The Herpetological Components of Florida Sandhill and Sand Pine Scrub Associations

by

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Abstract

Investigations of the herpetofauna of the peninsular Florida sandhills and sand pine scrub revealed a diverse complex composed of a minority of xeric-adapted species combined with an array of wide-ranging and aquatic species that can be found in many Florida habitats. The xeric-adapted species required sand for burrowing or sand-swimming. The tortoise (*Gopherus*) digs burrows that serve as shelter for several other species; the wide-ranging generalist species, however, require none of the specialized conditions of the sandhills and scrub. Sand scrub, especially early successional stages, contains 22 species of reptiles and amphibians, which is more than in any other of a wide range of peninsular Florida habitats. Apparently the herpetofauna is responding to the dry, well-drained soil and patches of sand free from roots rather than to any aspect of the vegetation. The sand-swimming species (*Eumeces egregius*, *Tantilla relicta*, and *Neoseps reynoldsi*) depend on periodic disturbance (e.g., fire and clear-cutting) to remove the matted understory and pine canopy. The widespread distribution of these forms attests to the continuous presence, throughout history, of a mix of successional stages in both the sandhills and sand pine scrub.

The sandhill and scrub pine plant associations are characteristic and well defined elements of the Florida environment. Although vegetatively distinct, they are closely related physically and geographically (Fig. 1) and have very similar herpetofaunas. Autecological studies of sandhill and scrub species are available (Telford 1959; Jackson 1972; Smith, this volume), but, in contrast to extensive literature on the vegetation, previous research has not dealt with the community of animals living in these plant associations. The sandhills and sand pine scrubs, along with xeric hammocks, form the principal habitats in Florida for a distinctive herpetofauna based on xeric-adapted forms.

We initiated studies (Florida Fish and Game Commission 1976) in these habitats in the spring of 1975 using the methods detailed elsewhere (Campbell and Christman, this volume). In 1976 we substantially increased our efforts in the various subtypes of sandhill and scrub in the Ocala National Forest in central Florida to determine the distribution and relative abundance of amphibian and reptile species in the various successional stages of sandhills and scrub.

Characterization of the Habitats

Sandhill Association

The sandhill association and its successional relations to other Florida plant associations have received considerable attention over the years (Laessle 1958), and there is general agreement on the physical and phytogeographic characteristics of the sandhills. References to the reptiles and amphibians occurring in the sandhills generally use the designators "High Pine" (Carr 1940) or "Longleaf-pine/Turkey-oak" (Laessle 1942). Similar habitats, differing only slightly in

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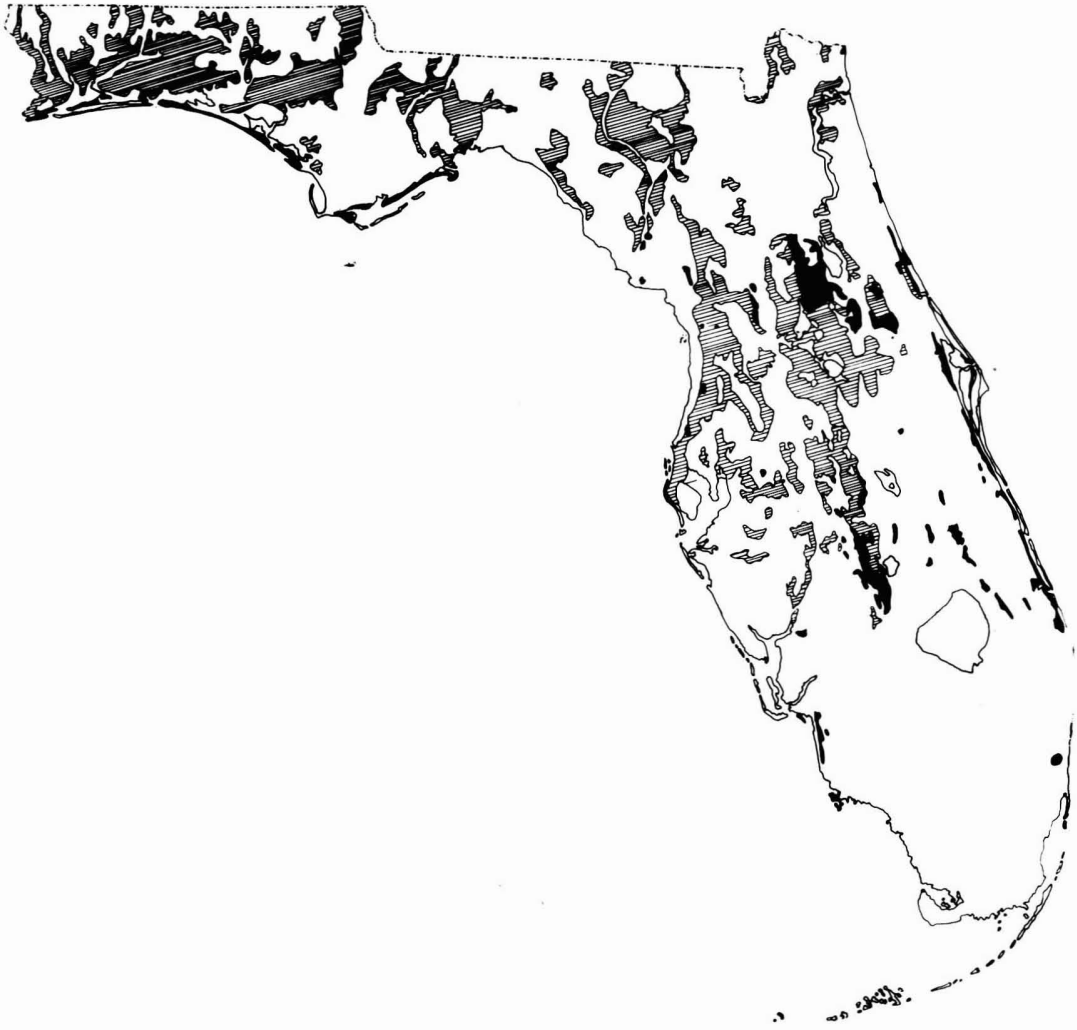

Fig. 1. Distribution of sandhills (hatched) and sand pine scrub (black) in Florida (Davis 1967).

their plant species, are found in scattered areas having suitable soils throughout the southern United States (Laessle 1958; Bozeman 1971), but the sandhills of the Florida peninsula support a herpetological community that is distinct from the sandhills of the Florida panhandle and other areas of the southeast. The following analysis will deal specifically with the peninsular sandhills.

Most sandhills in peninsular Florida occur on well-drained, sandy soils of the Lakeland series as defined by Gammon et al. (1953) and Laessle (1958). The physical characteristics of these soils and their similarity to the soils supporting sand pine scrub and xeric hammock, as well as the relative frequency of fire in these associations, are considered to be the factors determining which animals use these habitats. Sandhills are generally restricted to soils of slightly higher clay and silt content than those supporting the scrub association (Laessle 1958).

The sandhill association exists in two basic forms in peninsular Florida: the "typical" longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) association, and the turkey oak sandhills. The typical phase is a three-tiered habitat with widely-spaced longleaf pines forming the upper level, an understory of scattered turkey oak (bluejack oak, *Q. incana*, may replace turkey oak on lower soils of the Blanton series), and a

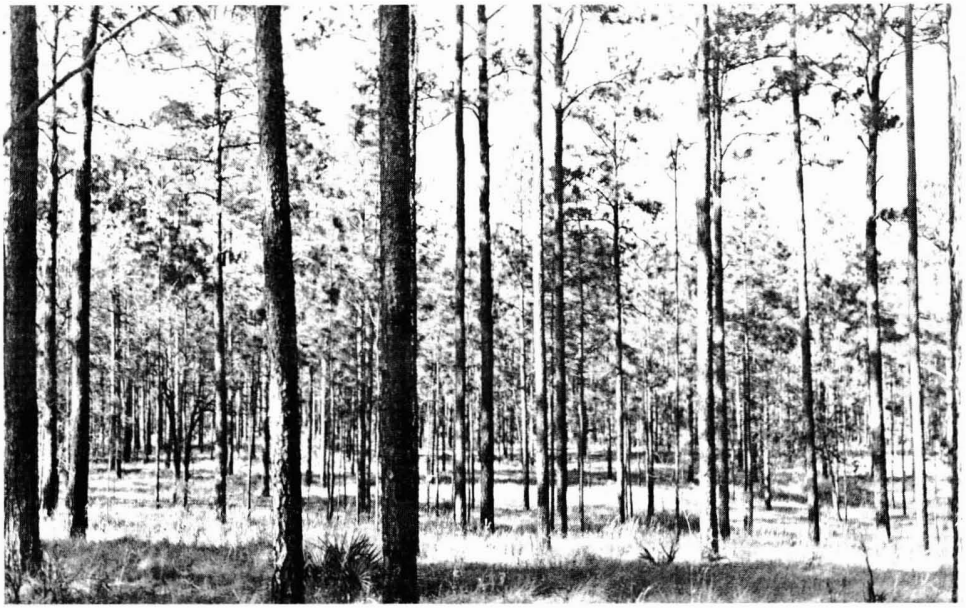

Fig. 2. Typical phase of the longleaf pine–turkey oak sandhill habitat in the Ocala National Forest, Florida.

ground cover dominated by wire grass (*Aristida stricta* and *Sporobolus gracilis*, Fig. 2). Fire is frequent in this habitat, perhaps the most widespread of the fire subclimax associations in Florida. The dominant plant species are fire resistant.

Where the longleaf pines are removed, the turkey oak increases in height, forming the canopy layer at 8–10 m, and the ground cover becomes less dense with frequent and extensive areas of bare sand interspersed with drifted piles of oak leaves and scattered vegetation (Fig. 3). Fire is also a frequent phenomenon in the turkey oak sandhill and often results in extensive areas of open sand and occasional damage to the oaks.

The turkey oak sandhill is by far the predominant phase of sandhill habitat remaining in peninsular Florida; lumbering demands on the longleaf pine long ago eliminated it over extensive areas of sandhill habitat. Today the Riverside Island area of the Ocala National Forest (Fig. 2) is perhaps the largest and least disturbed stand of the "typical" longleaf pine-dominated sandhill habitat remaining in the southeastern United States (Florida Game and Fresh Water Fish Commission 1976).

Sand Pine Scrub Association

The sand pine scrub association occurs throughout Florida in isolated patches, often associated with or adjacent to sandhills (Fig. 1). The soils that support scrub habitat are of the St. Lucie series and are essentially loose, unconsolidated sands, similar to but coarser and looser than those which support sandhills. There is never standing or running water in scrub habitats, as even the heaviest rains percolate immediately into the loose sand. Mulvania (1931: 528) referred to these soils as ". . . a bed of silica, to which the term soil is but remotely applicable." The Florida scrub has been called the ecological equivalent of the California chaparral (Laessle 1967).

Botanists have been intrigued with scrub since its description early in the last century (Vignoles 1823). Perhaps no plant community in Florida has stimulated more interest or more printed words (e.g., Vignoles 1823; Nash 1895; Whitney 1898; Harper 1914, 1921; Mulvania 1931; Webber 1935; Kurz 1942; Laessle 1942, 1958, 1967; Miller 1950; Cooper et al. 1959; Veno 1976).

Characteristic scrub tree species include the

Fig. 3. Turkey oak phase of the longleaf pine–turkey oak sandhill habitat in the Ocala National Forest, Florida.

sand pine (*Pinus clausa*), various evergreen oaks (*Quercus virginiana*, *Q. myrtifolia*, and *Q. chapmani*), and lyonia (*Lyonia ferruginea*). Scrubs can be divided into two major types: those with sand pine trees and those without. The latter are sometimes referred to as rosemary scrubs. It is not always clear why some scrubs lack sand pines. Where the pines have died of old age in the absence of fire, scrubs sometimes persist for many years (Laessle 1967). Other evergreen oak scrubs appear never to have had sand pines. The Florida scrub jay (*Aphelocoma coerulescens*), the sand skink (*Neoseps reynoldsi*), and the Florida scrub lizard (*Sceloporus woodi*) are largely restricted to the evergreen oak scrub without sand pines and to those scrubs with young sand pines.

Scrubs rarely burn but, when they do, the fire usually crowns, killing the sand pines. Under the extreme heat of a crowning fire, the sand pine seeds are released from the serotinous cones. More often than not, scrubs are adjacent to sandhill communities which burn frequently. Many authors have noted the tendency of ground fire in the sandhills to stop abruptly at the sandhill – scrub ecotone (e.g., Webber 1935; Laessle 1967). The dominant sandhill tree, longleaf pine, is well adapted to survive frequent ground fires which are readily kindled by the wire grass and deciduous oak leaves which accumulate rapidly. On the other hand, the evergreen oaks of the scrub provide little fuel for ground fires. Thus Webber (1935) referred to the scrub as a "fire fighting association." If fire is excluded from the scrub, the sand pines eventually die of old age and the habitat may ultimately succeed to hardwood (oak, magnolia) hammock (Veno 1976). When a scrub burns, however, the sand pines are killed, seeds are released, and the cycle begins again. At first there are extensive areas of open sand, but the vegetation gradually fills in to form an almost impenetrable tangle composed of a matted ground cover, a dense evergreen shrub layer, and a full pine canopy characteristic of a mature scrub.

Table 1. *Categories of reptile and amphibian species occurring in sandhills and scrubs in peninsular Florida.*

Characteristic
Xeric adapted
Eumeces egregius
Neoseps reynoldsi
Sceloporus woodi
Masticophis flagellum
Stilosoma extenuatum
Tantilla relicta
Cnemidophorus sexlineatus
Wide-ranging
Scaphiopus holbrooki
Gastrophryne carolinensis
Bufo quercicus
B. terrestris
Rhineura floridana
Anolis carolinensis
Eumeces inexpectatus
Scincella laterale
Cemphora coccinea
Coluber constrictor
Micrurus fulvius

Associated with Tortoise Burrows
Rana areolata
Gopherus polyphemus
Pituophis melanoleucus

Frequent
Hyla femoralis
H. gratiosa
Ophisaurus compressus
Diadophis punctatus
Heterodon platyrhinos
Lampropeltis triangulum
Opheodrys aestivus
Sistrurus miliarius

Occasional
Hyla cinerea
H. crucifer
H. squirella
Pseudacris ornata
Ophisaurus attenuatus
O. ventralis
Sceloporus undulatus
Drymarchon corais
Elaphe guttata
E. obsoleta
Heterodon simus
Storeria occipitomaculata
Thamnophis sirtalis
Crotalus adamanteus

Associated with Aquatic Habitats
Acris gryllus
Rana catesbeiana
R. grylio
R. sphenocephala
Ambystoma talpoideum
A. tigrinum
Notophthalmus perstriatus
N. viridescens
Pseudobranchus striatus
Siren intermedia
S. lacertina
Chrysemys floridana
C. nelsoni
Deirochelys reticularia
Kinosternon bauri
K. subrubrum
Sternotherus odoratus
Nerodia fasciata
Seminatrix pygaea
Thamnophis sauritus
Agkistrodon piscivorus

Results

General

Several distinct groups of amphibian and reptile species occur in the sandhills and scrub (Table 1): those that can be considered to be highly adapted to a xeric, sandy habitat (i.e., reaching maximum population levels or found only there); those that occur throughout a wide habitat spectrum; those species associated with burrows of tortoise (*Gopherus polyphemus*); and those species that occur in or near aquatic habitats surrounded by sandhills, scrub, or any other terrestrial habitat.

All of the xeric-adapted species except the Florida scrub lizard require loose, well-drained sand for burrowing or sand-swimming. *Gopherus* and associated species are also dependent on sandy soils for burrows. These species are restricted to sandhill, scrub, and xeric hammock habitats, although *Tantilla relicta* may rarely occur in more mesic habitats. *Gopherus polyphemus* deserves special mention as a focal species in providing burrow refuges for a wide variety of other species including *Rana areolata*

and *Pituophis melanoleucus*, which are essentially restricted to this microhabitat in peninsular Florida. *Drymarchon corais*, generally considered a characteristic gopher tortoise burrow inhabitant, is not so restricted in peninsular Florida and may actually reach greater population levels in certain more mesic hardwood habitats. Its close relation to gopher tortoise burrows and xeric habitats is encountered primarily at its range margins in Georgia and Alabama; in peninsular Florida the burrows are more commonly used by *Pituophis* and a variety of other snake species.

The aquatic species occurring in the sandhills and scrub may reach high population levels around appropriate habitat but are best considered fortuitous additions to the species list. The greatest number of species occurring in the sandhill and scrub habitats are ecological generalists which find suitable conditions in a wide variety of habitats. Unfortunately, we know too little of absolute population densities of amphibian and reptile species to be able to judge relative habitat quality for most species and thus cannot rank the value of sandhills and scrub to these generalist species. On inspection of Table 1, however, it is clear that the generalists are all species which require none of the specialized physical or vegetative conditions of the sandhill and scrub associations.

Table 2. *Results of the herpetological trapping program by habitat type, Cross Florida Barge Canal Wildlife Restudy.* Eleutherodactylus planirostris, *an exotic species, has been omitted.*

Habitat type	Total number of species	Number of individuals/array/day
River swamp	3	0.05
Slash pine flatwoods	7	0.07
Longleaf pine flatwoods	16	0.13
Pond pine flatwoods	6	0.17
Hydric hammock	17	0.23
Mesic hammock	12	0.21
Xeric hammock	10	0.15
Longleaf pine sandhills	13	0.22
Deciduous oak sandhills	16	0.11
Evergreen oak scrub	21	0.16
Sand pine scrub (mature)	19	0.14

Scrub Species Diversity

The community of herpetologists in Florida has long been familiar with the scrub endemics (*Neoseps reynoldsi* and *Sceloporous woodi*), but when our data showed that scrubs had the highest amphibian and reptile species richness of 11 terrestrial habitat types sampled (Table 2), we decided to look more closely at what Carr (1940:8) called, ". . . undoubtedly the most rigorous habitat in Florida. . . ."

We list 43 nonaquatic species of amphibians and reptiles as known to occur either characteristically, frequently, or occasionally in Florida scrubs and sandhills (Table 1). Two of these, *Neoseps reynoldsi* and *Sceloporus woodi*, are primarily restricted to scrub habitat. Others (e.g., *Eumeces egregius*, *Eumeces inexpectatus*, *Cemophora coccinea*, *Tantilla relicta*) may reach their greatest abundance in some successional stage of the scrub habitat. Still others occur in scrub only near its ecotone with sandhills or along roads through the scrub (e.g., *Gopherus polyphemus* and its symbionts).

The reptiles that inhabit the scrub proper fall into two categories: those that "swim" beneath the sand surface (Mosauer 1932) and those that run on the surface of the sand. Even lizards such as *Anolis carolinensis* and *Sceloporus woodi* spend much time on the surface, as pit-fall records indicate. *Neoseps reynoldsi*, *Eumeces egregius*, and *Tantilla relicta* are the principal sand swimmers, although other small species are frequently encountered beneath the sand surface (e.g., *Scincella laterale*, *Lampropeltis triangulum*, *Heterodon platyrhinos*). Smith (this volume) investigated the details of the niches of the three principal sand-swimming species.

Amphibians are poorly represented in the scrub. *Notophthalmus perstriatus* efts occasionally inhabit the scrub. Only the most xeric-adapted anurans will be found regularly in true scrub. Turtles are essentially lacking, although *Kinosternon bauri* may occasionally wander through scrubs, and *Gopherus polyphemus* will occur near roads and ecotones where the soil will sustain burrow construction. Snake and lizard diversity is high.

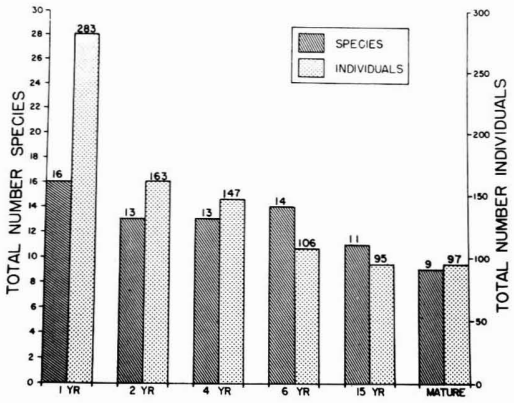

Fig. 4. Total numbers of species and individuals of reptiles and amphibians collected in various ages of sand pine scrub in the Ocala National Forest, Florida.

Scrub and Sandhill Succession

Our ongoing trapping program in the Ocala National Forest was designed to determine if there are any differences in the terrestrial herpetofauna between different-aged stands of sand pine scrub and between the facies of the sandhill association. We installed two standardized trapping arrays in turkey oak and longleaf pine sandhills and in each of six various-aged stands of even-aged sand pine. During the first 10 months of this sampling, we collected 891 specimens of 22 species in the scrub traps (Fig. 4). These results suggest strongly that some species are more abundant in the younger stands of scrub while others are more abundant in the more mature scrubs. No species is confined to the more mature scrubs, although several species collected in the younger stands have not been taken in the mature scrub. Of 22 species collected, only *Anolis carolinensis*, *Scincella lateralе*, and possibly *Eumeces inexpectatus* are more abundant in the older scrubs. On the other hand, at least six species occur more frequently in the younger scrubs. Notable among these are *Scaphiopus holbrooki*, *Cnemidophorus sexlineatus*, *Sceloporus woodi*, and *Tantilla relicta*. The 1-year, 2-year and 4-year-old sites have thus far produced 593 specimens of 20 species, whereas the 6-year, 15-year, and mature sites have yielded only 298 specimens of 16 species. A similar pattern characterized the turkey oak and longleaf pine sandhills. We believe that additional collecting will not appreciably change this trend; that is, it appears that species richness and animal abundance decrease as the pines mature or, to be more specific, as the ground cover increases.

Discussion

It appears to us that the amphibian and reptile fauna occurring in the sandhills and scrub is not actually responding to a particular plant association, but rather to the physical characteristics of the habitat. Where these physical characteristics are met in other plant associations (e.g., xeric hammock), many of the same vertebrate species occur. Thus the scrub lizard and the sand skink are really adapted to habitats that are dry, well-drained, and offer patches of open sand, free from rooted vegetation. We can think of no amphibian or reptile species in Florida that has a distribution restricted to a single plant association. Actually, we argue that the plant species occurring in a given habitat are responding to many of the same environmental factors as the animals. Perhaps wildlife habitats should be classified according to the significant physical characteristics to which both the plants and the animals are adapted rather than by plant associations. The present system can lead to misleading judgments, and we offer a single example: the Florida gopher tortoise is known from several "habitats" (i.e., plant associations): longleaf pine sandhills, deciduous oak sandhills, evergreen oak scrub, sand pine scrub, xeric hammock, dry flatwoods, and a host of ruderal situations. Does this mean that the gopher tortoise is a highly-adaptable, ubiquitous species? It does not. Gophers are essentially restricted to habitats with well-drained, sandy soils, and an abundance of grasses and forbs, and ultimately, with maximal light intensity at ground level (Auffenberg and Franz 1980). These conditions can be met in a variety of places regardless of the specific plant species living there.

A comparison between longleaf pine and turkey oak sandhill may shed light on the evolution of the highly adapted sandhill and scrub reptile and amphibian species. Aside from the presence or absence of a pine canopy and the corresponding dwarfing or enlargement of the understory oaks, these facies of the association are strikingly different in the nature of the ground cover. The

longleaf pine-dominated sandhill usually supports a dense ground cover of wire grass and forbs, whereas the turkey oak-dominated facies is more open, often with extensive areas of bare sand, and it receives more intensive surface insolation. The reptiles characteristic of the sandhills are, as noted, species which burrow and highly specialized sand "swimmers." Species such as *Tantilla relicta*, *Eumeces egregius*, and *Neoseps reynoldsi*, which require loose sand for sand swimming, historically have encountered such conditions in the sandhills only in areas of disturbance, such as the burrow mounds of *Gopherus polyphemus* and *Geomys pinetis*, or the open areas resulting from fire, especially under a turkey oak canopy. In the longleaf pine/turkey oak association such conditions (minus man's imposition of road shoulders and other disturbances) are localized islands of loose sand protruding from a cover of wire grass. Similarly, the mat of roots and humus covering the sand in the mature sand pine scrub would require breaks to provide suitable conditions for these species.

Neoseps reynoldsi, *Eumeces egregius*, *Tantilla relicta*, and *Stilosoma extenuatum* are also more abundant in early successional stages of sand pine scrub than they are in the advanced stages with a full pine canopy, dense evergreen shrub layer, and matted ground cover. To provide conditions for the evolution of the endemic or characteristic species of the sandhills and scrub, there must have always been such disturbed areas where loose surface sand was available. Despite the contention that the central sandhills of Florida were historically blanketed by a sheet of longleaf pine/turkey oak (Laessle 1958), it would appear more probable that a mix of successional stages, both in sandhills and sand pine scrub, has always existed. Breaks in the typical or mature stages of both habitats could, and probably did, result from severe fires, tornado or hurricane blow-downs of the canopy trees, outbreaks of pine-bark beetles, or other natural disasters. These factors would have maintained a mix of habitats amply supplied with the open, loose sand conditions needed for the evolution of the unique herpetological components of the peninsular Florida sandhill and scrub associations. These species, especially *Neoseps reynoldsi*, *Tantilla relicta*, and to a lesser extent, *Eumeces egregius*, are thus cast as "weed" species, colonizers of a patchy early successional or disturbed habitat type which occurs throughout the sandhill, sand pine scrub, and xeric hammock vegetative associations as a result of biological (*Gopherus*, etc.) or catastrophic (fire) factors.

Although most of the highly adapted scrub and sandhill fauna meet few or none of the biological requirements typically cited for colonizing species (see Baker and Stebbins 1965), they must be considered colonizers because of the short-lived nature of their required habitat. A population of sand skinks cannot persist to its maturity in a patch of sand pine scrub; they invade young scrubs opened by killing fires, scrubs without sand pine, and sandhills without wire grass and longleaf pines. Just how a species with a reproductive rate of only one or two young per female per year (Telford 1959) and such apparently poor vagility can do this is a question worth pursuing.

In our current study of the scrubs of the Ocala National Forest, we consistently trapped more species and more individuals in the younger sand pine scrubs. This suggests that there are either more animals in the younger stands or that those present are easier to trap. It is clear that the recently clear-cut scrub is more frequently used by "typical" scrub species; when we consider the natural history of scrub (i.e., fire ecology), this makes sense. It should come as no surprise that the scrub-adapted fauna is accustomed to survival in even-aged stands of sand pine. It thus appears that clear-cutting and even-age management of sand pine stands may mimic the natural situation of infrequent crown fire to which the scrub fauna is adapted.

The variables of a herpetological association or "community" in the scrub and sandhills habitat are difficult to define. Many of the most common species are broadly distributed and only fortuitously juxtaposed in the sandhills and scrub; the more specialized species occur only in restricted microhabitats. With only a few exceptions, the species list for these areas can be duplicated in various other habitat types in peninsular Florida. If we exclude aquatic habitats, the species list is virtually identical to that for xeric hammock.

It appears evident from these data that the concept of a herpetological association or "community" cannot be defined along plant association boundaries in the xeric habitats of peninsular Florida. The local distribution of species is

determined by a complex of physical and probability factors at least partially independent of the plant species of the area. The most heuristic approach is to view amphibian, reptile, and plant species as responding to a similar set of physical and biotic factors without assuming any interdependency between species. If the definition of a herpetological "community" is to be more than the fortuitous association of a group of individuals of a variety of species at a specific place and time, we must look beyond the plant association. In the xeric habitats of peninsular Florida, the particular plant associations appear less important than the presence or absence of areas of loose dry sand.

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References

Auffenberg, W., and R. Franz. 1981. The status and distribution of *Gopherus polyphemus*. *In* R. B. Bury, ed. North American tortoises: conservation and ecology. In press.

Baker, H. G., and G. L. Stebbins [eds.]. 1965. The genetics of colonizing species. Academic Press, New York. 588 pp.

Bozeman, J. R. 1971. A sociologic and geographic study of the sand ridge vegetation in the Coastal Plain of Georgia. Ph.D. Thesis, University of North Carolina, Chapel Hill. 243 pp.

Carr, A. F. 1940. A contribution to the herpetology of Florida. Biol. Sci. Ser., University of Florida Press, Gainesville 3:1–118.

Cooper, R. W., C. S. Shopmeyer, and W. H. D. McGregor. 1959. Sand pine regeneration in the Ocala National Forest. U.S. For. Serv. Prod. Res. Rep. 30: 1–37.

Davis, J. H. 1967. General map of natural vegetation of Florida. Agric. Exp. Stn., Univ. Florida, Gainesville.

Florida Game and Fresh Water Fish Commission. 1976. Cross Florida Barge Canal restudy report: Wildlife. Department of the Army, Jacksonville District Corps of Engineers.

Gammon, N., Jr., J. R. Henderson, R. A. Carringan, R. E. Caldwell, R. G. Leighty, and F. B. Smith. 1953. Physical, spectrographic and chemical analysis of some virgin Florida soils. Florida Agric. Exp. Stn. Tech. Bull. 524:1–130.

Harper, R. M. 1914. Geography and vegetation of northern Florida. Ann. Rep. Florida State Geol. Surv. 6:163–452.

Harper, R. M. 1921. Geography of central Florida. Ann. Rep. Florida State Geol. Surv. 13:71–307.

Jackson, J. F. 1972. The population phenetics and behavioral ecology of the Florida scrub lizard (*Sceloporus woodi*). Ph.D. Thesis, University of Florida, Gainsville. 119 pp.

Kurz, H. 1942. Florida dunes and scrub, vegetation and geology. Florida Geol. Surv. Bull. 23:1–154.

Laessle, A. M. 1942. The plant communities of the Welaka area. Biol. Sci. Ser., University of Florida Press, Gainesville 4:1–43.

Laessle, A. M. 1958. The origin and successional relationships of sandhill vegetation and sand pine scrub. Ecol. Monogr. 28:261–387.

Laessle, A. M. 1967. Relationship of sand pine scrub to former shore lines. Q. J. Fl. Acad. Sci. 30: 269–286.

Miller, R. 1950. Ecological comparisons of plant communities of the xeric pine type on sand ridges in central Florida. M.S. Thesis, University of Florida, Gainesville.

Mosauer, W. 1932. Adaptive convergence in the sand reptiles of the Sahara and of California. Copeia 1932:72–78.

Mulvania, M. 1931. Ecological survey of a Florida scrub. Ecology 12:528–540.

Nash, G. V. 1895. Notes on some Florida plants. Bull. Torrey Bot. Club 22:141–145.

Telford, S. R. 1959. A study of the sand skink, *Neoseps reynoldsi* Stejneger. Copeia 1959:110–119.

Veno, P. A. 1976. Successional relationships of five Florida plant communities. Ecology 57:498–508.

Vignoles, C. 1823. Observations upon the Floridas. Bliss, New York. 197 pp.

Webber, H. J. 1935. The Florida scrub, a fire fighting association. Am. J. Bot. 22:344–361.

Whitney, M. 1898. The soils of Florida. U.S. Dept. Agric. Bull. 13:14–27.