THE ECOLOGY OF A SANDHILLS POPULATION OF THE EASTERN NARROW-MOUTHED TOAD, *GASTROPHRYNE CAROLINENSIS*, DURING A DROUGHT

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ABSTRACT

The eastern narrow-mouthed toad, *Gastrophryne carolinensis*, is a common inhabitant of sandhill uplands in north-central Florida. From 1986 through 1990, I monitored a population of this species at a 0.16 ha wetland on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida. The pond held water only 14 mo during the 60-mo study. A drift fence-pitfall trap system encircled the pond basin to capture eastern narrow-mouthed toads as they entered and exited. A total of 5740 eastern narrow-mouthed toads (including recaptures) were captured despite a severe drought during the latter years of the study. In 1986 and 1988, approximately 900 eastern narrow-mouthed toads entered the pond, but the numbers fluctuated substantially in the other years. Few multi-year recaptures were recorded, although two eastern narrow-mouthed toads were captured four years after initial marking. Although eastern narrow-mouthed toads were active during all months of the year, peak activity occurred from June through September. Reproduction was successful only during the summer of 1985, and juveniles exited the pond basin through the spring of 1986. The adult population size-class structure remained consistent throughout the study, although the population size decreased. The adult sex ratio was male-biased in all years except 1990. Males were smaller than females in both snout-urostyle length (SUL) and weight, and differences were significant among years and between sexes. Drought eliminated reproduction for five years and seemed to reduce overall population size, but direct correlations between drought effects and natural stochastic variation are not yet possible. My data suggest that *G. carolinensis* survives long-term droughts by maintaining large populations scattered across a variety of habitats and because at least some individuals are opportunistic, rather than philopatric, in their choice of breeding sites. Long-term studies and manipulative field experiments will assist in answering some of the many questions raised by these results.

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DODD, C.K., JR. 1995. The ecology of a sandhills population of the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, during a drought. Bull. Florida Mus. Nat. Hist., Biol. Sci. 38, Pt. I(1):11-41.

RESUMEN

El sapo de boca angosta del Este, *Gastrophryne carolinensis*, es un habitante común de las tierras altas arenosas del centro norte de Florida. Yo monitoreé una población de esta especie entre 1986 y hasta 1990 en un humedal de 0.16 ha en la Catherine Orway Preserve- Swisher Memorial Sanctuary, en el Condado de Putnam, Florida. EL estanque contuvo agua durante sólo 14 de los 60 meses de estudio. Un sistema de reja-trampa en la cual los sapos caían, se ubicó rodeando todo el estanque con el objeto de capturar sapos de boca angosta del Este, a medida que éstos entraban o salían del estanque. A pesar de una severa sequía que ocurrió durante los últimos años de estudio, se capturó un total de 5740 sapos de boca angosta del Este (incluyendo recapturas). En 1986 y 1988, aproximadamente 900 sapos de boca angosta del Este entraron en el estanque, pero estos números fluctuaron substancialmente en los otros años. Aún cuando dos sapos de boca angosta del Este fueron capturados durante cuatro años después del marcaje inicial, se registraron escasas recapturas multianuales. Aunque los sapos de boca angosta del Este estuvieron activos durante todos los meses del año, el máximo de actividades ocurrió entre junio y septiembre. La reproducción fue exitosa sólo durante el verano de 1985, abandonando los juveniles la cuenca del estanque a lo largo de la primavera de 1986. La estructura etaria de la población adulta permaneció constante a lo largo del estudio, aún cuando el tamaño poblacional disminuyó. La razón de sexos estuvo sesgada hacia los machos en todos los años excepto 1990. Los machos fueron más pequeños que las hembras en longitud naso-urostilar y peso, existiendo diferencias significativas entre años y sexos. La sequía eliminó la reproducción por cinco años, y pareció reducir el tamaño general de la población. Correlaciones directas entre los efectos de la sequía y variación natural estocástica no son posibles todavía. Mis datos sugieren que *G. carolinensis* sobrevive prolongadas sequías a través de la mantención de grandes poblaciones repartidas a lo largo de una variedad de habitats y además al menos algunos individuos son oprtunistas en vez de filopátricos en la elección de sus sitios reproductivos. Estudios a largo plazo y experimentos manipulativos de campo permitirán responder algunas de las muchas preguntas que surgen de estos resultados.

INTRODUCTION

Droughts are common in Florida (Winsberg 1990), and have been an important natural agent in selecting xeric-adapted plant species that comprise the vegetation of many Florida ecosystems, including the sandhills community of central and north-central Florida (Myers 1990). Although tree ring records are not published for Florida, core samples from cypress trees (*Taxodium distichum*) in other parts of the southeast suggest that droughts occur in cycles that alternate with mesic or wet periods of varying duration (Stahle et al. 1988). Many Florida animals, particularly amphibians and reptiles, were derived from xeric-adapted western forms that migrated to the Southeast prior to the mid-Pleistocene (Auffenberg and Milstead 1965; Meylan 1982; Webb 1990).

Although droughts occur on a regular basis, there are no quantitative data on the responses of Florida's amphibian communities to prolonged drought. In other areas, drought suppresses reproduction in amphibians (Fitch 1956), results in the death of eggs or larvae prior to metamorphosis (Wright 1932; Tevis 1966; Heyer 1973; Shoop 1974; Seale 1982; Semlitsch 1983, 1987), and can lead to the decline or extinction of local populations (Blair 1957; Corn and Fogelman 1984; Osborne 1989). For temporary pond-breeding amphibians, drought may play an important role in population dynamics (e.g. Dodd 1993; Healy 1974; Harris et al. 1988;

Semlitsch and Wilbur 1989). Drought also has been suggested as a contributing factor in the apparent worldwide decline in amphibians, particularly anurans.

Temporary ponds are dispersed throughout Florida's xeric uplands. These ponds form in shallow clay-lined basins and typically fill during winter, spring, or summer rains (LaClaire and Franz 1990). Summer thunderstorms are frequent but scattered, and the often torrential rains help to maintain hydroperiod (i.e. the amount of time standing water is in a wetland). As summer progresses, sandhill ponds usually dry and remain without water through the autumn, unless rain from a tropical depression or hurricane refills them. The wet-dry cycles are not regular, however, and long periods with or without water are common.

Many ponds in sandhill habitats lack fishes because they are not connected with other wetlands. In addition, an unpredictable and locally variable hydroperiod results in variability in invertebrate populations, such that predacious species may or may not colonize particular ponds. The composition and population sizes of invertebrate species are not consistent within a geographic region because of variation in local wetland hydroperiod coupled with variation in predators' abilities to colonize spatially fragmented habitats. The absence of fishes and the potential for reduced levels of invertebrate predation allow amphibians, particularly those species that do not have well developed antipredator defenses (Kats et al. 1988), to reproduce in temporary ponds (Pechmann et al. 1989; Bristow 1991; Dodd 1993).

The importance of temporary ponds to a wide variety of wildlife is only beginning to be appreciated (Moler and Franz 1988; LaClaire and Franz 1990). In Florida sandhill communities, several species (e.g. *Notophthalmus perstriatus*, *Rana capito aesopus*) are obligate temporary pond breeders. Many other amphibians, however, also breed in temporary ponds. From March 1983 through February 1985, 13 anuran species bred in 10 temporary, isolated, clearwater, sandhill ponds averaging 0.1-0.3 ha on the Katharine Ordway Preserve/Swisher Memorial Sanctuary in Putnam Co., Florida (Moler and Franz 1988). Of 22 anuran species breeding in small isolated wetlands on the southeastern Coastal Plain, 10 use temporary ponds as their principal or exclusive breeding habitat (Moler and Franz 1988).

In 1985, I began a 5-year study of a temporary wetland in the "high pine" uplands of north-central Florida. The objectives of the project were to measure the species richness, diversity, and dominance of the community (Dodd 1992) and to gather basic information on the population biology of species that use the pond and adjacent uplands. However, a prolonged drought during the study provided the opportunity to examine the effects of drought on the amphibian community.

In this paper, I report the results from data gathered on the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, the most abundant amphibian that visited the pond. This toad is found from the Delmarva Peninsula south throughout Florida and west to Missouri and Texas (Conant and Collins 1991). The species is largely subterranean and secretive in habits, and its diet consists

almost entirely of ants and termites (Holman and Campbell 1958; Ashton and Ashton 1985). Breeding occurs in a wide variety of temporary water habitats, including ponds, ditches, and pools. Although commonly found in the Florida sandhills (Campbell and Christman 1982; Mushinsky 1985), *Gastrophryne* occurs in many other habitat types (Carr 1940; Anderson 1954).

Despite its large range and conspicuous nature during the breeding season, there have been few studies of its ecology (Wright 1932; Anderson 1954) or even of the timing of various activities, including reproductive phenophase (*sensu* Mitchell 1979; Trauth et al. 1990). In other parts of the Southeast, data consist mostly of observations on numbers at breeding ponds taken incidentally to other studies (e.g. Gibbons and Bennett 1974; Gibbons and Semlitsch 1982, 1991) or of anecdotal information on distribution, calling, coloration and feeding (Hecht and Matalas 1946; Duellman and Schwartz 1958; Nelson 1972; Dalrymple 1988). This paper presents data on the ecology of a Florida sandhills eastern narrow-mouthed toad population and its response to a prolonged drought. These results will form the baseline data for monitoring this population as part of a planned long-term assessment of amphibian status.

ACKNOWLEDGMENTS

I thank R. Altig, M. Crump, D. Forester, R. Franz, J. Palis and J.H.K. Pechmann for reviewing drafts of the manuscript and offering helpful suggestions. B. Charest, K. Enge, J. Stuart, M. Blouin, K. Studenroth, and R. Burke assisted in data collection. I especially thank R. Franz for advice and shared information over the years and L. LaClaire and L. Smith for information on the vegetation and physical structure of Breezeway Pond.

STUDY AREA AND METHODS

Field data were collected at Breezeway Pond, a 0.16 ha depression marsh (Florida Natural Areas Inventory 1990) located in a shallow 1.3 ha basin on the Katharine Ordway Preserve/ Swisher Memorial Sanctuary, Putnam Co., Florida. The pond is surrounded by a "high pine" community dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and wiregrass (*Aristida stricta*) to the south and west, a maidencane (*Panicum hemitomon*) meadow to the east, and a xeric oak hammock dominated by sand live oak (*Q. geminata*) and laurel oak (*Q. hemisphaerica*) to the north. Breezeway Pond is formed in a shallow sinkhole depression and is not part of a flow-through drainage system. Water enters the pond solely from rainfall and groundwater recharge. The hydroperiod is thus dependent upon the level of the water table in the nearby surrounding uplands. Water percolates downhill into the basin where it is trapped by stratified organic

soil layers beneath the soil surface (LaClaire and Franz 1990). The pond continuously held water for two years prior to the initiation of my study, but its soil profile suggests that periodic droughts are common (LaClaire and Smith unpubl.).

The pond area was enclosed by a 230-m drift fence made of galvanized metal flashing (36 cm above ground, 10-15 cm below the surface). No vegetation overhung the fence, and the fence and pond area were exposed to direct sunlight. Vegetation was kept cut and away from the fence exposing bare white sand for about 40 cm from the base of the fence in either direction. The distance from the drift fence to the nearest forest cover is generally 20 m, but extends to about 50-60 m behind the *Panicum* meadow. Within the enclosure, herbaceous hydrophytic vegetation dominated the basin although a few shrubs, including buttonbush (*Cephalanthus occidentalis*), myrtle holly (*Ilex myrtifolia*), and wax myrtle (*Myrica cerifera*), were present. Several sapling longleaf and slash pines (*P. elliottii*) grew within the enclosure. Maidencane and carpetgrass (*Axonopus furcatus*) comprised 76 percent of the ground cover on vegetation transects (LaClaire and Smith unpubl.).

Pitfalls (19-l black plastic buckets) were placed on opposite sides of the fence at 10-m intervals following the procedures outlined by Gibbons and Semlitsch (1982). In order to minimize the effects of direct sun, the buckets were partially shaded with pegboard slanted over the openings in such a manner that there was plenty of room for transit beneath the boards. Each board was laid flat across the bucket opening on days when the pitfalls were not to be checked in order to prevent desiccation of captured animals. Eastern narrow-mouthed toads were captured even when the boards covered the bucket openings because the seals were not complete.

The pitfalls were checked 5 days per week between 0700 h and 0900 h, depending on season, from October 1985 through September 1990 (1,273 days; 83,950 bucket nights). A year was defined as extending from October of one year through September of the following year (e.g. "1986" covers October 1985 through September 1986) for purposes of analysis. This yearly partition corresponds better than the calendar year with amphibian activity patterns in north-central Florida.

Frogs were measured in the field with a clear plastic ruler (snout-urostyle length [SUL], defined as the tip of snout to the posterior portion of the urostyle) and weighed to the nearest 0.1 g using a Pesola hand-held spring scale. Males have a clearly visible black chin that is present in varying levels of intensity year-round (Anderson 1954). In females the chin is mottled, light, and the same color as the belly (Wright 1932). Females also occasionally contained eggs visible through the ventral body wall. The sex was classified as "unknown" if there was any question about the sex of the animal. Animals smaller than 21 mm SUL generally were considered juveniles (Wright 1932; Anderson, 1954), although the sex of some individuals was difficult to determine at 22-24 mm SUL (also see Hecht and Matalas 1946). Anderson (1954) noted that *G. carolinensis* show adult secondary sex characteristics across a range of sizes and that determining gonadal

activity solely from external characters is impossible. I marked frogs by clipping toes using a year-specific cohort sequence; no more than one toe was clipped per foot. I carefully examined all captured animals for regenerated toes. Frogs were released on the opposite side of the fence from where they were captured.

In addition to biological data, I recorded maximum and minimum air and water temperature and rainfall since the pitfalls were last checked, current weather conditions, and the occurrence of cyclic weather patterns (e.g. cold fronts, severe storms, etc.).

Eastern narrow-mouthed toads marked in one year and recaptured in another year presented special data analysis problems, because I could not determine whether an individual had been caught more than once during the second year. Either combining or excluding counts of previously marked frogs with first-caught frogs will give an imprecise picture of population structure and sex ratio of the breeding population. In the results and discussion below, I arbitrarily chose to exclude multi-year recaptures; descriptive statistics relate to previously unmarked animals caught within a year cohort. Multi-year recaptures are treated separately in the paper.

RESULTS

Hydroperiod and Rainfall

From 1985 to 1990, generally small amounts of rain falling in the vicinity of Breezeway Pond resulted in short hydroperiods at various times of the year (Dodd 1992). Large lakes also dried as the water table dropped > 2.5 m throughout north-central and northeastern Florida from 1988 to 1990. Although the maximum recorded water depth at Breezeway Pond was 75 cm, the pond held water for only 14 mo from January 1985 through September 1990 (Fig. 1). The water table was located 60 cm below the ground surface of the bottom of the pond in October 1989 (LaClaire and Smith unpubl.). By February 1991, the water table had dropped to 2.5 m below the ground surface and the central pond area was colonized by a thick growth of *Panicum*.

The driest months at Breezeway Pond were April and October, whereas the wettest months generally were in the summer, except in 1987 and 1988 (Fig. 1). Less than 300 mm of rain fell in any one month except in September 1988, when a tropical depression brought 270 mm of rain in four days. Rainfall was sporadic, however, and very dry months occurred at all times of the year, especially from October 1988 through September 1990.

In the summer (mid-May through mid-September), thunderstorms provided most of the rainfall in the vicinity of Breezeway Pond. However, rainfall from thunderstorms was localized and, during the latter years of the study, was

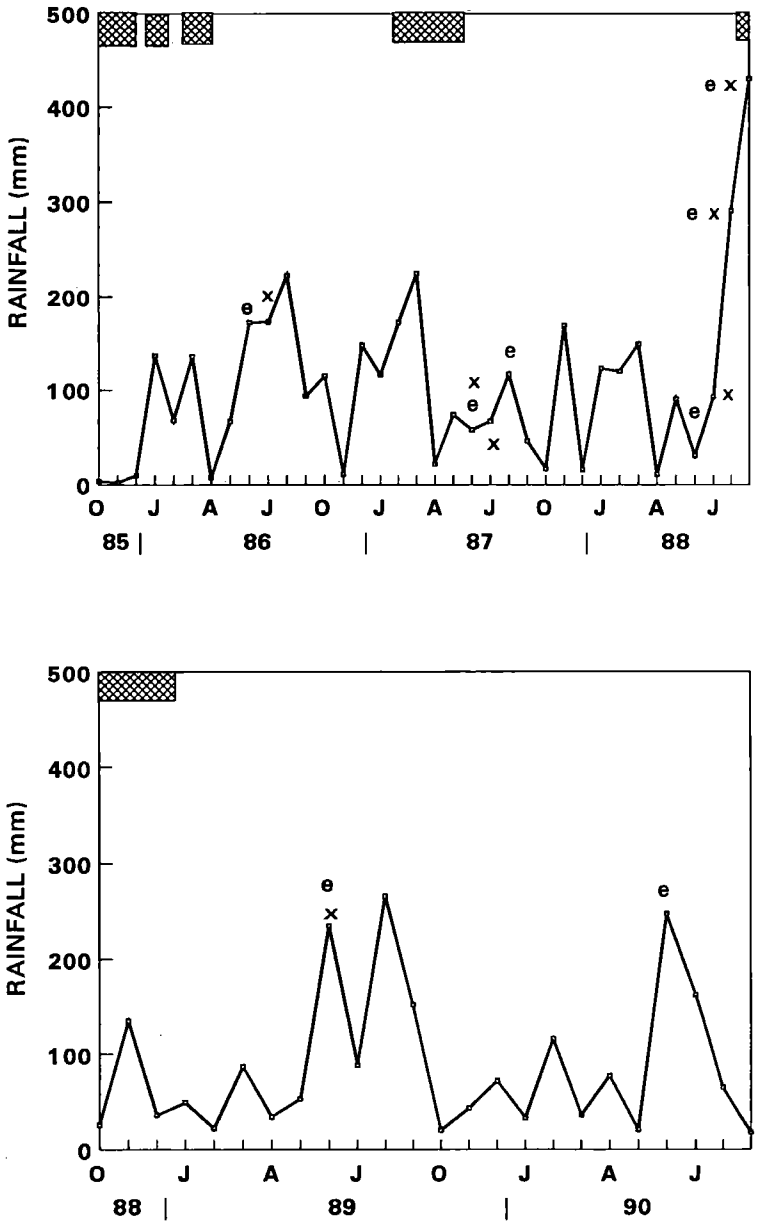

Fig. 1. Monthly rainfall totals at Breezeway Pond, Putnam Co., Florida, October 1985-September 1990. The stippled bars at the top of the figure illustrate the duration of the hydroperiod. No water was present in the pond at other times of the year. The stars indicate months with substantial movements of *Gastrophryne carolinensis* into (e) or away from (x) the pond.

insufficient to replenish groundwater depleted by regional drought. North-central Florida experienced a record drought during the latter half of the study based on hydrological data kept by the St. Johns River Water Management District. Other than the 1988 tropical depression, no weather patterns during that period resulted in substantial rainfall at Breezeway Pond.

Daily and Seasonal Activity

A total of 5740 eastern narrow-mouthed toads, including recaptures, were captured between 1985 and 1990 (Table 1). Most were captured during the first four years of the study, and captures declined dramatically in 1990 as the drought progressed. Eastern narrow-mouthed toads were captured during all months of the year (Table 2), although they were not captured in all months of any one year (Fig. 2). Juveniles were caught more often than adults during the winter months of December through February.

Adult males and females entered and exited the pond at all times of the year (Table 2). However, 98% of all adult captures occurred from May through September from 1986 through 1990. During the 1986, 1988, and 1990 field seasons, most activity occurred from June through September (Fig. 2). Juveniles exited the pond basin in the autumn of 1985 and during the spring of 1986, but entered the pond from September through early November 1988.

Adult males and females were active not only during the same months of the year (Fig. 2), but also on the same days. A visual examination of capture records from 1986 through 1990 for the months of June, July, and August revealed no temporal differences in the daily capture of males and females. A representative example of the daily capture data for males and females is shown for June 1989 (Fig. 3). Neither sex was active consistently before or after the other sex.

Although individuals might be active during very dry periods, rainfall triggered an immediate response. When rain fell from May through September, frogs became active and were encountered at the drift fence. For example, *Gastrophryne* moved in large numbers on only 10 occasions in June from 1986 through 1990. On eight of these occasions, rainfall totaled 29 mm or greater (Table 3). On the remaining two occasions, the rainfall occurred after long periods without rain. Most eastern narrow-mouthed toads were captured when most of the monthly rainfall was recorded (Table 3). Large numbers of toads moved to Breezeway Pond only in the presence of some rainfall.

The presence of standing water within the pond basin had no effect on eastern narrow-mouthed toad movements, i.e. animals went to the pond in mid-summer whether water was present or not (Fig. 1). Frogs entering Breezeway Pond encountered standing water only twice from 1985 through 1990, and in one of

Table 1. Captures of unmarked (first number) and marked (second number) *Gastrophryne carolinensis* at Breezeway Pond, Putnam County, Florida, 1986-1990. If the sex of an animal could not be determined, it was classified as "Unknown."

Year	Males	Females	Juveniles	Unknowns	Total
1986	193/76	142/48	37[1]	482/102	854/226
1987	180/164	189/107	1/0	9/3	379/274
1988	507/195	351/130	8/0	31/2	897/327
1989	219/122	181/120	240/35	----	640/277
1990	55/24	66/36	1/0	1/5	123/65
Total	1154/581	929/441	287/35	523/112	2893/1169

1 An additional 1678 recently metamorphosed juveniles were not marked in 1986.

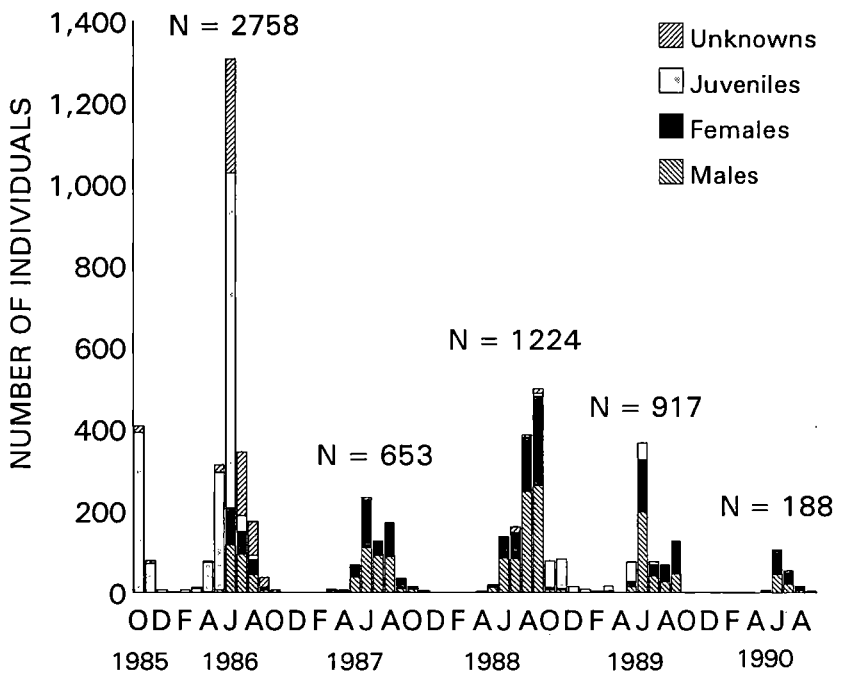

Fig. 2. Monthly and annual variation in activity patterns of adult and juvenile *Gastrophryne carolinensis* at Breezeway Pond, Putnam Co., Florida. Data combined for all captures (N=5740), entering and exiting.

Table 2. Capture of *Gastrophryne carolinensis* entering and exiting Breezeway Pond, Putnam County, Florida, by month, 1986-1990. The total includes animals for which the sex was not determined. N = 5740.

Month	Total		Adults Exit		Adults Enter		Juveniles	
	Exit	Enter	M	F	M	F	Enter	Exit
Jan	1	10	0	0	1	0	9	1
Feb	6	8	2	0	0	1	7	3
Mar	12	25	1	3	4	5	14	7
Apr	0	86	0	0	7	4	72	0
May	195	285	11	10	64	43	164	170
Jun	1130	1018	190	125	364	318	125	737
Jul	507	254	235	138	96	71	7	40
Aug	358	456	192	117	218	187	1	11
Sep	470	230	242	200	83	128	8	3
Oct	361	141	8	8	8	6	115	341
Nov	75	91	6	4	3	2	79	65
Dec	6	15	0	0	0	0	15	6
Total	3121	2619	887	605	848	765	616	1384

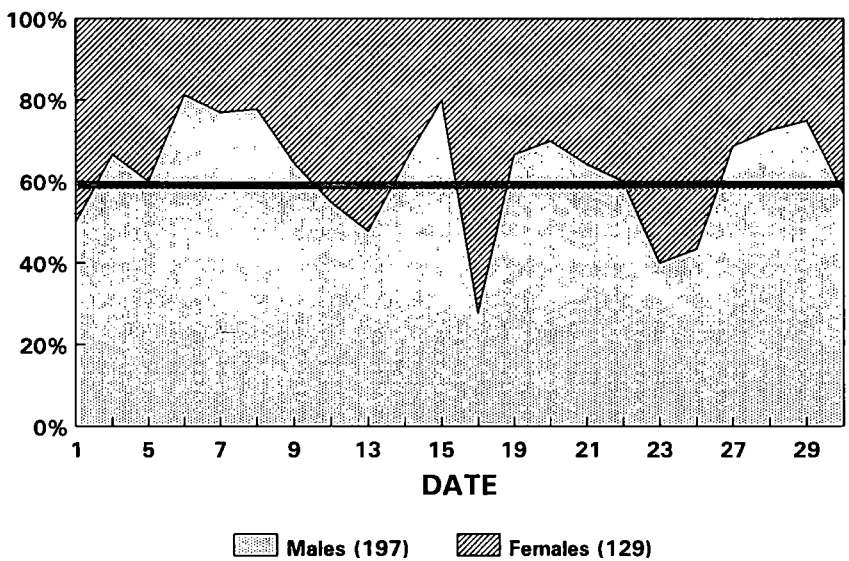

Fig. 3. Proportional capture of male and female *Gastrphryne carolinensis* at Breezeway Pond, Putnam Co., Florida, in June, 1989. Males comprised 60% of the sample. Both sexes always were captured on the same day.

Table 3. Relationship between the number of adult *Gastrophryne carolinensis* captured and daily rainfall during the month of June 1986-1990.

Year	Date	Rainfall (in mm)	Number Captured	% of Monthly Capture	% of Monthly Rain
1986	18-22	147	156	75.4	85.5
1987	15-18	2	96		
	22-26	42	60	68.7	75.9
1988	6-10	29	79		
	28	2	27	78.5	100
1989	5-14	51	139		
	20-23	108	89		
	26-28	67	53	86.1	96.1
1990	7-12	108	45		
	25-27	136	31	74.5	98.4

those years (1987), the pond dried in June. A cumulative high monthly rainfall total also was not associated with movement to or away from the pond (Fig. 1). The sole exception was associated with a September 1988 tropical depression that drenched north-central Florida. Individual frogs probably went back and forth between the pond basin and upland retreat sites, depending on weather conditions, throughout the breeding season.

Most of the eastern narrow-mouthed toads that were captured at the beginning of the activity season in May or June were unmarked (Figs. 4, 5). However, the relative proportion of unmarked to marked animals neither remained constant nor decreased, except in 1990. Instead, a second influx of unmarked animals appeared in August and September. The proportion of unmarked to marked animals changed from one year to the next as the activity season progressed, but the within-year patterns were similar between the sexes (Figs. 4, 5).

Population Structure

The overall sex ratio of unmarked adult (> 23 mm SUL) eastern narrow-mouthed toads was one female for every 1.30 males. A male bias in the sex ratio was present in all years except for 1990 (Table 4). The sex ratio of unmarked animals differed significantly from 1:1 in 1986 (χ^2=9.95, df=1, p =

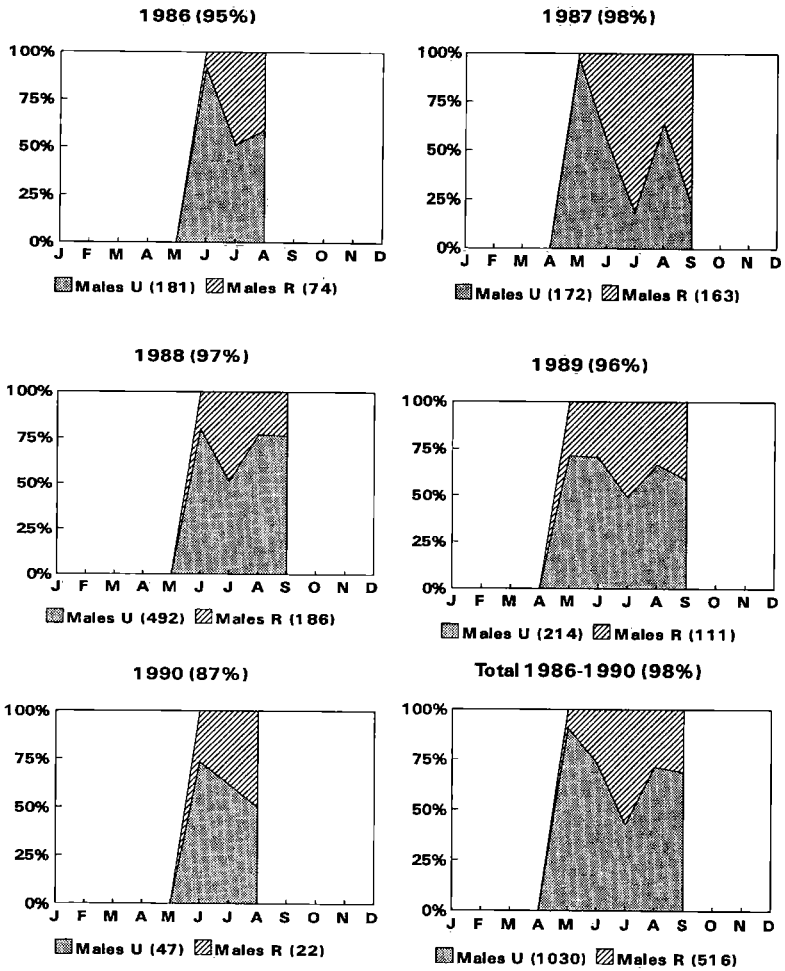

Fig. 4. Proportional capture of unmarked (U) to recaptured (R) male *Gastrophryne carolinensis* during the priciple activity season at Breezeway Pond, Putnam Co., Florida, 1986 - 1990. The number in parentheses after the year is the percentage of the total number of males captured within that year.

0.0016), 1988 (χ^2=30.57, df=1, $p < 0.0001$), and in the overall sex ratio from 1986 through 1990 (χ^2=28.76, df=1, $p < 0.0001$). In 1990, the ratio was nearly significant (χ^2=3.61, df=1, $p = 0.0574$). For recaptured animals, the adult sex ratio was one female for every 1.29 males and was male-biased in all years except 1990.

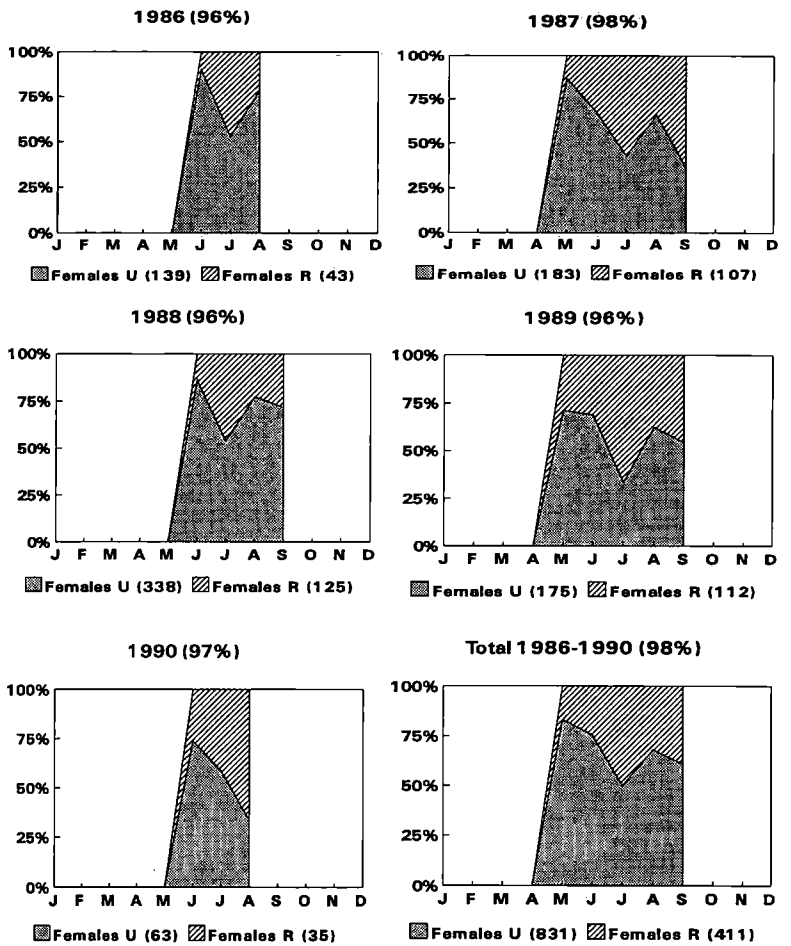

Fig. 5. Proportional capture of unmarked (U) to recaptured (R) female *Gastrophryne carolinensis* during the principle activity season at Breezeway Pond, Putnam Co., Florida, 1986 - 1990. The number in parentheses after the year is the percentage of the total number of females captured within that year.

There was no trend toward a 1:1 sex ratio as the season progressed in any year (Table 4).

Population size structure varied somewhat among years (Fig. 6). In 1987, 1988, and 1990, the population structure was unimodal with few or no juveniles and very large animals among the unmarked toads. In 1986 and 1988, the

Table 4. Summary of sex ratio data within and among years for all *Gastrophryne carolinensis* captured at Breezeway Pond, Putnam County, Florida, during the months of June, July, and August. The tabulation includes all adults captured within that month.

	June			July			August		
Year	M	F	Ratio	M	F	Ratio	M	F	Ratio
1986	117	90	1.3:1	94	55	1.7:1	44	37	1.2:1
1987	110	117	0.9:1	91	35	2.6:1	88	82	1.1:1
1988	85	50	1.7:1	84	63	1.3:1	247	133	1.9:1
1989	197	129	1.5:1	41	27	1.5:1	27	40	0.7:1
1990	45	57	0.8:1	21	29	0.7:1	4	12	0.3:1

Table 5. Analysis of variance of differences in snout-urostyle length (SUL) and weight among years between the sexes of unmarked adult *Gastrophryne carolinensis*, 1986-1990. No weight data were available for 1987. Values are for Type III sums of squares.

Variable	Year	Sex	Year*Sex
SUL	F=115.24	F=186.53	F=16.56
	p=0.0001	p=0.0001	p=0.0001
	4 df	1 df	4 df
Weight	F=46.85	F=329.52	F=1.43
	p=0.0001	p=0.0001	p=0.2316
	3 df	1 df	3 df

population structure was bimodal with the appearance of recently metamorphosed young from the 1985 breeding season (exiting Breezeway Pond in 1986) and from immigrants from some other location in 1988 (entering Breezeway Pond in September, October, and November). Despite the lack of reproduction at Breezeway Pond from 1986 through 1990, the population structure did not shift appreciably toward large adults as the study progressed. In 1990, a small number of eastern narrow-mouthed toads came to the pond, but the adult size structure did not differ from previous years.

Table 6. Descriptive statistics for snout-urostyle length showing number, range, mean, and standard deviation (in mm) of unmarked *Gastrophryne carolinensis* caught at Breezeway Pond, Putnam County, Florida, 1986-1990.

Year	Males	Females	Juveniles	Unknowns
1986				
N	137	89	36	326
Range	(22-33)	(23-35)	(14-19)	(20-33)
Mean	27.8	28.8	18.1	22.8
S.D.	1.52	2.36	1.18	1.78
1987				
N	180	189	—	5
Range	(22-34)	(21-34)	—	(21-26)
Mean	26.4	26.5	—	22.8
S.D.	1.50	2.60	—	1.92
1988				
N	376	239	8	—
Range	(24-31)	(24-34)	(11-14)	—
Mean	27.5	29.1	12.9	—
S.D.	1.31	0.38	1.13	—
1989				
N	219	181	222	—
Range	(24-32)	(24-35)	(11-24)	—
Mean	28.1	30.1	15.9	—
S.D.	1.43	1.99	2.37	—
1990				
N	55	66	1	1
Range	(24-30)	(25-33)	—	—
Mean	27.1	29.0	22	25
S.D.	1.26	1.68	—	—

Significant differences in SUL and weights occurred among years and between sexes (Table 5), except for the year*sex interaction in weight. Differences among mean adult SULs and weights were generally small (Tables 6, 7). Adult males were shorter and weighed less than adult females in all years, although the difference was slight in 1987. The largest mean SUL for both males and females

Table 7. Descriptive statistics for weight showing number, range, mean, and standard deviation (in mm) of unmarked *Gastrophryne carolinensis* caught at Breezeway Pond, Putnam County, Florida, 1986-1990. Weights were not recorded in 1987.

Year	Males	Females	Juveniles	Unknowns
1986				
N	137	89	33	318
Range	(1.0-2.9)	(0.8-4.8)	(0.2-0.7)	(0.5-2.5)
Mean	1.93	2.29	0.52	1.10
S.D.	0.30	0.66	0.11	0.30
1988				
N	301	177	8	—
Range	(0.6-2.5)	(1.2-3.0)	(0.1-0.3)	—
Mean	1.62	2.04	0.19	—
S.D.	0.20	0.38	0.06	—
1989				
N	206	176	198	—
Range	(1.1-2.8)	(0.9-3.2)	(0.1-1.0)	—
Mean	1.75	2.23	0.35	—
S.D.	0.24	0.44	0.16	—
1990				
N	54	66	1	1
Range	(1.2-2.7)	(1.5-3.4)	—	—
Mean	1.93	2.42	1.1	0.6
S.D.	0.29	0.43	—	—

was in 1989, whereas the smallest mean SUL for both was in 1987. The largest male was 32 mm SUL, whereas the largest female was 35 mm SUL. Adult females weighed more than adult males in all years. Weights were greatest for adult males in 1986 and 1990, and for females in 1990.

Multi-Year Recaptures

Most recaptured eastern narrow-mouthed toads were caught within the same year they were marked (Table 1), but 134 multi-year recaptures were

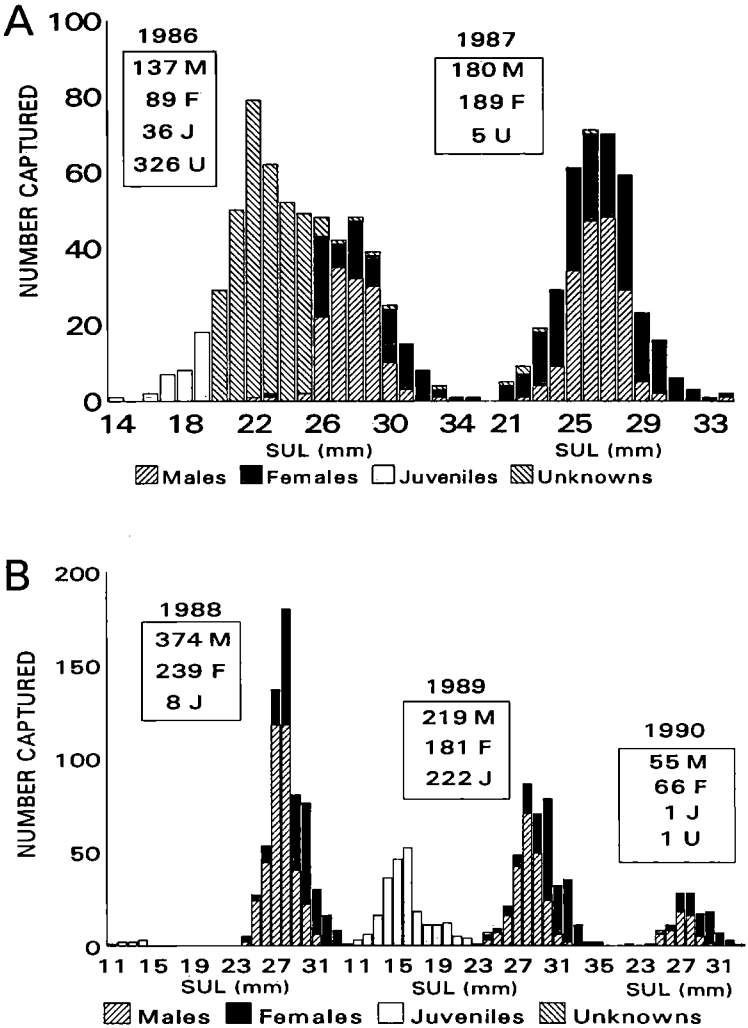

Figure 6. Annual variation in size-class structure of *Gastrophryne carolinensis* at Breezeway Pond, Putnam Co., Florida. A. 1986 -1987. B. 1988-1990. An additional 1679 juveniles < 15 mm SUL were captured in 1986. Note the difference in scale.

recorded (Table 8). Most multi-year recaptures were marked in one year and observed during the following year. Multi-year recaptures included both immigrants to and emigrants from the pond throughout the activity season, and made it impossible to determine how often they were caught within a season.

The size-class distribution of toads captured after one year spanned nearly the entire range of size classes captured during the study (Fig. 7). However, the size-class distributions of eastern narrow-mouthed toads captured after two and three

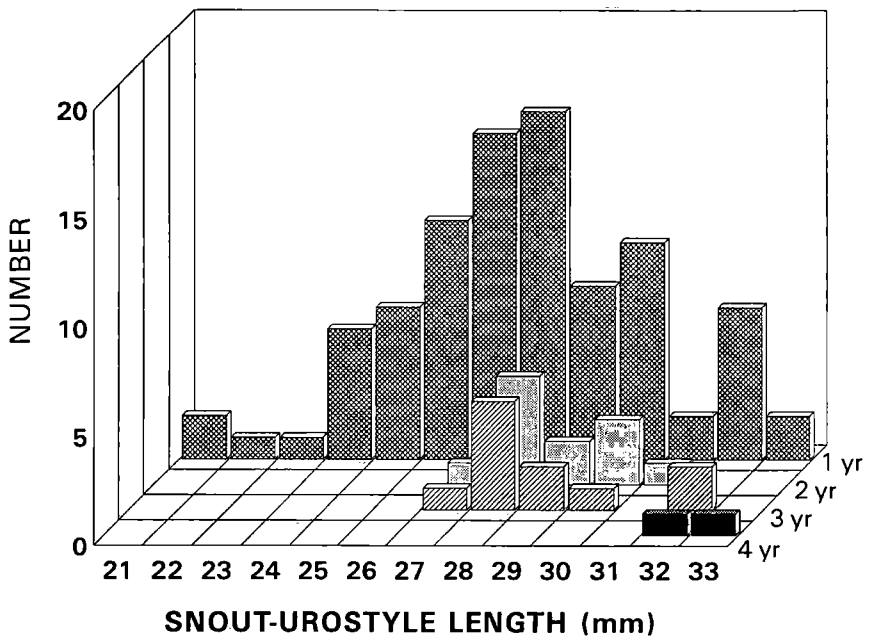

Figure 7. Size-class structure of multi-year recaptured *Gastrophryne carolinensis* at Breezeway Pond, Putnam Co., Florida, 1986 - 1990. Recaptures occurred after 1 year (N = 88), 2 years (N = 12), 3 years (N = 11), or 4 years (N = 2).

years were quite similar to one another and included only larger adults. Only two toads were captured four years after marking.

For the three years with the most multi-year recaptures, recaptured males were larger than unmarked males in 1987 (mean=26.6 mm, N=13) but smaller than unmarked males in 1988 (mean=27.3 mm, N=27) and 1989 (mean=27.8 mm, N=30). Lengths for multi-year recaptured females were larger in 1987 (mean=26.9 mm, N=10) and 1989 (mean=30.6 mm, N=17) but slightly smaller in 1988 (mean=29.0 mm, N=20) than unmarked females. The weights of multi-year recaptured males were nearly identical with unmarked males in 1988 (mean=1.6 g, N=11), but multi-year recaptured females were substantially heavier (mean=2.3 g, N=6) than unmarked females. In 1989, female weight was nearly identical between marked and unmarked (mean=2.2 g, N=17) animals, whereas unmarked males weighed more than multi-year recaptured males (mean=1.6 g, N=30). The sex ratio of multi-year recaptured animals in 1987 was one female per 1.3 males; in 1988, one female per 1.35 males; and in 1989, one female per 1.76 males.

Table 8. Multi-year recapture data for *Gastrophryne carolinensis* at Breezeway Pond, Putnam County, Florida, 1986-1990.

Year Initially Marked	Total Marked	Year Recaptured				
		1986	1987	1988	1989	1990
1986	847	—	23	20	11	2
1987	379		—	42	2	0
1988	893			—	34	0
1989	640				—	0

Reproduction and Size at Metamorphosis

Breezeway Pond held water only from 7 June through 13 December 1985 (189 day hydroperiod) and from 24 February through 19 June 1987 (139 day hydroperiod) during the reproductive season of *G. carolinensis*. Juvenile eastern narrow-mouthed toads left the pond in October and November 1985 and from April through June 1986. These animals were derived from the 1985 juvenile cohort. Eastern narrow-mouthed toads did not reproduce successfully in 1987, because the pond dried before metamorphosis could be completed. The other times that the pond held water (Fig. 1) were outside the breeding season of *G. carolinensis* and no reproduction occurred from 1986 through 1990.

From September through November 1988, 146 unmarked juvenile eastern narrow-mouthed toads were recorded at Breezeway Pond. Of these, 105 (72%) were captured as they entered the pond. Because of their small size and the lack of water for the previous 13 months, it is unlikely that the remaining 41 animals originated from within the enclosed pond. I suggest instead that they probably trespassed the fence (Dodd 1991). The movement of this large group of juveniles occurred after a tropical depression in September 1988. All originated from other breeding sites and were not part of any reproduction at Breezeway Pond during the summer of 1988.

All of the juveniles captured in the autumn of 1985 as they left Breezeway Pond were < 14 mm SUL. The long hydroperiod during the summer of 1985 allowed larvae to complete metamorphosis without the threat of desiccation, and toadlets probably foraged in the pond basin for several weeks or months prior to

Table 9. Trap mortality of *Gastrophryne carolinensis* at Breezeway Pond, 1986-1990.

Year	Male	Female	Juvenile	Unknown	Total
1986	0/269	0/190	178/1715	22/584	200/2758
					7.25%
1987	0/344	3/296	1/1	7/12	11/653
					1.68%
1988	2/702	3/381	0/8	20/33	25/1224
					2.04%
1989	4/341	1/301	20/275	—	25/917
					2.73%
1990	2/79	1/102	0/1	5/6	8/188
					4.25%
Total	8/1735	8/1270	199/2000	54/635	269/5740
%	0.46	0.63	9.95		4.69

exiting. Thus, the size of the juveniles exiting the pond from the 1985 cohort probably exceeded their size at metamorphosis. The smallest eastern narrow-mouthed toad measured at Breezeway Pond was 11 mm SUL. If this size can be taken as the minimum size at metamorphosis at Breezeway Pond, then the juveniles that were captured in the spring of 1986 grew from 3-8 mm prior to exiting the pond.

Mortality

Relatively few adult *G. carolinensis* died in bucket traps from 1986 through 1990 (Table 9). Most mortality occurred in the juvenile size class, particularly in 1986 as large numbers of juveniles left the pond basin. The chief cause of mortality seemed to be from desiccation despite the presence of moist sponges in the bucket. In the hot summer, particularly during periods of drought, sponges often dried within 20 h of hydration. After desiccation, the principal mortality source was predation by ants, spiders (*Geolycosa* sp.), and carabid beetles (*Pasimachus strenuus*, *P. subsulcatus*, *Dicaelus* sp.). In most instances, it was not

possible to determine whether the invertebrate killed the toad or the predator scavenged a carcass.

DISCUSSION

Life-history of *Gastrophryne carolinensis*

Population Size.—There are no comparable studies on the eastern narrow-mouthed toad in Florida with which to compare the results of this study. At least 900 adult *G. carolinensis* visited the pond basin (unmarked animals with allowances for a few animals presumed to trespass the fence; Dodd 1991) in each of two of the five years that the fence was checked. The number of animals visiting the pond in 1987 is inexplicably low in relation to 1986, 1988, and 1989. This could be due to a natural population fluctuation, but it makes the interpretation of the 1990 collection data difficult. The most parsimonious explanation for the low pond visitation in 1990 is that the effects of the long-term drought were becoming apparent. Alternatively, the low numbers in 1990 could represent a natural fluctuation. The numbers of breeding adults and juveniles that complete metamorphosis of pond-breeding amphibians are known to fluctuate widely (Shoop 1974; Gibbons and Bennett 1974; Semlitsch 1987; Pechmann et al. 1989; Raymond and Hardy 1990; Pechmann et al. 1991).

Recaptures.—Relatively few *G. carolinensis* were recaptured. Most recaptured individuals were captured in the same season as originally marked, presumably as the toads crossed back and forth between the core of the pond basin and refugia in the surrounding uplands. Other studies on *Gastrophryne* also report low recapture rates (Anderson 1954; Fitch 1956; Franz et al. 1989). Freiburg (1951) recaptured 33.5% of marked *G. olivacea* in his 1-year study but only 12.7% more than once. Fitch (1956) marked 1215 *G. olivacea* between 1949 and 1954, but only 13 "yielded series of records, well spaced, in two or more different years." Of 69 tattooed *G. carolinensis* trapped in April and May in Louisiana, only five were recaptured (Anderson 1954).

Gastrophryne carolinensis may regenerate clipped toes rapidly, become trap-shy or otherwise learn to avoid recapture, move to breeding ponds only once or twice within a 5-year period thus minimizing the chances of recapture, or have very high mortality rates. Rates of toe regrowth are unknown, but little evidence of regrowth was apparent in this study or in studies of *G. olivacea* (Freiburg 1951). Unpublished data on movements based on cobalt tagging suggest that *G. carolinensis* may be sedentary and trap-shy (Franz et al. 1989). *G. carolinensis* also easily crawl vertically upwards (Wright 1932) and cross drift fences (Dodd 1991). Alternative forms of marking and long-term studies are needed to evaluate capture efficiency and individual recognition.

Low recapture rates in amphibian studies have led some authors to conclude that mortality rates are very high from one year to the next (e.g. Given 1988). Although *G. carolinensis* possesses noxious skin secretions (Garton and Mushinsky 1979), many vertebrates and invertebrates probably prey on this abundant resource. This species also seems particularly sensitive to desiccation (Anderson 1954; Wygoda 1984). Mortality at the pond or in refugia certainly occurs, but whether it accounts for the low multi-year recapture percentages cannot be ascertained.

Seasonal Activity.--Some *G. carolinensis* were active throughout the year at Breezeway Pond, although adult activity was greatly reduced from October through April. Juveniles were active in all months, especially in the autumn, presumably as they dispersed. Peak population activity occurred from June through September as adults moved toward and away from Breezeway Pond. This period is similar to that reported elsewhere for this species (Wright 1932), although the breeding season extends from April through September in the southern parts of the range (Anderson 1954; Mount 1975; Dundee and Rossman 1989). April and May were very dry months at Breezeway Pond from 1986 through 1990, perhaps accounting for the lack of activity in these months.

Activity of *Gastrophryne* is definitely influenced by rainfall (Deckert 1914; Wright 1932; Freiburg 1951; Anderson 1954; Fitch 1954). Heavy rains from June through September stimulated adult animals to move to breeding sites. Movement occurred during the rainy period, and there was no evidence of a lag effect. The amount of rain needed to trigger movement varied with previous weather conditions. If rainfall was regular, high amounts of rain were required to stimulate movement. However, during droughts, rainfall of as little as 2 mm stimulated substantial numbers of toads to move toward or away from the pond.

Although small amounts of rainfall can trigger movements to breeding ponds by amphibians (e.g. Semlitsch 1985; Dodd and Charest 1988; Sexton et al. 1990), most *G. carolinensis* move to ponds only after heavy rains, except after prolonged periods without rain. Rainfall in April and May was never greater than 20 mm on any one day from 1986 through 1990 at Breezeway Pond. Amounts were generally 1-10 mm. Few *G. carolinensis* moved during these months, although eastern narrow-mouthed toads breed in April and May elsewhere in Florida (Carr 1940; Duellman and Schwartz 1958) and nearby southern Georgia (Wright 1932). Presumably, movement and reproductive behavior would have commenced in April or May at Breezeway Pond if heavy rainfall had occurred.

Two peaks of immigration by unmarked animals of both sexes were evident annually from 1986 through 1989. The first occurred in June, and the second occurred in August. Two hypotheses are possible. The first is that two temporally segregated groups of toads breed in Breezeway Pond. Alternatively, the August pulse of unmarked animals represents toads that bred elsewhere and were moving

through the area on their way to terrestrial refugia. No August peak was observed in 1990, but its absence might have been a consequence of drought.

One way to test these hypotheses would be to mark animals with different two-week cohort marks and resample the pond from June through September. If the August toads remain in the pond for the same amount of time that June toads remain, the first explanation is reasonable. However, if the August toads exit the pond rapidly after initial capture, the second explanation is more appropriate. Neither explanation seems better than the other in the absence of sequential capture data, but the large movement of juvenile toads through Breezeway Pond in the autumn of 1988 suggests that migration through the area by transitory animals is possible.

Reproduction.—*Gastrophryne carolinensis* successfully reproduced in only one year from 1985 through 1990. Except in 1987, reproduction was unsuccessful because of the lack of standing water. In 1987, water was present in Breezeway Pond from February 24 through June 19. Given that the larval period for the eastern narrow-mouthed toad varies from 20 to 70 days (Wright and Wright 1949), eggs deposited in April, May, or even early June might have had enough time to hatch and for larvae to complete metamorphosis. However, little rain fell from April through June, few *G. carolinensis* migrated to the pond, and environmental conditions in the pond became more and more unfavorable for larval survival (shallow water, with maximum water temperature reaching 40°C which is only slightly below the average critical thermal maximum for larval eastern narrow-mouthed toads (Cupp 1980). If reproduction occurred, it was unsuccessful.

Population Size-Class Structure.—It is difficult to make statements about the significance in the general lack of annual variation in population size-class structure of *G. carolinensis* at Breezeway Pond. Little is known about the population structure of *G. carolinensis* at other breeding or non-breeding sites. Also, the composition of the population at a breeding site is biased at any point in time because it is only a sample of the population in surrounding habitats (Crump 1982).

However, among-year differences have two explanations. First, the population structure at a breeding site could be influenced by differences in annual and seasonal variation in activity, reproductive behavior, and movements between the sexes and among size classes. Second, environmental conditions may stimulate or inhibit activity at the breeding pond. Although differences were not found, it is hard to believe that these factors had no influence on the population structure of eastern narrow-mouthed toads from 1986 through 1990 at Breezeway Pond.

If the 1985 cohort had been followed in subsequent years, it might have been possible to monitor age-class changes in the population structure. However, the population structure remained nearly identical from 1986 through 1990 despite the

effects of drought and lack of recruitment. If the 1985 cohort had any effect on the population's size-class or age structure, it was not apparent.

Sex Ratio.–Skewed sex ratios have been observed in other *Gastrophryne* populations. Anderson (1954) also reported a male bias of eastern narrow-mouthed toads trapped in Louisiana, but he captured the sexes in a 1:1 ratio by hand. Freiburg (1951) captured more females than males in three of the four months that he sampled.

Male frogs are generally more abundant at breeding sites than females (Crump 1982; Woodward 1984 and references therein) and remain for longer periods of time. However, a drift fence should capture all animals irrespective of the length of time that they remain at the breeding site. Thus, in the absence of *a priori* reasons to suspect that the sex ratio is different from 1:1 in the local population of eastern narrow-mouthed toads, a skewed sex ratio over the course of a breeding season was not expected. The preponderance of females caught after August 1989 also is difficult to explain. I suggest several hypotheses that might account for the observed skewed sex ratios.

First, the actual sex ratios really may be skewed, and the capture data mirror the population's sex ratio, although sex ratio theory suggests that this is not typically the case for iteroparous species (Fisher 1930). Alternatively, males may move more often and remain at the breeding site longer than females. However, if males move more often than females, they should be exposed to greater risks of predation and desiccation. If they continued to do so during the early stages of a severe multi-year drought, male mortality might be greater than female mortality and lead to skewed sex ratios as the drought progressed. Finally, there may be different tendencies between the sexes in their propensity to move to breeding sites, especially during an environmental stress. For example, males might be less likely than gravid females to leave secure refugia and move to breeding sites during drought conditions. Also, individuals may not breed every year (Bull and Shine 1979; Gill 1985). One of the cobalt tagged adult females followed by Franz et al. (1989) for more than one year lived 20 m from Breezeway Pond but never went to the pond or made any other long-distance movements. Unfortunately, available data are not sufficient to select among these hypotheses.

Individual Size.–Breezeway Pond *G. carolinensis* are within the SUL range reported elsewhere in the literature for this species (Hecht and Matalas 1946; Wright and Wright 1949; Anderson 1954; Duellman and Schwartz 1958). Anderson (1954) reported a maximum size of 32.2 mm for males and 34.3 mm for females in Louisiana. Weights have never previously been reported, except for five *G. carolinensis* used in experiments on evaporative water loss (Wygoda 1984). Sexual dimorphism is common in anurans, with males usually smaller than females (Shine 1979; Duellman and Trueb 1986).

Gray (1989) suggested that the mean body size of numerically dominant species should be reduced during an environmental perturbation. *G. carolinensis* is clearly the dominant species in the amphibian community at Breezeway Pond (Dodd 1992). However, the mean body size (both SUL and weight) did not change significantly during the study. In fact, the greatest weights occurred in 1990, the year of the most severe drought effects, although the population size declined. These results mirror those obtained for the striped newt at the same site (Dodd 1993). Hence, my data do not substantiate Gray's (1989) predictions.

Longevity.—The oldest wild-caught *G. carolinensis* at Breezeway Pond were at least in their fourth year, the same age that Fitch (1956) reported for *G. olivacea* in Kansas. Eastern narrow-mouthed toads captured after four years were probably in their first or second year when initially caught. Fitch (1956) suggested that the plains narrow-mouthed toad might live a few years beyond four, and that most of the breeding population consisted of 3-year olds. A similar scenario seems reasonable for *G. carolinensis* at Breezeway Pond.

Mortality.—Trap mortality resulted primarily from desiccation. *G. carolinensis* seem particularly prone to desiccation despite attempts to minimize its impact. Smaller animals are more susceptible than larger animals. Anderson (1954) noted similar results and suggested that desiccation made the toads more vulnerable to predation by the ant *Iridomyrmex humilis*. Such a hypothesis seems reasonable inasmuch as dehydration reduces locomotor capacity in frogs (Moore and Gatten 1989). Invertebrate predation undoubtedly occurs in the confines of a bucket, but its effects are unknown in wild populations.

Response to Drought

Drought, especially long-term drought, may have serious consequences for amphibians that breed in isolated temporary ponds in sandhill habitats (Dodd 1993). This is because most Nearctic amphibians, including *Gastrophryne*, usually lack special reproductive adaptations to resist or avoid drought conditions. Because they are bound to water, a severe reproductive cost will be realized when environmental conditions are not favorable for reproduction. Yet, drought occurs regularly in the southeastern United States and is quite common in the Upper Etonia Creek Basin that contains the Ordway Preserve (Motz et al. 1991).

Dodd (1993) suggested that drought might have three effects on populations of striped newts, *Notophthalmus perstriatus*, sympatric with *G. carolinensis* in upland sandhill habitats. Localized newt populations might be extirpated, newts could move to other nearby breeding sites if available, or newts could outlast the drought in favorable refugia and take advantage of predator-free habitats once the

drought ended. In this regard, striped newts exemplify a version of the "storage effect" whereby reproduction is maximized during favorable periods and curtailed at other times (Warner and Chesson 1985). Newts may outlast a drought in reduced population size because interdemic migration is rare and newts presumably have a long life span (Gill 1985). Local extinctions undoubtedly occur during very severe droughts, but it is rarely possible to prove this is responsible for the absence of newts from what seem to human observers to be appropriate breeding sites. Below, I examine whether *G. carolinensis* populations in dry sandhill habitats might respond in a similar manner to droughts.

Localized Extinction.—Casual observations suggest that most aquatic habitats that might be expected *a priori* to contain breeding adult *G. carolinensis* usually do so under favorable conditions. Eastern narrow-mouthed toads were found on other parts of the Ordway Preserve during the drought and still visited Breezeway Pond 5 years after they last successfully reproduced in the pond. Still, during severe droughts extending more than several breeding seasons, localized extinction of eastern narrow-mouthed toad populations might occur. However, no data on localized extinctions of this species are available. The extent to which the eastern narrow-mouthed toads using Breezeway Pond constitute a reproductively closed population is unknown, so the definition of what might constitute a population-level local extinction is unclear.

If localized extinctions occur but breeding ponds are quickly recolonized, the temporary loss of a portion of a breeding population, or even the entire breeding population, might be overlooked without long-term monitoring. Environmental perturbations or predation preclude successful amphibian reproduction in some years (this study; Pechmann et al. 1989; Pechmann et al. 1991; Dodd 1993), but it is unknown how long a population might persist without reproducing. The average life span of *G. carolinensis* under natural conditions remains unknown.

Interdemic Migration.—Nothing is known of the potential for interdemic migration of eastern narrow-mouthed toads. Individual *Gastrophryne* occasionally may travel long distances (300-600 m in Fitch 1956; Franz et al. 1989). However, *G. carolinensis* (N = 353) captured at drift fence arrays 40-290 m from Breezeway Pond were never captured at the pond from 1987 to 1989, nor were toads marked at Breezeway Pond captured at the arrays. Thus, even relatively short distance movements were not demonstrated.

Non-reproductive movements of both *G. carolinensis* and *G. olivacea* seem to be quite localized (Freiburg 1951; Fitch 1956; Franz et al. 1989). Fitch (1956) estimated the home range of *G. olivacea* to be about 46 m in diameter whereas two cobalt-tagged *G. carolinensis* near Breezeway Pond had home ranges averaging only 273 m^2. Presumably, breeding adults faced with a dry pond are capable of traveling elsewhere, if appropriate habitats are nearby, but whether they actually do so is unknown.

Although many amphibians show site fidelity to a particular breeding pond (Martof 1953; Shoop 1965; Gill 1978, 1985; Semlitsch 1981; Duellman and Trueb 1986; Smith 1987), this had not been demonstrated previously for *G. carolinensis*. Anderson (1954) reported that a population of eastern narrow-mouthed toads in Louisiana attempted to breed at the site of a pond bulldozed the previous year. In the present study, multi-year recaptures suggest some degree of site fidelity in breeding site choice. If site fidelity is strong, interdemic migration probably is not significant. Even if most of the population never moves to another breeding site, however, a few toads might do so. Only a few wandering reproductive toads could recolonize a new or former breeding site.

Refugia.--*Gastrophryne carolinensis* could stay in terrestrial refugia until drought conditions end, if they can live long enough to outlast the drought. The two toads captured four years after initial marking are the longest lived individuals reported from a free-ranging population of this species. Fitch (1956) also captured several *G. olivacea* known to be in their fourth year and speculated that some individuals can live a few more years. Droughts that result in the loss of breeding sites more than four years in a row might begin seriously to deplete a local population. If this is the case, the study at Breezeway Pond ended at a critical juncture.

CONCLUSIONS

To understand how an amphibian population is affected by drought, it is necessary to recognize that the frogs that visit a pond represent a fraction of the total population (Crump 1982). The population of eastern narrow-mouthed toads that inhabits the Breezeway Pond region includes juveniles, non-reproductive adults, and breeding adults. The reproductive population of *G. carolinensis* probably contains a large number of individuals dispersed at substantial distances from a breeding site. The population is widely distributed, with toads dispersing evenly toward the various environments surrounding the pond (sandhills, xeric hammock, meadow) (Dodd unpubl.). Eastern narrow-mouthed toads have been seen in sandhills more than 500 m from the nearest potential breeding location (pers. obs.).

Amphibians living in unpredictable environments should be flexible in life history traits (Wilbur 1972; Crump 1982). Unlike the sympatric striped newt (Dodd 1993), I suggest that the eastern narrow-mouthed toad probably does not survive a drought through a combination of long life span and opportunistic timing of reproduction. Subterranean habits, the abundance of ants and termites for food, a short larval period, and the ability to use a wide variety of temporary wetlands for breeding probably allows *G. carolinensis* to colonize the otherwise harsh sandhills

of northern and central Florida. I further suggest that *G. carolinensis* survives long-term droughts because of its large population size and use of a broad range of habitats, and because at least some individuals are opportunistic, rather than philopatric, in their choice of breeding sites. I predict that localized extinctions occur during severe droughts at certain breeding sites, although this remains to be proven.

Although the trend in amphibian community studies has been toward controlled manipulative experiments (Jaeger and Walls 1989; Morin 1989; Wilbur 1989), the value of long-term ecological monitoring is increasingly recognized (Franklin 1989; Taylor 1989). Franklin (1989) noted that long-term studies are needed to examine ecological processes that are slow, rare, episodic, or which contain high degrees of variability, or involve subtle and complex phenomena, or to test and formulate theory. The response of the population of *G. carolinensis* at Breezeway Pond and its surrounding uplands to episodic drought is certainly complex, subtle, and probably extends over time. Population parameters (e.g. sex ratio, age and size-class structure, larval duration, and survivorship) are certainly variable, even without environmental uncertainty. Although lasting five years, this study could not answer many important questions about this and other amphibian species' responses to environmental perturbations.

Until monitoring encompasses longer time periods, the long-term effects of environmental perturbations on a species or community must remain speculative. If prolonged drought severely stresses amphibian communities, the response probably lasts many years, and the effects probably vary locally and species-specifically. On the other hand, short-term droughts may have no lasting effects (Cypert 1961). Population recovery will depend on a drought's duration, the presence of refugia, a species' colonization abilities and life history plasticity, and its habitat requirements and their availability. These considerations are important for determining the long-term effects of drought-induced declines in amphibian populations. Separating natural fluctuations in community composition and structure from human-caused or environmentally related declines will not be possible without long-term monitoring studies. The baseline data gathered in the present study provide an example of the information that will be needed.

LITERATURE CITED

Anderson, P. K. 1954. Studies in the ecology of the narrow-mouthed toad, *Microhyla carolinensis carolinensis*. Tulane Stud. Zool. 2:15-46.

Ashton, R. E., Jr., and P. S. Ashton. 1985. Handbook of Reptiles and Amphibians of Florida. Part 3. The Amphibians. Windward Publ., Inc., Miami.

Auffenberg, W., and W. W. Milstead. 1965. Reptiles in the Quaternary of North America. Pp. 557-568 *in* The Quaternary of the United States, VII Congress. Intl. Assoc. Quaternary Research. Princeton Univ. Press.

Blair, W. F. 1957. Changes in vertebrate populations under conditions of drought. Cold Spring Harbor Symp. Quant. Biol. 22:273-275.

Bristow, C. E. 1991. Interactions between phylogenetically distant predators: *Notophthalmus viridescens* and *Enneacanthus obesus*. Copeia 1991:1-8.

Bull, J. J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. Amer. Nat. 114:296-303.

Campbell, H. W., and S. P. Christman. 1982. The herpetological components of Florida sandhill and sand pine scrub associations. Pp. 163-171 *in* N.J. Scott, Jr., ed. Herpetological Communities. Fish Wildl. Serv., Wildl. Res. Rept. 13.

Carr, A. F., Jr. 1940. A contribution to the herpetology of Florida. Univ. Florida Publ., Biol. Sci. 3(1): 1-118.

Conant, R., and J. T. Collins. 1991. A Field Guide to the Reptiles and Amphibians. Eastern and Central North America. Houghton Mifflin Co., Boston.

Corn, P. S., and J. C. Fogleman. 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. J. Herp. 18:147-152.

Crump, M. L. 1982. Amphibian reproductive ecology on the community level. Pp. 21-36 *in* N.J. Scott, Jr., ed. Herpetological Communities. Fish Wildl. Serv., Wildl. Res. Rept. 13.

Cupp, P. V., Jr. 1980. Thermal tolerance of five salientian amphibians during development and metamorphosis. Herpetologica 36:234-244.

Cypert, E. 1961. The effects of fires in the Okefenokee Swamp in 1954 and 1955. Amer. Midl. Nat. 66:485-503.

Dalrymple, G. H. 1988. The herpetofauna of Long Pine Key, Everglades National Park, in relation to vegetation and hydrology. Pp. 72-86 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, eds. Management of Amphibians, Reptiles, and Small Mammals in North America. U. S. Dept. Agric. For. Serv., Gen. Tech. Rept. RM-166.

Deckert, R. F. 1914. Further notes on the salientia of Jacksonville, Fla. Copeia 1914(9):1-3.

Dodd, C. K., Jr. 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. J. Herp. 25:296-301.

_____. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodivers. Cons. 1:125-142.

_____. 1993. The cost of living in an unpredictable environment: The ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. Copeia 1993: 605-614.

_____, and B. G. Charest. 1988. The herpetofaunal community of temporary ponds in north Florida sandhills: Species composition, temporal use, and management implications. Pp. 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. Dept. Agric. For. Serv., Gen. Tech. Rept. RM-166.

Duellman, W. E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus., Biol. Sci. 3(5):181-324.

Duellman, W. E., and L. Trueb. 1986. Biology of Amphibians. McGraw-Hill Book Co., New York.

Dundee, H. A., and D. A. Rossman. 1989. The Amphibians and Reptiles of Louisiana. Louisiana St. Univ. Press, Baton Rouge.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford Univ. Press, Oxford, England.

Fitch, H. S. 1956. A field study of the Kansas ant-eating frog, *Gastrophryne olivacea*. Univ. Kansas Publ. Mus. Nat. Hist. 8:275-306.

Florida Natural Areas Inventory. 1990. A Guide to the Natural Communities of Florida. Florida Nat. Areas Invent. and Florida Dept. Nat. Resources, Tallahassee.

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. Pp. 3-19 *in* G. E. Likens, ed. Long-term Studies in Ecology. Approaches and Alternatives. Springer-Verlag, New York.

Franz, R., R. E. Ashton, Jr., and W. W. Timmerman. 1989. Behavior and movements of certain small sand hill amphibians and reptiles in response to drift fences. Project No. GFC-87-023. Rept. to Nongame Wildl. Prog., Florida Game and Fresh Water Fish Comm., Tallahassee.

Freiburg, R. E. 1951. An ecological study of the narrow-mouthed toad (*Microhyla*) in northeastern Kansas. Trans. Kansas Acad. Sci. 54:374-386.

Garton, J. D., and H. R. Mushinsky. 1979. Integumentary toxicity and unpalatability as an antipredator mechanism in the narrow-mouthed toad, *Gastrophryne carolinensis*. Can. J. Zool. 57:1965-1973.

Gibbons, J. W., and D. H. Bennett. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:236-243.

_____, and R. D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: An effective technique for quantitative sampling of animal populations. Brimleyana 7:1-16.

Gibbons, J. W., and R. D. Semlitsch. 1991. Guide to the Reptiles and Amphibians of the Savannah River Site. Univ. Georgia Press, Athens.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecol. Monogr. 48:145-166.

_____. 1985. Interpreting breeding patterns from census data: A solution to the Husting dilemma. Ecology 66:344-354.

Given, M. 1988. Territoriality and aggressive interactions of male carpenter frogs, *Rana virgatipes*. Copeia 1988:411-421.

Gray, J. S. 1989. Effects of environmental stress on species rich assemblages. Biol. J. Linn. Soc. 37:19-32.

Harris, R. N., R. A. Alford, and H. M. Wilbur. 1988. Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. Herpetologica 44:234-242.

Healy, W. R. 1974. Population consequences of alternative life histories in *Notophthalmus v. viridescens*. Copeia 1974:221-229.

Hecht, M. K., and B. L. Matalas. 1946. A review of the middle North American toads of the genus *Microhyla*. Amer. Mus. Nov. 1315, 21 pp.

Heyer, W. R. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. J. Herp. 7:337-361.

Holman, J. A., and H. Campbell. 1958. An interesting feeding activity of *Microhyla carolinensis*. Herpetologica 14:205.

Jaeger, R. G., and S. C. Walls. 1989. On salamander guilds and ecological methodology. Herpetologica 45:111-119.

Kats, L. B., J. W. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1865-1870.

LaClaire, L. V., and R. Franz. 1990. Importance of isolated wetlands in upland landscapes. Pp. 9-15 *in* M. Kelly, ed. Proc. 2nd Ann. Mtg., Florida Lake Mgmt. Soc., Winter Haven.

Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans*. Ecology 34:529-543.

Meylan, P. A. 1982. The squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida). Bull. Florida State Mus., Biol. Sci. 27(3):111-195.

Mitchell, J. C. 1979. The concept of phenology and its application to the study of amphibian and reptile life histories. Herp. Rev. 10:51-54.

Moler, P. E., and R. Franz. 1988. Wildlife values of small, isolated wetlands in the Southeastern coastal plain. Pp. 234-241 *in* R. R. Odom, K. A. Riddleberger, and J. C. Ozier, eds. Proc. 3rd Nongame & Endang. Wildl. Symp., Georgia Dept. Nat. Resources, Social Circle.

Moore, F. R., and R. E. Gatten, Jr. 1989. Locomotor performance of hydrated, dehydrated, and osmotically stressed anuran amphibians. Herpetologica 45:101-110.

Morin, P. J. 1989. New directions in amphibian community ecology. Herpetologica 45:124-128.

Motz, L. H., J. P. Heaney, W. K. Denton, and G. Leiter. 1991. Upper Etonia Creek hydrologic study. St. Johns Water Mgmt. Dist., Spec. Publ. SJ 91-SP5.

Mount, R. H. 1975. The Reptiles and Amphibians of Alabama. Agric. Exper. Sta., Auburn Univ., Auburn.

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

Myers, R. L. 1990. Scrub and high pine. Pp. 150-193 *in* R. L. Myers and J. J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando.

Nelson, C. E. 1972. *Gastrophryne carolinensis* (Holbrook). Eastern narrow-mouthed toad. Cat. Amer. Amphib. Rept. 120.1-120.4.

Osborne, W. S. 1989. Distribution, relative abundance and conservation status of the Corroboree frogs, *Pseudophryne corroboree* Moore (Anura: Myobatrachidae). Aust. Wildl. Res. 16:537-547.

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 Ecol. Mgmt. 1:3-11.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. Science 253:892-895.

Raymond, L. R., and L. M. Hardy. 1990. Demography of a population of *Ambystoma talpoideum* (Caudata: Ambystomatidae) in northwestern Louisiana. Herpetologica 46:371-382.

Seale, D. B. 1982. Physical factors influencing oviposition by the woodfrog, *Rana sylvatica*, in Pennsylvania. Copeia 1982:627-635.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Can. J. Zool. 59:315-322.

_____. 1983. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia 1983:608-616.

_____. 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. Copeia 1985:477-489.

_____. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61-69.

_____, and H. M. Wilbur. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 43:105-112.

Sexton, O. J., C. Phillips, and J. E. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). Copeia 1990:781-787.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297-306.

Shoop, C. R. 1965. Orientation in *Ambystoma maculatum*: Movements to and from breeding ponds. Science 149:558-559.

_____. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology 55:440-444.

Smith, D. C. 1987. Adult recruitment in chorus frogs: Effects of size and date at metamorphosis. Ecology 68:344-350.

Stahle, D. W., M. K. Cleaveland, and J. G. Hehr. 1988. North Carolina climate changes reconstructed from tree rings: A.D. 372 to 1985. Science 240:1517-1519.

Taylor, L. R. 1989. Objective and experiment in long-term research. Pp. 20-70 *in* G. E. Likens, ed. Long-term Studies in Ecology. Approaches and Alternatives. Springer-Verlag, New York.

Tevis, L., Jr. 1966. Unsuccessful breeding by desert toads (*Bufo punctatus*) at the limit of their ecological range. Ecology 47:766-775.

Trauth, S. E., R. L. Cox, B. P. Butterfield, D. A. Saugey, and W. E. Meshaka. 1990. Reproductive phenophases and clutch characteristics of selected Arkansas amphibians. Proc. Arkansas Acad. Sci. 44:107-113.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. Amer. Nat. 125:769-787.

Webb, S. D. 1990. Historical biogeography. Pp. 70-100 *in* R. L. Myers and J. J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando.

Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. Ecology 53:1-21.

_____. 1989. In defense of tanks. Herpetologica 45:122-123.

Winsberg, M. D. 1990. Florida Weather. Univ. Central Florida Press, Orlando.

Woodward, B. D. 1984. Arrival to and location of *Bufo woodhousei* in the breeding pond: Effect on the operational sex ratio. Oecologia 62:240-244.

Wright, A. H. 1932. Life-histories of the Frogs of Okefinokee Swamp, Georgia. MacMillan Co., New York.

_____, and A. A. Wright. 1949. Handbook of Frogs and Toads. Cornell Univ. Press, Ithaca, New York.

Wygoda, M. L. 1984. Low cutaneous evaporative water loss in arboreal frogs. Physiol. Zool. 57:329-337.