SEASONAL ABUNDANCE AND HABITAT USE OF SELECTED SNAKES TRAPPED IN XERIC AND MESIC COMMUNITIES OF NORTH-CENTRAL FLORIDA

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ABSTRACT

We studied the upland snake community on the Katharine Ordway Preserve-Swisher Memorial Sanctuary during the years 1989 and 1990. A total of 220 wire-mesh funnel traps were deployed at seven xeric and three mesic habitats for a total of 39,162 trap nights. Habitats were sampled from March or April to September or November, depending on year and location. Fourteen species (276 individuals plus 53 recaptures) of snakes were captured, nearly all in traps, of which the five most abundant were *Cemophora coccinea, Coluber constrictor, Masticophis flagellum, Micrurus fulvius,* and *Sistrurus miliarius.* The high-pine snake-community was slightly more diverse and evenly distributed than that of the other xeric or mesic habitats. Snakes were active throughout the sampling period but showed complex rather than strictly modal patterns of activity. In general, there appears to be little seasonal or macro-level habitat partitioning among the five most commonly trapped snakes. Neither monthly rainfall nor temperature appeared to influence capture. The black racer (*Coluber constrictor*) was the most commonly trapped species in all habitat types, with larger racers caught in more structurally diverse habitats. Sampling biases may account for the lack of capture of certain species or the underrepresentation of species known to be more common than capture data indicate. Funnel traps should be used in conjunction with other techniques to remove sampling biases when inventorying and monitoring snake communities.

RESUMEN

Estudiamos la comunidad de culebras, habitante de las tierras altas en la Katharine Ordway Preserve-Swisher Memorial Sanctuary, durante 1989 y 1990. Se instaló un total de 220 trampas de alambre

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tubulares en siete habitats xéricos y tres habitats mésicos, por un total de 39.162 trampas-noche. Los habitats fueron muestrados de marzo o abril, a septiembre o noviembre, dependiendo del año y la localidad. Se capturaron 14 especies (276 individuos, además de 53 recapturas) casi todas en trampas, siendo las cinco especies más abundantes *Cemophora coccinea, Coluber constrictor, Masticophis flagellum, Micrurus fulvius* y *Sistrurus miliarius*. La comunidad de culebras de sitios altos con pinos, fue levemente más diversa y más homogéneamente distribuida que las comunidades de otros habitats xéricos o mésicos. Las culebras estuvieron activas a lo largo del período de muestreo, aunque mostraron patrones de actividad más complejos que estrictamente modales. En general, parece haber poca partición de habitat estacional o a un nivel macro, entre las cinco culebras más comunmente capturadas. Las capturas no parecieron estar influenciadas por pluviosidad mensual ni temperatura. La corredora negra (*Coluber constrictor*) fue la especie más comunmente atrapada en todos los tipos de habitats, siendo las corredoras más grandes capturadas en habitats más estructuralmente diversos. La ausencia de captura de algunas especies o la subrepresentación de otras especies conocidas como más comunes que lo que indican los datos de captura, puede deberse a sesgos de muestreo. Las trampas tubulares debieran ser usadas en conjunto con otras técnicas con el objeto de remover sesgos de muestreo cuando se inventorean y monitorean comunidades de culebras.

INTRODUCTION

Relatively few studies have focused on snake community ecology, especially because of sampling difficulties (Vitt 1987). In order to fully appreciate the importance of snakes in community organization, however, species richness, abundance, and annual and seasonal variation in activity patterns must be determined. Sampling a variety of habitats using standardized techniques helps record variation in habitat use that is then subject to investigation using experimental procedures.

At one time, the longleaf pine (*Pinus palustris*)-turkey oak (*Quercus laevis*)-wiregrass (*Aristida stricta*) community stretched along the Atlantic and Gulf coastal plain from Virginia south to Florida, including a major portion of the Florida peninsula (Myers 1990), and westward to Texas. The community comprised approximately 28.3 million hectares, of which less than 10 percent remains (Croker 1979; Means and Grow 1985; Noss 1989). Interspersed within the longleaf pine forests are other communities, such as hardwood and swamp forests and xeric and mesic hammocks (Myers and Ewel 1990), which developed in response to local soil, fire, and hydrological conditions or resulted from past anthropogenic causes. All these communities are collectively termed uplands. Many species of vertebrate and invertebrate animals occur in these botanically rich communities. Little is known, however, concerning the life history and habitat use of most of the snakes that reside within upland communities.

The Katharine Ordway Preserve-Swisher Memorial Sanctuary includes a variety of upland habitats. From 1983 through 1988, RF conducted a general inventory of resident vertebrates, including snakes. From 1985 through 1990, CKD monitored the herpetofaunal community inhabiting a temporary pond located between a longleaf pine and xeric oak hammock (Dodd 1992). As a result of our efforts, 23 snake species now are known from the Ordway Preserve (Franz this vol.). The present study was undertaken to provide a more systematic inventory of the snakes inhabiting upland communities on the Ordway Preserve, and to examine factors that might influence sampling results. Throughout this paper, we use the term community as defined by Begon et al. (1986), i.e. "an assemblage of species populations which occur together in space and time."

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STUDY AREA

The Katharine Ordway Preserve-Swisher Memorial Sanctuary (hereinafter referred to as the Ordway Preserve) is a 3750 ha tract located approximately 5 km SE of Melrose, Putnam County, Florida. This upland sandhill region lies within the Interlachen Karstic Highland at the southern flank of Trail Ridge. The area represents a portion of a dune complex that probably formed in association with active beach development during periods of higher sea levels. The dunes have been secondarily modified by solutioning activities in the underlying limestones to form sinkholes and karst basins. Many of these solution features hold water to form the ponds, lakes, and wetlands of the Ordway Preserve. Two types of aquatic systems occur on the Ordway Preserve, a series of isolated clear water ponds and lakes and Mill Creek. Mill Creek is an extensive creek system that drains the eastern parts of Trail Ridge and the Interlachen Karstic Highlands. It flows through Etonia and Rice creeks into the St. Johns River. On the Ordway Preserve, the basin includes an extensive swamp forest, eight tannin-stained lakes, and four freshwater marshes. Franz and Hall (1991) provided a detailed discussion of the physical setting of the Ordway Preserve.

HABITATS

General information and references on Florida communities are in Myers and Ewel (1990). Franz and Hall (1991) identified eight vegetative communities on the Ordway Preserve, five of which were sampled during this study. Approximately 66% of the property is composed of upland and ruderal vegetation types, while the rest consists of open water pond and lakes or wetlands. More than 70 water bodies existed on the property prior to a severe drought that began in 1985. This number was reduced to seven at the height of the drought in 1990.

Most communities have been influenced by human disturbance and past fire histories. Between 15% and 25% of the property is believed to have been cleared for agriculture and human habitation since 1850. Several of these areas have regrown through old field succession to xeric sand live oak and mesic hardwood hammocks. Regular prescribed burning of high pine forests was established in 1983 as a part of the Ordway Preserve's management protocol for the purpose of reestablishing the native longleaf pine ecosystem and reducing fuel loads.

High Pine Forest.-- Also known as sandhill, this community type is dominated by longleaf pine (*P. palustris*), turkey oak (*Q. laevis*), and wiregrass (*A. stricta*). High pine requires frequent fires in order to maintain its open aspect, to sponsor pine and wiregrass regeneration, and to control invasive weed species. Located on Candler and Apopka soil types, the community occurs on deep sands associated with dune ridges.

Sand Live Oak Hammock.-- This community naturally occurs as fringes around certain wetland types. It also occurs on ruderal sites. Dominated by sand live oak (*Q. geminata*) and occasionally by laurel oak (*Q. hemisphaerica*), sand live oak hammocks can have dense understories composed of sapling oaks, blueberries (*Vaccinium* spp.), myrtle oak (*Q. myrtifolia*), and other woody plants. Reindeer lichens (*Cladonia* spp. and *Cladina* spp.) and herbaceous species are more prevalent in open hammocks. Prescribed fires rarely intrude into sand live oak hammocks because of sparse fuels and higher moisture conditions than adjacent high pine forest. For purposes of this paper, sand live oak hammocks are termed open (very little understory) or closed (very dense understory with complex habitat structure) xeric hammocks.

Mesic Hardwood Hammocks.-- Located on the lower slopes of the Mill Creek valley, most mesic hardwood hammocks are dominated by mesic species, particularly sweet gum (*Liquidamber styraciflua*), pignut hickory (*Carya glabra*), wild olive (*Osmanthus americanus*), water oaks (*Q. nigra*), and southern magnolia (*Magnolia grandiflora*), although more xeric-adapted pines and oaks commonly occur on some sites. The interior of most mesic hammocks tend to remain open, except where saw palmettos (*Serenoa repens*) form dense thickets. Fires rarely burn into this community, although they historically have invaded the upper Mill Creek valley as evidenced by fire-scarred slash pines (*P. elliotti*) in the vicinity of Mill Creek ford.

Swamp Forest.-- Dominated by red maple (*Acer rubrum*), sweet bay (*Magnolia virginiana*), black gum (*Nyssa sylvatica*), and dahoon holly (*Ilex cassine*), this community type is restricted to the Mill Creek valley bottomland. In some areas, slash pines and pond cypress (*Taxodium ascendens*) form important components. Ericaceous shrubs often are common understory species. Ferns and sphagnum moss can form an extensive ground cover on wetter sites.

Freshwater Marshes.-- Extensive wet prairies occur in four large solution depressions associated with the Mill Creek basin. Certain of these marshes are dominated by semi-woody species, such as swamp loosestrife (*Decodon verticillatus*), fetterbushes (*Lyonia lucida*), Virginia willow (*Itea virginica*), and buttonwood (*Cephalanthus occidentalis*), while others are composed of maidencane (*Panicum hemitomon*) and various sedges. Both types of marshes frequently have small to large localized stands of sawgrass (*Cladium jamaicense*) associated with depressions in the peat. Fires probably have played important roles in these marsh systems in the past, which probably helped to control invasive woody species. Currently, Ordway Preserve managers are not burning these sites.

METHODS

Xeric Community Sampling

In 1989, 100 individually numbered screen wire mesh double-opening funnel traps (90 cm long by 18-25 cm diameter; see Fitch 1987) were placed at six upland sites as follows: 31 traps in closed xeric (sand live oak) hammock (11 at the Fennell homestead [Ordway Preserve site location 12]; 20 south of Enslow Lake [Ordway Preserve site location 21]); 59 traps in sandhill (high pine) habitat (9 at the Fennell homestead; 10 in the vicinity of Polecat Flats [Ordway Preserve site location 19]; 10 in the vicinity of Dry Pond [Ordway Preserve site location 20]; 30 in the vicinity of Single Shot Pond [Ordway Preserve site location 23]); 10 traps in open xeric (sand live oak) hammock (all in the vicinity of the McCloud homestead [Ordway Preserve site location 22]). The locations of the sampling areas are shown in Figure 1.

In most cases, the traps were set along fallen trees and branches that formed natural drift fences. At locations 19 and 20, traps were set along drift fences made of 10 m sections of galvanized metal set in 4-pronged arrays (Campbell and Christman 1982, fig. 1). The traps were covered with palmetto fronds to prevent captured animals from overheating in the direct sun and to provide cover. The traps were checked daily from April 4 through November 17 (23,800 trap nights) between 0700 and 1200 h.

Trapped snakes were returned to the laboratory. Prior to measurement, they were cooled for 1-4 h depending on size. The following data were recorded: snout-vent and tail length (in mm using a ruler), wet mass body weight (in g using a Pesola spring scale), sex (using standard reptile sex probes to determine the

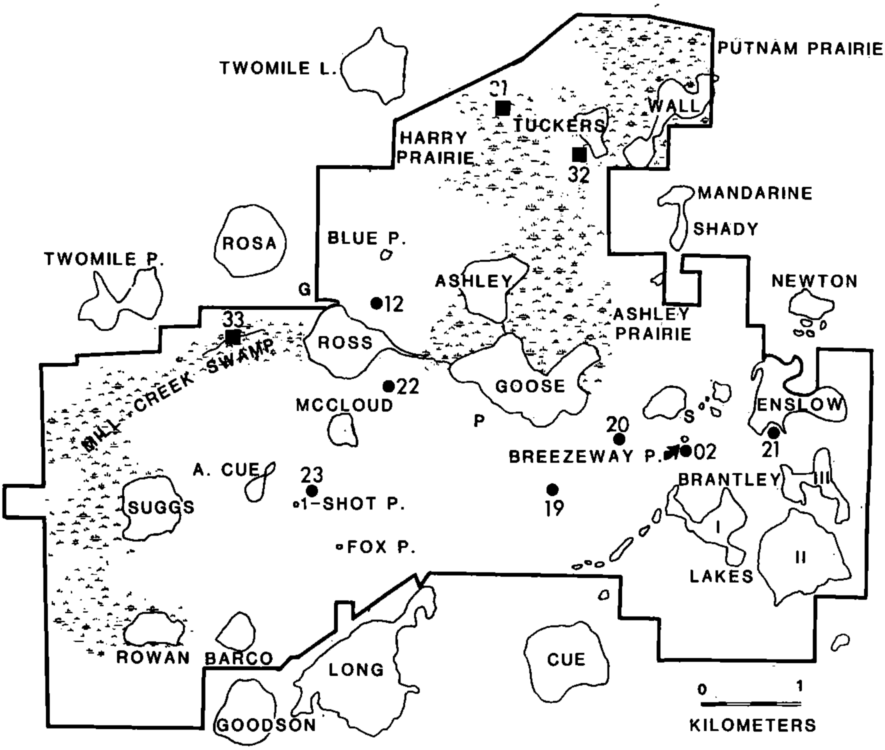

Figure 1. Map showing the locations of the sampling sites on the Katharine Ordway Preserve-Swisher Memorial Sanctuary. 02 = Breezeway Pond; 12 = Fennell Homestead; 19 = Polecat Flats; 20 = Dry Pond; 21 = Hammock south of Enslow Lake; 22 = McCloud Homestead; 23 = Sandhill northeast of Single Shot Pond; 31 = Harry Prairie; 32 = Timmons' Creek; 33 = Mill Creek ford. The dots represent xeric sites; the squares are mesic sites.

presence of hemipenes in males), and whether injuries or unusual scale patterns were present. Each snake was given a unique identification number by clipping or branding ventral and subcaudal scales (Lang 1992). Scale clips, injuries, and unusual scale patterns were drawn on a standardized data form for cross-reference. Snakes were released the following day in the vicinity of where they were trapped.

In 1990, the same areas were sampled using the same general techniques except that all sites were not sampled simultaneously. In addition, 30 traps were set in closed xeric hammock habitat in the vicinity of Breezeway Pond (Ordway Preserve location site 02, Fig. 1). This protocol resulted in a total sampling period of 4,490 trap nights. Traps were placed in the exact same position as in 1989. The dates that the sites were sampled were as follows: Site 02, 5 April-1 June; Site 12, 3 July-1 August; Sites 19 and 20, 2 June-30 June; Sites 21 and 22, 5 September-27 September; and Site 23, 2 August-31 August.

Mesic Hammock and Swamp Forest Community Sampling

Funnel traps were set along fallen logs and covered with saw palmetto fronds, similar to the methods described above. Traps were checked daily between 0700 and 1000 h. Snakes captured in funnel traps were handled in the manner described above except that they were processed at the time of capture without cooling.

Traps were installed on three mesic and wetland sites. Traps at Harry Prairie (Ordway Preserve site location 31, Fig. 1) sampled the edges of a drying freshwater marsh. Sampling was discontinued after five days in June 1989 (100 trap nights) because of frequent trap disturbances by alligators. Traps at Timmons' Creek (Ordway Preserve site location 32) were set for 34 days in 1989 (June and September-October) and for 71 days in 1990 (March-August and October). At Mill Creek ford (Ordway Preserve site location 33), traps were set for 17 days in 1989 (September-October) and for 71 days in 1990 (March-August and October). Total traps nights in mesic hardwood hammock totalled 10,872. Traps at Timmons' Creek and Mill Creek ford sampled both mesic hardwood hammock and swamp forest communities.

Data Analysis

Capture data are reported separately for xeric and mesic sites because of differences in sampling methods. Analysis of habitat associations and seasonal abundance concentrated on the data set derived from sampling the high pine and xeric hammock communities in 1989, because all traps were set and checked daily throughout the sampling period. We compared the number of individuals trapped in 1989 and 1990 at the high pine and xeric hammock sites by using data from identical sampling periods.

We computed the Shannon-Weiner species diversity index using $\log_e$ (H') and values for evenness (J') for snakes trapped in high pine, closed xeric hammock, and mesic hammock (Krebs 1989). H' was not computed for the other habitats because of small sample size. For all data, we calculated the number of snakes trapped in each habitat type in relation to sampling effort (with sampling effort defined as the relative amount of effort expended at each site, referring to the amount of time sampled, number of traps per site, or a combination thereof); the number of snakes per funnel trap versus the number of funnel traps, in each habitat type; and the total number of snakes per individual funnel trap. For the 1989 xeric habitat data, we tabulated the number of individuals trapped during each biweekly sampling period for the five most commonly trapped species as well as the mean number of days between captures at each trap for all species combined.

We divided the 1989 xeric sampling season into three general periods: Spring (biweekly sampling periods 1-4, 4 April-29 May); Summer (periods 5-12, 30 May-18 September); Autumn (periods 13-17, 19 September-17 November). We computed Hurlbert's measure of niche overlap (L) (Hurlbert 1978) for the five most abundant snakes because resource states, i.e. amounts of available habitat and seasonal activity, varied in abundance during the sampling period (Krebs 1989). Hurlbert's measure of niche breadth (B') was calculated for the four most abundant snakes, because it is sensitive to the selectivity of rare resources (Hurlbert 1978; Krebs 1989). The scarlet snake (*Cemophora coccinea*) was excluded, because it was not trapped in open xeric hammock.

A sufficient sample size was available to compare snout-vent lengths of black racers (*Coluber constrictor*) among xeric habitat types to determine if size-related habitat partitioning occurred. The data on snout-vent lengths in different habitats first were tested for normality. Inasmuch as the data were not normally distributed, comparisons were made using the nonparametric procedure NPAR1WAY which corresponds to a Kruskal-Wallis test (SAS Institute, Inc. 1988).

The effects of monthly rainfall and monthly maximum, minimum, and average temperatures on the total number of snakes trapped were examined using Spearman Rank Correlation. Statistical analyses were performed using the SAS program for microcomputers (SAS Institute, Inc. 1988), ABSTAT version 4 (Anderson Bell 1987), and ecological programs in Krebs (1988). The level of significance was set at $\alpha = 0.05$.

RESULTS

Habitat Associations

We captured 10 snake species (234 individuals plus 48 recaptures) in xeric habitats (Fig. 2) and 11 species (42 individuals plus 5 recaptures) in mesic habitats (Fig. 3). A few snakes were captured by hand (7) while checking traps and data from these snakes are included in the results that follow, where appropriate. Most recaptures occurred within a few days at the same or a nearby trap. The most commonly trapped snake in both habitat types was the black racer. The next most commonly captured species were trapped primarily in the xeric habitats, including the coachwhip (*Masticophis flagellum*), coral snake (*Micrurus fulvius*), and the pygmy rattlesnake (*Sistrurus miliarius*). Small snake species known from the Ordway Preserve (*Diadophis punctatus, Opheodrys aestivus, Regina alleni, Seminatrix pygaea, Tantilla relicta*) (Franz this vol.) were never trapped.

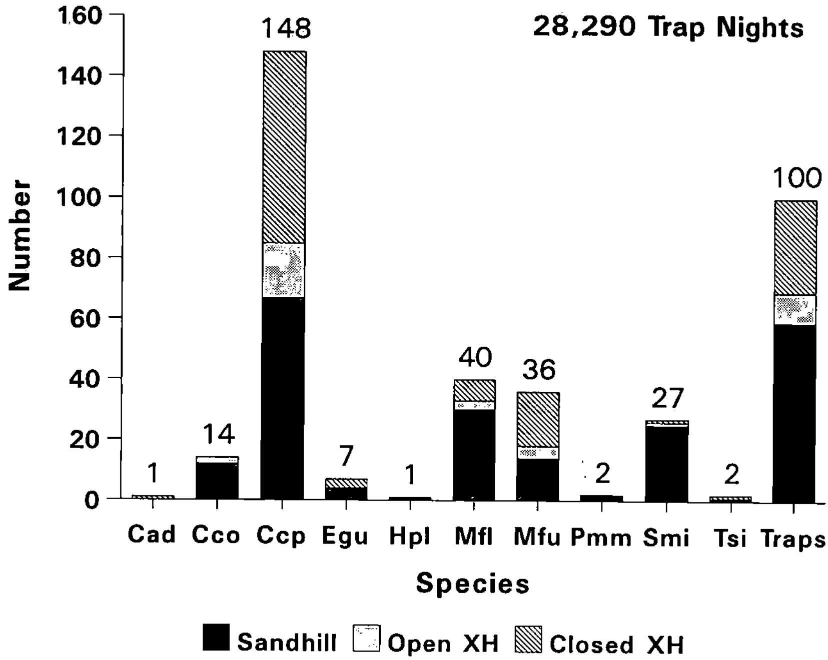

Figure 2. Snakes caught in traps by habitat type in xeric habitats. Cad = *Crotalus adamanteus*; Cco = *Cemophora coccinea*; Ccp = *Coluber constrictor*; Egu = *Elaphe guttata*; Hpl = *Heterodon platyrhinos*; Mfl = *Masticophis flagellum*; Mfu = *Micrurus fulvius*; Pmm = *Pituophis melanoleucus*; Smi = *Sistrurus miliarius*; Tsi = *Thamnophis sirtalis*. "Traps" refers to the percentage of trap effort in each habitat type.

The high pine snake community was more diverse ($H' = 2.31$) and evenly distributed ($J' = .729$) than the closed xeric hammock community ($H' = 1.49$; $J' = .531$). Mesic hammocks were intermediate in diversity and evenness ($H' = 2.02$ and $J' = .639$). Within the xeric habitats, most species were found in more than one habitat type, and those species found in only one habitat type were rarely trapped. In contrast, the mesic hammock accounted for the vast majority of captures in mesic habitats although trap sampling bias probably accounts for the lack of representation of more species in other mesic habitats. Habitat niche overlap values for the five most common species trapped in xeric habitats are in Table 1 and niche breadth values are in Table 2.

Snakes trapped in both xeric and mesic communities included juveniles and large adults (Table 3). However, black racers appeared to be larger in more structured habitats than in open habitats. Mean SVLs in high pine were smaller

Table 1. Niche overlap values for season (upper triangular matrix) and habitat (lower triangular matrix) in the five most abundant snakes trapped in the uplands of the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida.

	Species				
Species	*Cemophora coccinea*	*Coluber constrictor*	*Masticophis flagellum*	*Micrurus fulvius*	*Sistrurus miliarius*
Cemophora coccinea	—	1.153	1.069	1.242	0.897
Coluber constrictor	0.934	—	1.152	1.197	0.849
Masticophis flagellum	1.300	0.918	—	1.153	0.861
Micrurus fulvius	0.695	1.096	0.762	—	0.838
Sistrurus miliarius	1.364	0.856	1.306	0.669	—

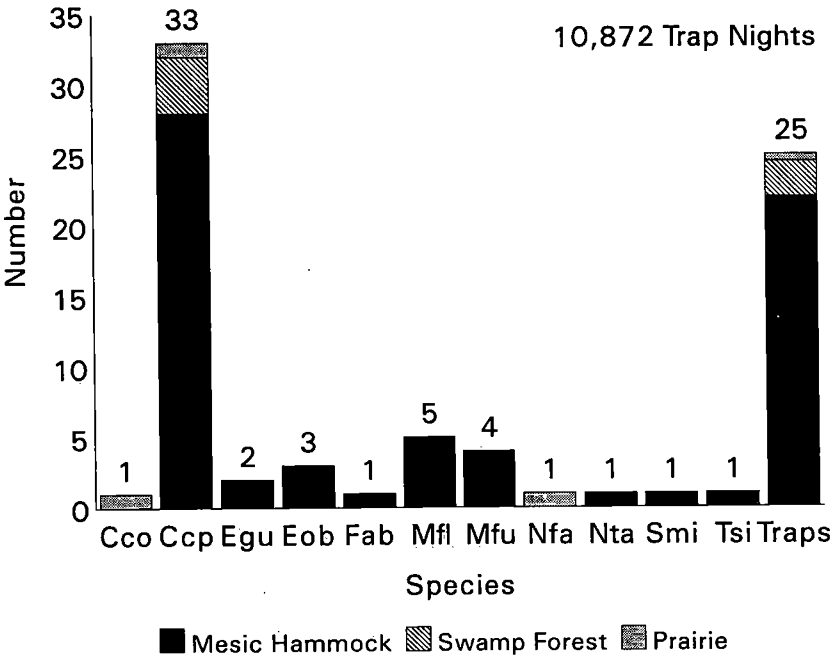

Figure 3. Snakes caught in traps by habitat type in mesic habitats. Cco = *Cemophora coccinea*; Ccp = *Coluber constrictor*; Egu = *Elaphe guttata*; Eob = *E. obsoleta*; Fab = *Farancia abacura*; Mfl = *Masticophis flagellum*; Mfu = *Micrurus fulvius*; Nfa = *Nerodia fasciata*; Nta = *N. taxispilota*; Smi = *Sistrurus miliarius*; Tsi = *Thamnophis sirtalis*. "Traps" refers to the relative percentage of trap effort in each habitat type.

Table 2. Niche breadth for four most abundant snakes trapped in uplands on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida.

	Species			
Parameter	*Coluber constrictor*	*Masticophis flagellum*	*Micrurus fulvius*	*Sistrurus miliarius*
Habitat	0.934	0.795	0.775	0.657
Season	0.804	0.829	0.742	0.844

(556.6 mm, N=61) than in open xeric hammock (665.9 mm, N=31) and closed xeric hammock (686.7 mm, N=19). The difference among means is significant (χ^2=16.84, df=2, p=0.0002). The mean SVL of *Coluber* in mesic habitats was 752.4 mm (N=25).

Seasonal Abundance

With the exception of *Cemophora*, at least one specimen of the five most common species was caught each month of the study. In 1989, the majority of *C. constrictor* was trapped during the first 12 weeks of the survey (i.e. from early April through mid-June) with later peaks in late August to early September and again in late October (Fig. 4). *Micrurus fulvius* were trapped most often in early May, but capture sharply dropped thereafter, whereas *S. miliarius* were trapped throughout the sampling period with a slight peak in the early autumn. No general patterns of seasonal capture are apparent for the other two most commonly trapped xeric habitat species. *Cemophora coccinea* was trapped only during the warmer months (Fig. 4), and *Masticophis flagellum* was trapped at low levels nearly throughout the sampling period. When temporal sampling periods were matched, more individuals were caught in 1990 than in 1989 for four of the five most commonly trapped species (Fig. 5). Seasonal values for niche overlap are in Table 1 and niche breadth in Table 2.

Inasmuch as all traps were not open simultaneously throughout the potential snake activity period in mesic habitats, it is not possible to determine seasonal activity patterns unless sampling effort is considered. Figure 6 shows total monthly snake capture in mesic habitats in relation to sampling effort during that month. A peak of snake activity is apparent in March. From April to August, the number of snakes trapped was proportional to sampling effort. In September and October, trap

Table 3. Descriptive statistics for snakes trapped in uplands and mesic habitats on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam Co., Florida, in 1989 and 1990. Snout-vent lengths in mm; wet mass body weight in g. SD = standard deviation.

	Snout-vent Length				Body Weight			
Species	N	Mean	Range	SD	N	Mean	Range	SD
Uplands Habitats								
Cemophora coccinea	10	304.8	(210-364)	46.7	10	9.2	(3.4-14)	3.4
Coluber constrictor	111	609.4	(230-875)	145.2	110	71.4	(3.1-181)	40.3
Crotalus adamanteus	1	457.0			1	56.0		
Elaphe guttata	7	548.1	(360-772)	155.6	7	57.1	(14.5-120)	43.2
Heterodon platyrhinos	1	375.0			1	70.0		
Masticophis flagellum	37	939.7	(356-1415)	273.1	36	176.8	(8.5-580)	122.2
Micrurus fulvius	33	552.4	(392-715)	65.2	31	31.5	(15-62)	10.9
Pituophis melanoleucus	2	1320	(1300-1340)	28.3	2	770.0	(680-860)	127.3
Sistrurus miliarius	26	339.7	(156-449)	56.6	26	30.0	(5-60)	12.8
Thamnophis sirtalis	2	404.0	(362-446)	59.4	2	24.5	(19-30)	7.8
Mesic Habitats								
Coluber constrictor	25	752.3	(412-884)	118.6	25	140.0	(16-241)	53.9
Elaphe guttata	2	480.5	(368-593)	159.1	2	31.8	(12-52)	27.9
E. obsoleta	3	553.3	(220-980)	553.3	3	135.1	(18-207)	102.0
Farancia abacura	1	688.0			1	111.8		
Masticophis flagellum	2	730.0	(260-1200)	664.7	2	162.7	(6-319)	221.4
Nerodia fasciata	1	350.0			1	57.0		
N. taxispilota	1	370.0			1	37.6		
Thamnophis sirtalis	1	518.0			1	52.0		

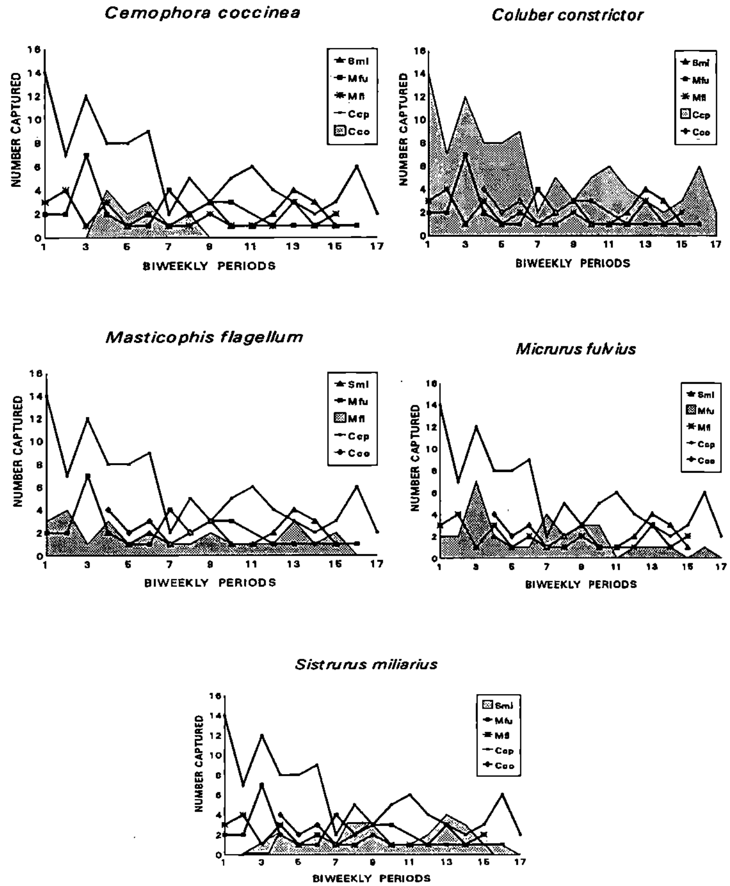

Figure 4. Biweekly seasonal activity of the five most common species trapped in xeric habitats in 1989. Cco = *Cemophora coccinea*; Ccp = *Coluber constrictor*; Mfl = *Masticophis flagellum*; Mfu = *Micrurus fulvius*; Smi = *Sistrurus miliarius*. Trapping extended from April 4 to November 17.

effort far exceeded the number of snakes caught, indicating a decline in seasonal snake activity. *Coluber constrictor* was the most commonly trapped snake in mesic habitats, and captures of this species accounted for the large number of snakes trapped in March. Secondary peaks in number of snakes trapped also occurred in June and July in mesic hammocks, because many *Coluber* were trapped, but it is impossible to separate trap effort from capture effort because of the temporal sampling protocol in mesic habitats. As with capture in xeric habitats, other species showed no trends in seasonal activity.

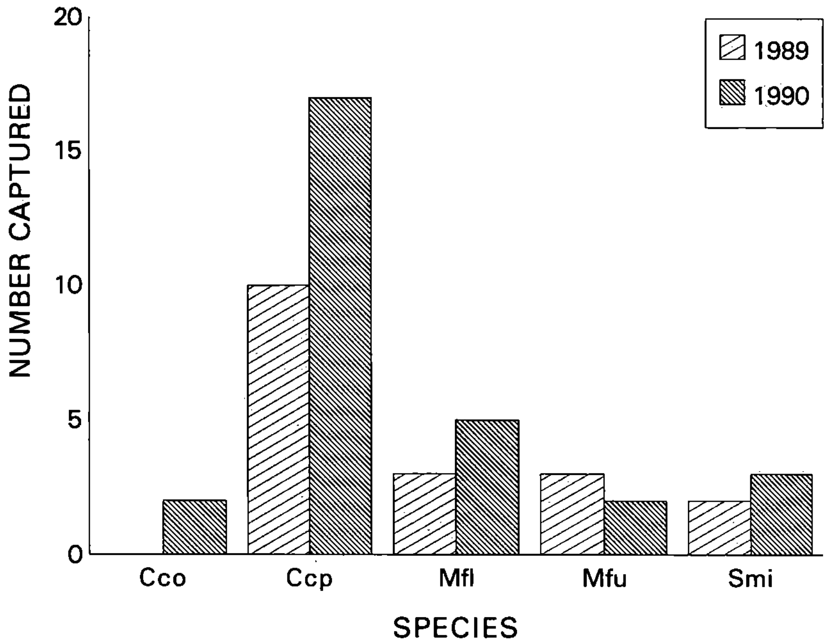

Figure 5. Comparison of trap results during identical sampling periods in xeric habitats in 1989 and 1990. Cco = *Cemophora coccinea*; Ccp = *Coluber constrictor*; Mfl = *Masticophis flagellum*; Mfu = *Micrurus fulvius*; Smi = *Sistrurus miliarius*.

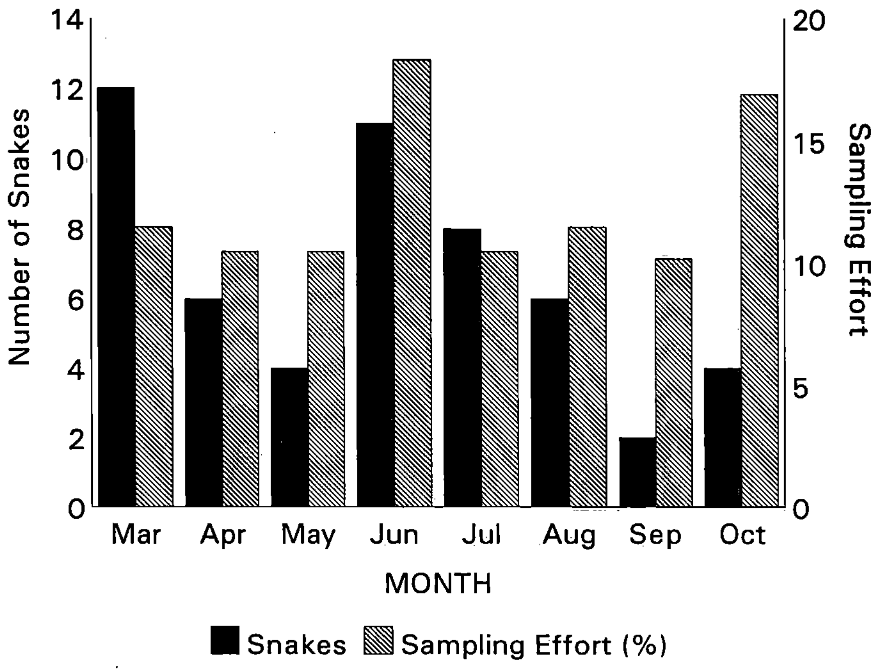

Figure 6. Monthly capture of snakes trapped in mesic habitats in 1989 and 1990 in relation to sampling effort.

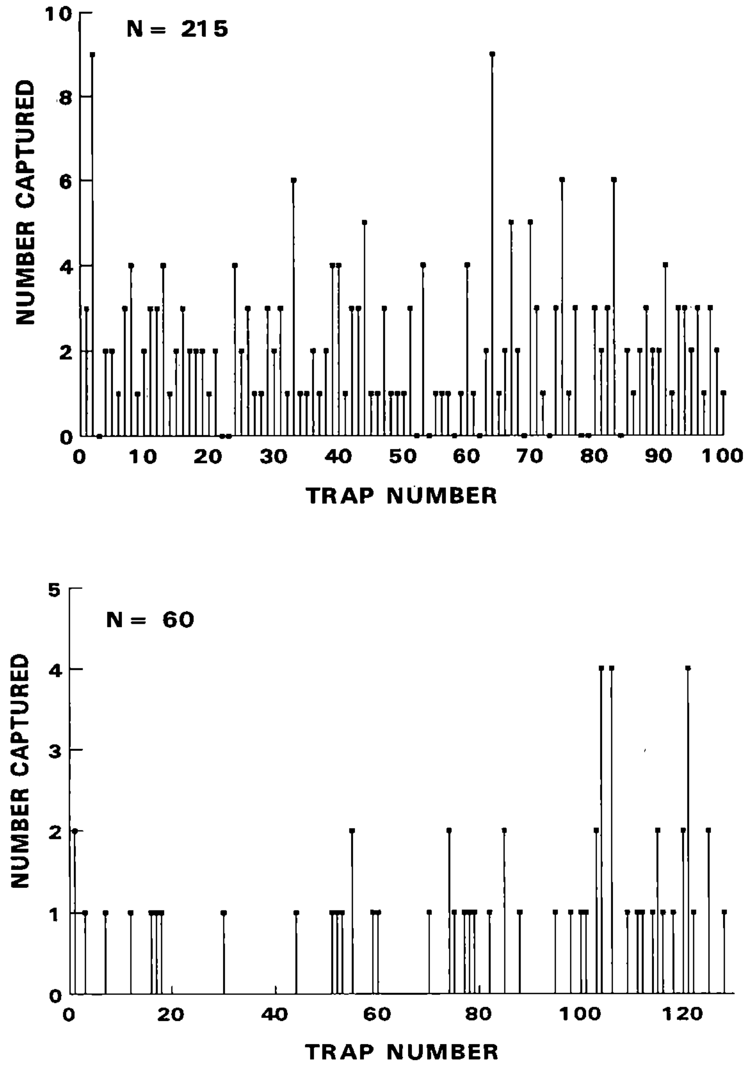

Figure 7. Total number of snakes captured by individual traps in xeric habitats. (A) 1989; (B) 1990.

Sampling Considerations

Throughout the long 1989 sampling period in xeric habitats, snakes were caught at least once in 88% of all traps, but only 5% of the traps accounted for six or more snakes (Fig. 7A). Snakes were caught in only 33.1% of traps in xeric habitats during the abbreviated sampling period in 1990, and only 2.3% of the traps caught three or more snakes (Fig. 7B). In mesic habitats, only 25.3% of traps captured one or more snakes during the 2-year sampling period, and only 1.2% of traps caught three or more snakes (Fig. 8).

We further examined the effectiveness of certain traps to catch snakes by calculating the mean number of days between captures, regardless of species trapped, and plotting this mean against the number of capture intervals (Fig. 9). As might be expected, increasing the number of intervals between captures resulted in a decrease in the mean number of days between captures. However, little variation exists in the mean of the mean number of days between captures when the capture interval was below four (1 interval mean = 81.9 days; 2 intervals mean = 92.6 days; 3 intervals mean = 97.0 days; 4 intervals mean = 90.8 days).

Habitat appeared to have little effect on the number of snakes caught per funnel trap. In 1989, most traps in xeric habitats caught one to three snakes, although the total number of snakes captured per funnel trap in open xeric habitat was rather uniform (Fig. 10). The number of snakes captured per funnel trap in 1989 is not different from a Poisson distribution both in high pine (χ^2=3.11, df=4) and closed xeric hammock (χ^2=2.87, df=3). Generally fewer snakes were captured per funnel trap during the abbreviated sampling period in 1990 xeric habitats and in the mesic habitats in both years. A high percentage of traps captured zero snakes regardless of habitat type (Figs. 11 and 12).

The average monthly temperatures were similar among years with the exception of April and May 1990 which were cooler than 1989 (Fig. 13). North-central Florida experienced a severe drought throughout the study (Dodd 1992 1993). Total rainfall amounts varied considerably among years; 1990 was dryer than 1989 (Fig. 13). The total number of snakes trapped per month was not correlated with rainfall (r_s = 0.245, $p > 0.05$), average monthly temperature (r_s = 0.248, $p > 0.05$), maximum monthly temperature (r_s = 0.431, $p > 0.05$), or minimum monthly temperature (r_s = 0.219, $p > 0.05$).

DISCUSSION

Species Richness and General Habitat Use.-- The xeric and mesic habitats on the Ordway Preserve appear to have similar snake species richness, at least on a macrohabitat level. Sampling was conducted on a relatively coarse scale, i.e. no trapping was undertaken in specialized habitats such as fossorial or arboreal locations within the xeric and mesic habitats. No new records were obtained for the Preserve, and our subjective impressions of the relative abundance of some species were substantiated. The Ordway Preserve has similar species richness with

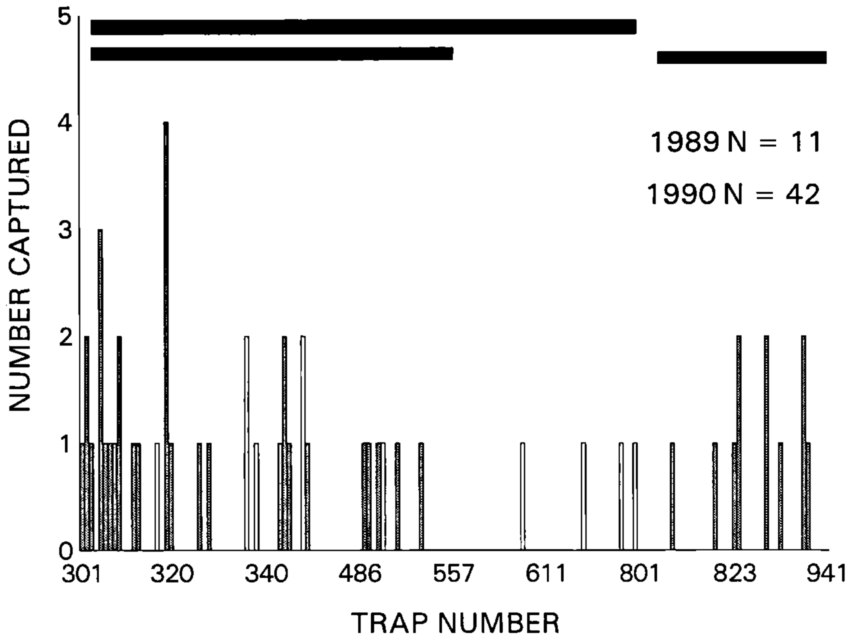

Figure 8. Total number of snakes captured by individual traps in mesic habitats, 1989-1990. The dark bars at the top of the graph show which traps were open in 1989 (top) and 1990 (bottom). N refers to the total number of snakes captured.

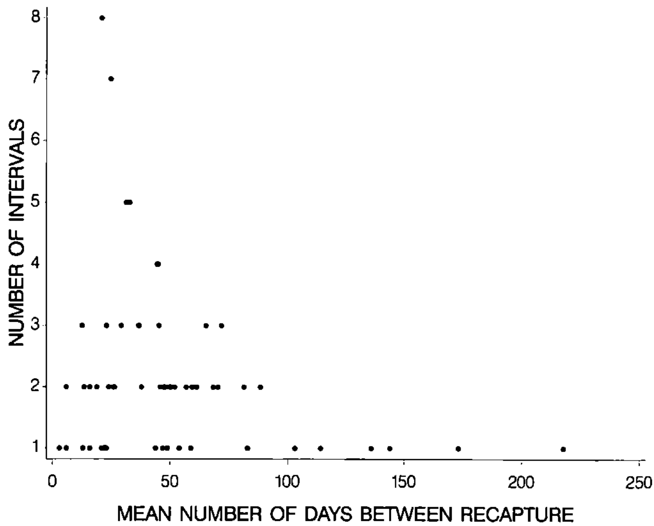

Figure 9. The relationship between the number of intervals between snake captures at a trap and the mean number of days between capture.

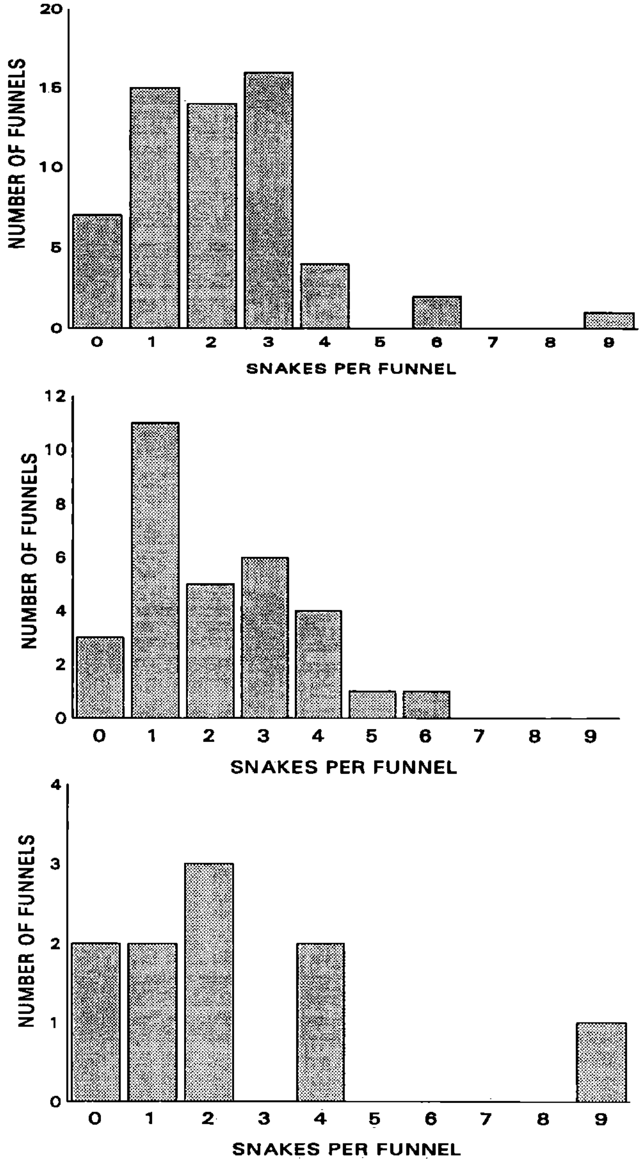

Figure 10. The relationship between the number of traps and the total number of snakes captured per trap in different xeric habitats in 1989. (A) Sandhills; (B) Closed xeric hammock; (C) Open xeric hammock.

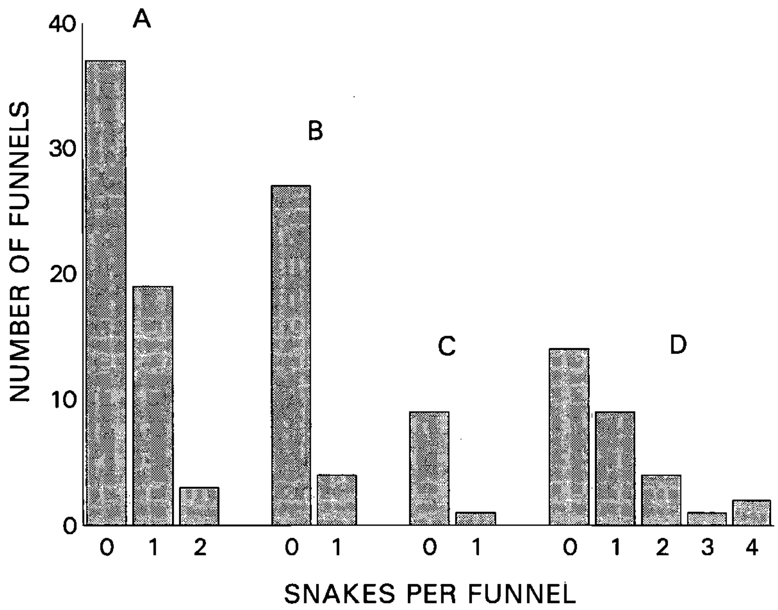

Figure 11. The relationship between the number of traps and the total number of snakes captured per trap in different xeric habitats in 1990. (A) Sandhills; (B) Closed xeric hammock; (C) Open xeric hammock; (D). Sample site surrounding Breezeway Pond.

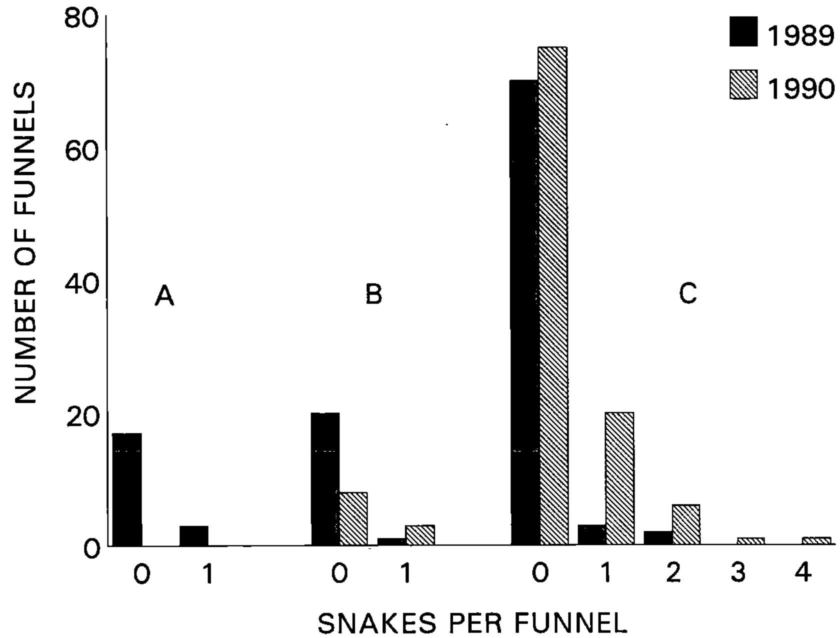

Figure 12. The relationship between the number of traps and the total number of snakes captured per trap in different mesic habitats in 1989 and 1990. (A) Prairie; (B) Swamp Forest; (C) Mesic hammock.

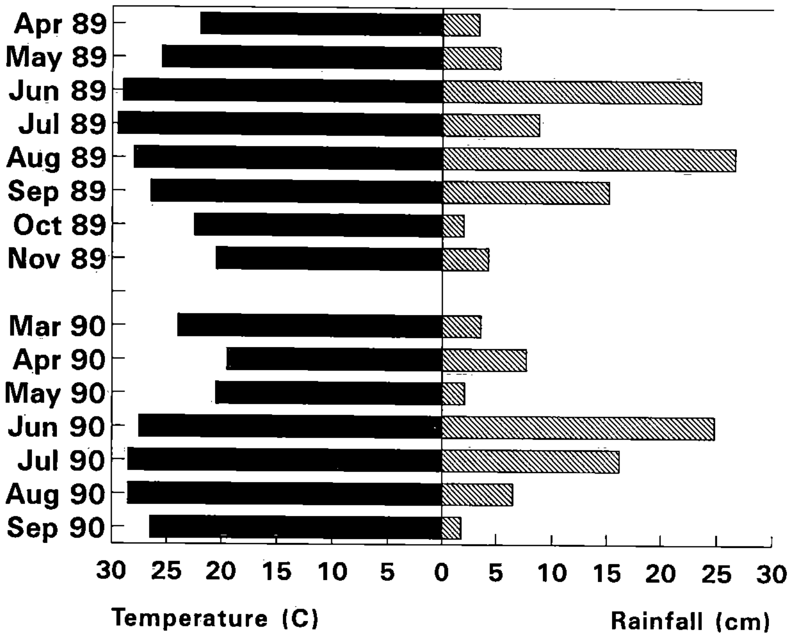

Figure 13. Average monthly temperature and total rainfall amounts on the Katharine Ordway Preserve-Swisher Memorial Sanctuary during the 1989 and 1990 sampling period.

comparable sized habitats at the same latitude (Vitt 1987). However, sampling in other habitat types, particularly the wetlands, may increase the number of species known to occur on the Preserve.

The black racer was trapped in substantial numbers in all habitat types. Relatively more black racers were found in mesic hammocks than in xeric habitats, especially considering differences in sampling effort, but whether this reflects habitat selection by different size classes or a response to different prey abundance (Toft 1985; Vitt 1987) is unknown. In xeric habitats, racers were nearly equally abundant in both high pine and in closed xeric hammock. In all habitats, capture frequency was proportional to sampling effort. The ubiquitous distribution and general abundance of *Coluber* suggests that it is an upland habitat generalist.

The next four most commonly trapped species (*Cemophora coccinea*, *Masticophis flagellum*, *Micrurus fulvius*, *Sistrurus miliarius*) were found both in xeric and mesic habitats, but the numbers trapped seemed to indicate a preference for the dryer habitats. A narrowing in habitat preference from that shown by *C. constrictor* is reflected by the lower niche breadth values for these species. With the exception of *S. miliarius*, considerable niche overlap occurs. In upland habitats, the pygmy rattlesnake was the most xerophilic of the common snakes trapped during this study although in other areas they are common in wetlands (e.g. Hudnall 1979).

The rest of the snakes trapped during the study were caught infrequently. Based on other observations (see below), several of them (e.g. *Crotalus adamanteus*, *Pituophis melanoleucus*) are known to be common on the Ordway Preserve (Timmerman 1989; CKD and RF unpubl. data). Others are wetland-associated species. Only *Heterodon platyrhinos* appears to be rare on the Ordway Preserve and was trapped infrequently. Additional sampling, using a variety of techniques in more habitat types, will be necessary before the habitat associations of these species on the Ordway Preserve can be discerned.

We suggest that a possible explanation of the similarity of the upland snake faunas in different habitat types on the Ordway Preserve is that they share a similar derivation. Approximately 47 percent of the uplands presently are in high pine vegetation. Xeric hammocks are found surrounding the numerous lakes in formerly cultivated areas on the property and in the Mill Creek valley. Examination of aerial photographs taken more than 30 years ago and conversations with elderly residents familiar with the land confirm that most xeric hammocks were cleared for agriculture or homesteads at one time, usually 50 to 70 years ago. These hammocks probably were in high pine vegetation prior to cultivation. Thus, the xeric hammocks are of relatively recent origin and do not contain species, such as *Storeria occipitomaculata*, found in historically undisturbed hammocks.

Seasonal Activity Patterns.— The five most commonly trapped species did not show similar seasonal activity patterns, and the activity patterns (Fig. 4) often were different from literature records. For example, *Coluber constrictor* is reported to have a bimodal seasonal activity period in Nebraska, based on road kills (Oliver 1955), and a unimodal activity period centered on the late spring to early summer in South Carolina (Gibbons and Semlitsch 1987) and southern Florida (Dalrymple et al. 1991b). *Micrurus* is active year-round in Florida with a bimodal activity season in spring and autumn (Jackson and Franz 1981; Dalrymple et al. 1991b). Our observations are similar to literature records for *Sistrurus* (Hudnall 1979; Dalrymple et al. 1991b), *Masticophis* (Ford et al. 1991), and *Cemophora* (Reynolds 1980; Gibbons and Semlitsch 1987; Dalrymple et al. 1991b).

The four most trapped species were active throughout the sampling period, as reflected in niche breadth values. *Micrurus* overlapped seasonally least with the other species, whereas the warm weather xeric habitat species *Cemophora, Masticophis*, and *Sistrurus* had the greatest seasonal niche overlap. The spring activity peak in *Coluber* and the autumn increase in *Sistrurus* are reflected in their medial niche overlap values. In general, there does not appear to be much seasonal partitioning of activity, perhaps because of the generally long activity seasons of most species.

Gibbons and Semlitsch (1987) suggested that Temperate Zone snakes showed two general activity patterns, a unimodal pattern centered on warm weather activity and a bimodal pattern centered on spring and autumn activity peaks. On the Ordway Preserve, such patterns were observed, but the patterns were more complex with less adherence to a particular modality. Failure to conform to recognized patterns suggests that sampling may be biased, that 1989 may have been an unusual year in terms of snake activity, that concepts of modality in subtropical snake activity patterns need to be refined to incorporate the possibility of both variation and complex patterns, or that all of these factors may be true. In areas with year-round activity, snakes seem to keep the general patterns observed in more northern latitude relatives but retain the plasticity to modify activity in accordance with local environmental conditions (Dalrymple et al. 1991b).

Sampling considerations.-Funnel traps have been used successfully to obtain data on both individual snake species and communities (Fitch 1960 1987; Ford et al. 1991). Clearly, the technique is effective at capturing certain upland species, such as *Coluber*, *Micrurus*, and *Sistrurus*. Six or more snakes were captured in only five traps throughout the study, providing little evidence of biased trapping. Although more traps had zero capture success in xeric habitats in 1990 than in 1989, the sampling effort was only 16% of that in 1989. Likewise, many mesic habitat traps had zero capture success during the two-year study, but mesic habitats were sampled for only 28% of the sampling total. Snakes did not shy away from any cluster of traps in any habitat type.

On the other hand, why did most traps capture few snakes? Several hypotheses are possible, including insufficient sampling effort, generally poor trap placement, low snake density, or escape from traps before the observer checked them. Snakes also may avoid traps in which other snakes had been caught, perhaps due to chemoreceptive cues left by previous occupants (but see Weldon et al. 1990). None of these hypotheses can be ruled out, and all may affect capture success.

The 14 species of snakes trapped during the study represent 61 percent of the snakes known from the Ordway Preserve (Franz this vol.). Other snake species (*Diadophis punctatus*, *Drymarchon corais*, and *Tantilla relicta*) are known from upland habitats on the Ordway Preserve but were not trapped. In addition, general collecting, radio-telemetry studies, and subjective impressions suggest that additional species, such as *Crotalus adamanteus* (Timmerman 1989), *Elaphe guttata*, *E. obsoleta*, and *Pituophis melanoleucus*, were underrepresented in funnel traps in relation to their probable abundance. Such discrepancies suggest that funnel trapping alone is inadequate to sample all species of an upland snake community.

Snake size, habitat specificity, and foraging mode may play an important role in the effectiveness of funnel traps to sample communities. Those upland species either not trapped or underrepresented were generally small as adults (*Diadophis*, *Tantilla*) or very large and robust as adults (*Crotalus*, *Drymarchon*, *Pituophis*). On the other hand, small robust *Sistrurus* and large slender *Masticophis* were trapped. Habitat specificity, such as fossorial (*Tantilla*) or arboreal (*E. guttata*, *Opheodrys*) habitat preferences, may restrict the effectiveness of funnel trap sampling. Ford et al. (1991) also were unable to capture *Tantilla* in funnel traps.

Several species that were trapped, such as *Nerodia fasciata* and *N. taxispilota*, are aquatic species and as such were unexpected in xeric upland habitats. However, Dodd (1992) found some non-resident aquatic or wetland-associated species that regularly visited a small isolated temporary pond located in upland habitat on the Ordway Preserve. Snakes normally associated with wetland habitats may travel across unfavorable habitat to find foraging areas or to disperse during unfavorable environmental conditions (Dodd 1993; Seigel et al. ms). On the Ordway Preserve, six additional wetland-associated species (*Farancia abacura*, *Nerodia floridana*, *Opheodrys aestivus*, *Regina alleni*, *Seminatrix pygaea*, *Thamnophis sauritus*) are known to at least occasionally cross upland habitat (Dodd 1992; unpubl. observ.) but were not trapped during the study. The likelihood of trapping wetland-associated species as they move across upland habitat would seem to be small, unless the uplands were located adjacent to wetlands subject to periodic desiccation. In such locations, seasonal snake activity is influenced by fluctuations in the water table resulting in increased capture as wetlands dry (Bernardino and Dalrymple 1992).

Finally, active foragers, such as *Masticophis* and *Coluber*, should be more likely to encounter funnel traps than sit-and-wait predators such as *Crotalus*. Active foragers, especially those that take a wide range of prey, also are more likely than sit-and-wait predators to be drawn to traps through intra- or interspecific chemical cues or the activity of prey species (lizards, other snakes, or rodents) caught in the traps.

Based on our results and those of other recent investigators (Fitch 1992; Grant et al. 1992; Rodda and Fritts 1992), we suggest that funnel traps should not be employed as the sole method for community sampling. All sampling techniques have biases and limitations, but certain questions, such as those involving the determination of activity patterns, often can be addressed using a non-trap biased approach (Reynolds 1982; Price and LaPointe 1990; Dalrymple et al. 1991a; Dalrymple et al. 1991b; Bernardino and Dalrymple 1992). Inventory sampling should use a variety of techniques, such as pitfall traps with drift fences (Gibbons and Semlitsch 1982), road-cruising (Klauber 1939), coverboards (Grant et al. 1992), and time-constraint sampling (Campbell and Christman 1982), to supplement funnel trap data (Fitch 1992).

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