S
Thamnophis proximus	<.01			
T. sauritus	.30			
T. sirtalis	.10			
Virginia striatula	.60	R		I-S
V. valeriae	.30	R		I-S
Elapidae				
Micrurus fulvius	.70	R	GA,LA,NC,SC	V-F
Viperidae				
Agkistrodon contortrix	.30	R		V-S
A. piscivorus	.70	R		V-W
Crotalus adamanteus	.90	RS	LA,NC,SC	V-S
C. horridus	.30	R		V-S
Sistrurus miliarius	.50	R	NC	V-S
Testudines				
Chelydridae				
Chelydra serpentina	.20			
Macroclemys temminckii	.40			
Emydidae				
Chrysemys picta	.20			
Clemmys guttata	.30			
Deirochelys reticularia	.80			
Graptemys barbouri	1.00			
G. flavimaculata	1.00			
G. kohnii	.50			
G. nigrinoda	1.00			
G. oculifera	.70			
G. pseudogeographica	<.01			
G. pulchra	.70			
Malaclemys terrapin	.50			
Pseudemys alabamensis	1.00			
P. concinna	.50			
P. floridana	.90			
P. nelsoni	.70			
P. rubriventris	.10			
Terrapene carolina	.40	R		P(+I)-S
T. ornata	<.01	R	LA	P-S
Trachemys scripta	.40			

Taxon	Overlap	Habitat Use	Conservation Status	Guilds
Kinosternidae				
Kinsternon baurii	.80			
K. subrubrum	.50			
Sternotherus carinatus	1.00			
S. minor	.60			
S. odoratus	.30			
Testudinidae				
Gopherus polyphemus	.90	RS	AL,FL,GA,LA,MS,SC	P-F
Trionychidae				
Apalone ferox	.80			
A. mutica	.10			
A. spinifera	.10			

LITERATURE CITED

Arnold, E.N., and J.A. Burton. 1978. A field guide to the reptiles and amphibians of Britain and Europe. William Collins and Sons, London.

Arnold, S.J. 1972. Species densities of predators and their prey. American Naturalist 106:220-236.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). Pages 95-126 in North American tortoises: conservation and ecology. Wildlife Research Report 12. U.S. Fish and Wildlife Service, Washington, D.C.

Bailey, M.A. 1990. Movements of the dusky gopher frog (*Rana areolata sevosa*) at a temporary pond in the lower Coastal Plain of Alabama. Pages 27-43 in C.K. Dodd, R.E. Ashton, R. Franz, and E. Wester, eds. Proceedings of the 8th Annual Meeting of the Gopher Tortoise Council. Florida Museum of Natural History, Gainesville.

Bryan, T.W. 1991. Effects of Black Creek Seed Orchard establishment on a population of gopher tortoises (*Gopherus polyphemus* Daudin) in southeastern Mississippi. Masters thesis, Auburn University, Auburn, Alabama.

Campbell, H.W., and S.P. Christman. 1982. The herpetological components of Florida sandhill and sand pine scrub associations. Pages 163-171 in N.J. Scott, ed. Herpetological communities. U.S.D.I. Wildlife Research Report 13.

Carr, A.F. 1982. Armadillo dilemma. Animal Kingdom 85:40-43.

Causey, M.K., and C.A. Cude. 1978. Feral dog predation of the gopher tortoise, *Gopherus polyphemus*, in southeast Alabama. Herpetological Review 9:94-95.

Chew, R.M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio Journal of Science 74:359-370.

Conant, R., and J.T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin, Boston.

Cox, J., D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on land slated for large-scale development in Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report no. 4. Tallahassee, Florida.

Dial, N.A., and C.A. Dial. 1987. Lethal effects of diquat and paraquat on developing frog embryos and 15-day-old tadpoles, *Rana pipiens*. Bulletin of Environmental Contamination and Toxicology 38:1006-1011.

Diemer, J.E., and P.E. Moler. 1982. Gopher tortoise response to site preparation in northern Florida. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 36:634-637.

Dobie, J.L. 1986. Alabama red-bellied turtle. Pages 38-39 in R.H. Mount ed. Vertebrate animals in need of special attention. Alabama Agricultural Experiment Station, Auburn Univ.

Dodd, C.K. and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336-350.

Dodd, C.K., and B.G. Charest. 1988. The herpetofaunal community of temporary ponds in North Florida Sandhills: species composition, temporal use, and management implications. Pages 87-97 in R.C. Szaro, K.E. Severson, and D.R. Patton, eds. Management of amphibians, reptiles, and small mammals in North America. U.S.D.A. Forest Service General Technical Report, RM-166.

Fauth, J.E., and W.J. Resetarits. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. Ecology 72:827-838.

Greene, H.W. 1986. Natural history and evolutionary biology. Pages 99-108 in M.E. Feder and G.V. Lauder, eds. Predator-prey relationships: perspectives and approaches from the study of lower vertebrates. University of Chicago Press.

Greene, H.W. 1988. Species richness in tropical predators. Pages 259-280 in F. Alameda and C.M. Pringle, eds. Tropical rainforests: diversity and conservation. California Academy of Science, San Francisco.

Hillis, D.M., and S.K. Davis. 1986. Evolution of ribosomal DNA: fifty million years of recorded history in the frog genus *Rana*. Evolution 40:1275-1288.

Humphries, C.J., and L.R. Parenti. 1986. Cladistic biogeography. Oxford Monographs on Biogeography no. 2.

Jackson, D.R., and E.G. Milstrey. 1989. The fauna of gopher tortoise burrows. Pages 86-98 in J.E. Diemer, D.R. Jackson, J.L. Landers, J.N. Layne, and D.A. Wood, eds. Gopher Tortoise relocation symposium proceedings. Nongame Wildlife Program Technical Report #5, Florida Game and Fresh Water Fish Commission, Tallahassee.

Kaczor, S.A. and D.C. Hartnett. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. Am. Midl. Nat. 123:100-111.

Klauber, L.M. 1972. Rattlesnakes. University of California Press, Berkeley.

Lamb, T., J.C. Avise, and J.W. Gibbons. 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizi*), and evolutionary relationships among the North American gopher tortoises. Evolution 43:76-87.

Landers, J.L., and J.L. Buckner. 1981. The gopher tortoise: effects of forest management and critical aspects of its ecology. Southlands Experimental Forest Technical Note, No. 56:1-7.

Landers, J.L., and D.W. Speake. 1980. Management needs of sandhill reptiles in southern Georgia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 34:515-529.

Landers, J.L., W.A. McRae, and J.A. Garner. 1980. Reproduction of gopher tortoise (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica 36:353-361.

Landers, J.L., W.A. McRae, and J.A. Garner. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. Bulletin of the Florida State Museum Biological Sciences 27:81-110.

Lanner, R.M. 1981. The Pinon pine: a natural and cultural history. University of Nevada Press, Reno.

Larsen, K.R., and W.W. Tanner. 1975. Evolution of the sceloporine lizards (Iguanidae). Great Basin Naturalist 35:1-20.

Lohoefener, R., and L. Lohmeier. 1981. Comparison of gopher tortoise (*Gopherus polyphemus*) habitats in young slash pine and old longleaf pine areas of southern Mississippi. Journal of Herpetology 15:239-242.

Martin, P.S., and B.E. Harrell. 1957. The Pleistocene history of temperate biotas in Mexico and eastern North America. Ecology 38:468-480.

McCranie, J.R., and L.D. Wilson. 1987. The biogeography of the Pine-Oak woodlands of the Sierra Madre Occidental of Mexico. Milwaukee Public Museum Contributions in Biology and Geology 72:1-30.

Means, D.B., and H.W. Campbell. 1981. Effects of prescribed burning on amphibians and reptiles. Pages 89-96 in G.W. Wood, ed. Prescribed fire and wildlife in southern forests. Belle W. Baruch Forest Science Institute of Clemson University, Georgetown, South Carolina.

Means, D.B., and G. Grow. 1985. The endangered longleaf pine community. ENFO Report 85:1-12.

Mirov, N.T. 1967. The genus *Pinus*. Ronald Press, New York.

Moler, P.E., and R. Franz. 1988. Wildlife values of small, isolated wetlands in the southeastern coastal plain. Pages 234-241 in R.R. Odum, K.A. Riddleberger, and J.C. Ozier, eds. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department of Natural Resources, Athens, Georgia.

Morin, P.J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212:1691.

Mount, R.H. 1975. The reptiles and amphibians of Alabama. Alabama Agricultural Experiment Station, Auburn, Alabama.

Mount, R.H. 1981. The red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), as a possible serious predator on some native southeastern vertebrates: direct observations and subjective impressions. Journal of the Alabama Academy of Science 52:71-78.

Mushinsky, H.R. 1985. Fire and the Florida sandhills herpetofaunal community: with special reference to responses of *Cnemidophorus sexlineatus*. Herpetologica 41:333-342.

Myers, C. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bulletin of the American Museum of Natural History 153:1-262.

Myers, R.L. 1990. Scrub and high pine. Pages 150-193 in R.P. Myers and J.J. Ewel, eds. Ecosystems of Florida. University of Central Florida Press, Orlando.

Nickerson, M.A., and C.E. Mays. 1973. The hellbenders. Milwaukee Public Museum Publications in Biology and Geology no. 1:1-106.

Noss, R.F. 1988. The longleaf pine landscape of the southeast: almost gone and almost forgotten. Endangered Species Update 5:1-6.

Outcalt, K.W., and C.E. Lewis. 1990. Response of wiregrass (*Aristida stricta*) to mechanical site preparation. Pages 1-12 in L.C. Duever and R.F. Noss eds. Wiregrass biology and management: maintaining ground cover integrity in longleaf pine ecosystems. Proc. of the Symposium, Oct. 5, 1988 (Valdosta, GA). KBN Engineering and Applied Science. Gainesville, FL.

Pacala, S., and J. Roughgarden. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). Oecologia 64:160-162.

Pechmann, J.H.K., D.E. Scott, J.W. Gibbons, and R.D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3-11.

Pielou, E.C. 1979. Biogeography. Wiley and Sons, Toronto.

Platnick, N.I., and G. Nelson. 1978. A method of analysis for historical biogeography. Systematic Zoology 27:1-16.

Pough, F.H. 1983. Amphibians and reptiles as low-energy systems. Pages 141-188 in W.P. Aspey and S.I. Lustick, eds. Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus.

Reilly, S.M. 1990. Biochemical systematics and evolution of the eastern North American newts, genus *Notophthalmus* (Caudata: Salamandridae). Herpetologica 46:51-59.

Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. Systematic Zoology 27:159-188.

Sattler, P.W. 1980. Genetic relationships among selected species of North American Scaphiopus. Copeia 1980: 605-610.

Savage, J.M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? Annals of the Missouri Botanical Gardens 69:464-547.

Schoener, T.W., and D.A. Spiller. 1987. Effects of lizards on spider populations: manipulative reconstruction of a natural experiment. Science 236:949-952.

Shaffer, B.H., J.M. Clark, and F. Kraus. 1991. When molecules and morphology clash: a phylogenetic analysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). Syst. Zool. 40:284-303.

Smith, C.R. 1987. Ecology of juvenile and gravid eastern Indigo snakes in North Florida. MS thesis, Auburn University, AL.

Speake, D.W., and R.H. Mount. 1973. Some possible ecological effects of "rattlesnake roundups". Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 27:267-277.

Stebbins, R.C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston.

Tanner, G., and W. Terry. 1981. Effect of roller chopping and web plowing on gopher tortoise burrows in southern Florida. Page 66-72 in R. Lohoefener, L. Lohmeier, and G. Johnston, eds. The future of gopher tortoise habitats. Proceedings of the 2nd Annual Meeting of the Gopher Tortoise Council.

Van Devender, T.R., and R. Conant. 1990. Pleistocene forests and copperheads in the eastern United States, and the historical biogeography of New World *Agkistrodon*. Pages 601-614 in H.K. Gloyd and R. Conant, eds. Snakes of the *Agkistrodon* complex. Contributions to Herpetology, no. 6, Society for the Study of Amphibians and Reptiles.

Wilbur, H.M. 1984. Complex life cycles and community organization in amphibians. Pages 195-225 in P.W. Price, C.N. Slobodchikoff, and W.S. Gaud, eds. A new ecology: novel approaches to interactive systems. Wiley and Sons, New York.

Williams, E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quarterly Review of Biology 44:345-389.

Williams, T. 1990. Driving out the dread serpent. Audubon 26-32.