

Annual Variation in the Population Ecology of the Endangered Gopher Frog, *Rana sevosa* Goin and Netting

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We studied variation in the population ecology of dusky gopher frogs, *Rana sevosa* Goin and Netting, in southern Mississippi from 1996–2001. Specifically, we measured adult size structure, adult survivorship, residency length within the pond, and juvenile recruitment using a drift fence that completely enclosed the study pond. Population size structure shifted among years because of lack of recruitment in previous years, adult mortality, and differential age at maturity. Age at maturity was 6–8 months for males and 24–36 months for females. Annual survival ranged from 65 to 92%; however, the rate at which adults returned to breed among years was low (16–22%). The average number of seasons that adults bred was 1.2, although nine individuals bred in 3–5 seasons. Our data suggest that *R. sevosa* has high population turnover among years and that most adults live less than 7 yr. Because of the low rate of return of adults among years and complete isolation of the population, the viability of the population is contingent on consistent recruitment of juveniles with minimal years of reproductive failure.

WORLDWIDE reports of amphibian declines are becoming increasingly common (reviewed in Alford and Richards, 1999), but data on the population biology of most declining species are less readily available. Many reports of amphibian declines only provide changes in numbers of individuals detected over some period of years (e.g., Beebee et al., 1996), temporal changes in age structure of populations (e.g., Ishchenko, 1996), or results of a catastrophic event, such as mass mortality resulting from disease (e.g., Laurance et al., 1996). Although valuable, the absence of data on changes in population variables such as size structure, sex ratio, survivorship, and recruitment makes understanding amphibian declines difficult (Green, 1997). For example, changes in sex ratio over time might be indicative of higher mortality rates on one of the two genders, something that cannot be determined using simple counts alone.

Gopher frogs (*Rana capito* and *Rana sevosa*) are rare and poorly studied amphibians whose historic geographic range extended throughout the southeastern coastal plain upland longleaf pine (*Pinus palustris*) forests (Goin and Netting, 1940; Wright and Wright, 1949; Conant and Collins, 1991). They breed in temporary, upland ponds and spend the nonbreeding season in adjacent longleaf pine forests (Richter et al., 2001). Habitat has been greatly diminished across the geographic distribution of gopher frogs because of logging and conversion of longleaf pine ecosystems to off-site pine plantations (Bailey, 1991). In addition to habitat loss, gopher frogs are threatened by habitat

fragmentation, fire suppression, introduction of fish to breeding ponds, and road mortality (Bailey, 1990). The number of breeding populations of gopher frogs has been drastically reduced, especially in the western portion of the range. Gopher frogs are considered extirpated in Louisiana (R. Thomas, pers. comm.), and although they were once abundant in coastal Mississippi (Allen, 1932), breeding populations are currently known from only a single pond (Glen's Pond) located in the Desoto National Forest in Harrison County, Mississippi. A recent study by Young and Crother (2001) indicated that this population was genetically distinct from other populations of gopher frogs and elevated it to specific status by resurrecting *R. sevosa* Goin and Netting. In December 2001, *R. sevosa* was listed under the U.S. Endangered Species Act as endangered (LaClaire, 2001). Thus, the need for information on the biology of this last known population is crucial.

Information on the life history and general ecology of gopher frogs of both *R. capito* and *R. sevosa* is scarce. Published data on *R. sevosa* are limited to population genetics (Young and Crother, 2001), egg mass mortality (Richter, 2000), and postbreeding movement patterns (Richter et al., 2001). Information on *R. capito* is more common, including population and reproductive data from southern Alabama (Bailey, 1990), the Panhandle of Florida (Palis, 1998), central Florida (Greenberg, 2001), and South Carolina (Semlitsch et al., 1995). However, only Palis (1998) provided detailed information on population biology, albeit for only a single year. Our goals were to determine yearly variation in

such key demographic traits as population size structure, sex ratio, within-season and among-season survival, and age at maturity for the only known breeding population of *R. sevosa*.

MATERIALS AND METHODS

Study site.—Glen's Pond is an ephemeral pond, approximately 440 m in circumference (fairly circular in shape) and fills to a maximum depth of about 1.1 m, typically holding water from early winter (December or January) until mid- to late summer (June through August). The surrounding habitat is primarily longleaf pine forest and is burned by the U.S. Forest Service at approximately four-year intervals. Private lands abut the Forest Service property approximately 250 m to the north and east of the pond. These private lands were clearcut in 1994 and 2001.

Study period.—We present breeding seasons, which typically spanned two calendar years (winter to summer), as the latter year (e.g., December 1995 to June 1996 breeding season = 1996). In December 1995, a 525-m drift fence completely enclosing Glen's Pond was installed above the high-water line. The fence was composed of fine-woven, Department of Transportation grade, black plastic mesh (so-called silt fencing), and approximately 90 cm high. It was installed 8–10 cm beneath the soil and equipped with 68 pairs of 25-liter buckets serving as pitfall traps (one on either side of the fence) at intervals of 8 m. Direct observations of gopher frogs along the fence indicated they made no attempt to dig under the fence or jump over it; most frogs moved slowly along the fence until they fell into a pitfall trap or stayed motionless until captured. Thus, we believe this method was highly effective in sampling both adults and metamorphs. The fence was equipped with gates that could be opened when the fence was not in use, allowing transit by frogs and other animals. Each pitfall trap was equipped with a large sponge to minimize the desiccation of amphibians. The drift fence was operational during six breeding seasons, from December 1995 to July 2001. Months of operation for the fence began with initial rains and ended after the pond dried, usually December to June for each breeding season, but as early as September (in the 1999 season) or as late as August (in 1997). The drift fence was monitored continuously in 1996 (from 18 December 1995 to 9 June 1996), 1997 (28 December 1996 to 6 August 1997), and 1998 (27 November 1997 to 14 June 1998) and during periods of

rainfall and breeding activity in 1999, 2000, and 2001.

During periods when the fence was operational, the pitfall traps and fence were checked at least once per day. The fence was checked multiple times after dark during rainy periods. During periods of clear weather, the pitfalls and fence were checked between 0700 and 1000 h. Water levels were measured every other day with a permanent meter stick placed at the center of the pond. Rainfall was measured with a rain gauge daily.

Marking and measurements.—Adults were individually marked using unique toe-clips in 1996 and PIT tags (passive integrated transponders; AVID®) from 1997–2001. Unique toe-clips followed the scheme of figure 29B of Donnelly et al. (1994). Frogs marked with PIT tags had the PIT tag injected into the abdomen through the muscle. Direct observation on recaptured frogs indicated that all incisions healed, and there was no necrotic tissue present upon recapture. All PIT-tagged frogs received a cohort toe-clip, and for 1997 and 1998, only two recaptured frogs lost their PIT tags, a loss rate of 0.01.

All adult frogs captured were checked for missing digits and for PIT tags using a handheld AVID® PIT-tag scanner. They were then measured (snout-vent length, SVL) to the nearest mm using a plastic caliper, weighed to the nearest 0.5 g using a 50-g or 100-g spring balance (Pesola®), given an unique identity and released at the point of capture. Males were distinguished from females by the vocal sacs and the thumbs, which enlarge during the breeding season. If not evident from the vocal sacs or thumbs, the sex was determined by provoking a distress call. When giving this call, females extended their median subgular areas, whereas males extended their paired, lateral vocal sacs.

All metamorphs captured were measured (SVL) to the nearest 0.1 mm using a plastic caliper and weighed to the nearest 0.01 g using an electronic scale (Acculab®). Presence or absence of a tail bud was assessed. Metamorphs were not PIT tagged but were given an annual cohort mark by clipping the same toe on every individual within a given year.

Statistical methods.—Advanced statistical tests were performed using SAS® version 8.1 (ANOVA and ANCOVA) and SYSTAT® 7.0 (contingency table analyses). Multiple comparison procedures were calculated by hand using methods described below. All means are followed by \pm 1 SE. Alpha was set at 0.05.

We tested for differences among and within

years of adult residency length and SVL using a two-way analysis of variance and in body mass using a two-way analysis of covariance (PROC GLM in SAS®). All initial models incorporated the two main effects (sex and year) and interactions between the main effects; the model for mass also incorporated a covariate (SVL) and an interaction of the main effects with the covariate (SVL) to test the homogeneity of slopes assumption. If the slopes were heterogeneous (significant covariate-main effect interaction), the interaction was retained in the model, which allotted degrees of freedom to estimating separate slope parameters for levels of main effects. When the effect of an interaction was not significant, the interaction with the highest *P*-value was dropped and the model was recomputed. This was repeated until all interactions included in the model were significant. Following tests of main effects, we used a GH multiple comparison procedure (Games and Howell, 1976) with a Cicchetti means parameter correction to determine differences between cell means across years and sexes. The GH procedure is appropriate when sample sizes are unequal, and the Cicchetti correction incorporates the number of posthoc comparisons to be performed in the calculation of statistical critical values (Toothaker, 1991).

We compared metamorph SVL using a one-way ANOVA, and body mass using a one-way ANCOVA with SVL as covariate, both of which were followed by a GH multiple comparison procedure to determine differences among years.

We tested among-year differences in within-season survivorship by sex using a contingency table analysis. Within-year data of intersexual differences in survivorship were analyzed using 2×2 contingency tables, and within-season data on sex ratios were tested using a chi-square test. We used a chi-square to test the goodness of fit of the observed circular frequency distribution of metamorph and adult emergence to a theoretical distribution (Zar, 1984).

RESULTS

Drift fence data.—During 1996–1998, adult capture data are complete (i.e., adults migrating to and from the pond were captured), sex was identified, and measurements were taken as described above. In September 1998, though Glen's Pond filled and gopher frogs migrated to the pond, the drift fence was destroyed by Hurricane Georges; thus adult captures were not complete. The hurricane was followed by a severe drought (from a "La Nina" event) from

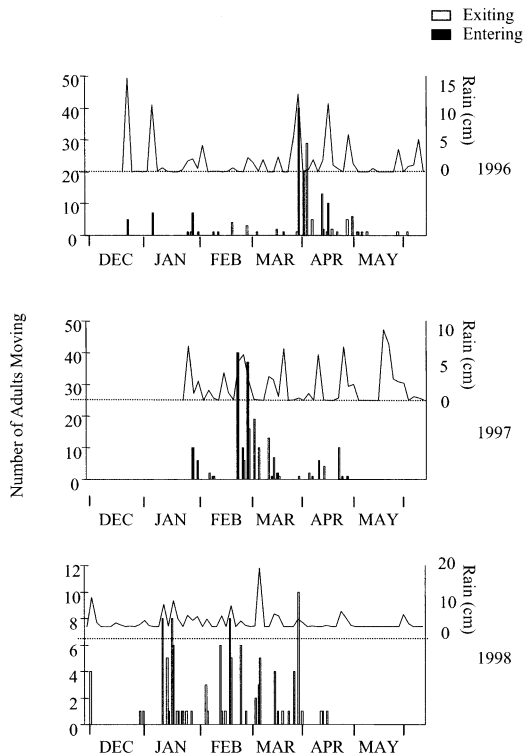


Fig. 1. Adult *Rana sevoosa* movement patterns and associated rainfall as determined by drift fence captures of frogs entering and exiting Glen's Pond during 1996, 1997, and 1998.

November 1998 to October 2000, and adult movement was minimal. Beginning in November 2000, the drift fence was fully operational; however, the sex of all frogs was not accurately determined. Therefore, the capture data for 1999–2001 were not used in gender-specific analyses.

Adult movements.—A total of 301 adult frogs was marked during 1996–2001 (97 in 1996, 94 in 1997, 47 in 1998, three in 1999, zero in 2000, and 61 in 2001). The total number of individuals captured at the drift fence (including among-year recaptures) was 350 (97 in 1996, 110 in 1997, 67 in 1998, eight in 1999, zero in 2000, and 68 in 2001). Based on these count data alone, return among years is low. Almost all instances of adult frog movements were associated with rainfall (e.g., 1996–1998; Fig. 1). Movement to the pond by adults typically began with the onset of winter rains as the pond began to fill, and movements away from the pond began after the initial deposition of egg masses. Adults entered and exited the pond in a non-random pattern for all years (Enter: $\chi^2 = 34.86$,

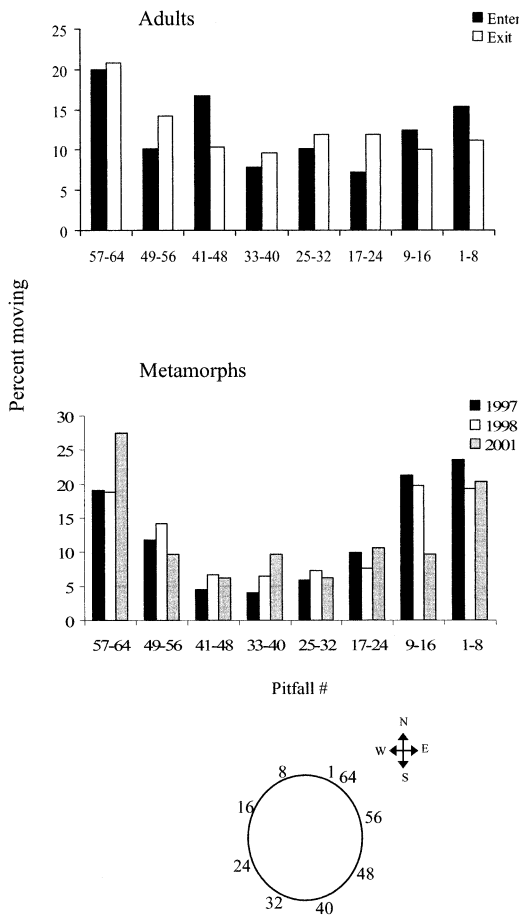


Fig. 2. Pattern of emergence of adult and metamorphic *Rana sevosa* captured exiting Glen's Pond during 1997, 1998, and 2001. The circle with numbers represents the orientation of the drift fence (circle) and pitfall traps (numbers). See Richter et al. (2001: fig. 1) for habitat features.

df = 7, $P < 0.001$; Exit: $\chi^2 = 19.32$, df = 7, $P = 0.007$) and tended to exit toward the north and east, which was in an uphill direction toward the recent clearcut (Fig. 2; Richter et al., 2001: fig. 1) and similar to metamorph emergence pattern (see below; Fig. 2).

TABLE 2. RESULTS OF TWO-WAY ANOVA (SVL AND RESIDENCY LENGTH) AND TWO-WAY ANCOVA (BODY MASS) MODELS. Initial models are as follows: SVL = Sex Year Sex \times Year; Residency = Sex Year Sex \times Year; Mass = SVL Sex Year Sex \times Year SVL \times Sex SVL \times Year SVL \times Sex \times Year. Following the AN(C)OVA analyses, multiple comparison statistics were calculated using the Games-Howell procedure (see Fig. 3).

Source	Ndf,Ddf	F	P
SVL (mm)			
Overall Model	5,270	64.20	<0.0001
Sex	1,270	277.23	<0.0001
Year	2,270	0.41	0.465
Year \times Sex	2,270	21.48	<0.0001
Body mass (g)			
Overall Model [†]	6,242	306.78	<0.0001
Sex	1,242	39.34	<0.0001
Year	2,242	4.54	0.012
SVL	1,242	578.75	<0.0001
Sex \times Year ^c	2,240	0.81	0.448
SVL \times Sex ^a	1,237	0.31	0.580
SVL \times Year	2,242	5.19	0.006
SVL \times Sex \times Year ^b	3,237	0.65	0.585
Residency length (d)			
Overall Model	5,180	17.56	<0.0001
Sex	1,180	70.73	<0.0001
Year	2,180	13.62	<0.0001
Year \times Sex	2,180	9.88	<0.0001

[†] Overall model with ^{a-c} removed.
^{a-c} Order (alphabetic; based on highest P-value) that variables were removed from model.

Sex ratios and body size.—Although there were always more females present during each breeding season (Table 1), the adult sex ratio did not significantly differ from 1:1 in any year (1996: $\chi^2 = 0.412$, df = 1, $P = 0.521$; 1997: $\chi^2 = 0.004$, df = 1, $P = 0.948$; 1998: $\chi^2 = 1.91$, df = 1, $P = 0.167$). Mean male SVL significantly increased from 1996 to 1997, and mean female SVL significantly decreased from 1996 to 1997 and 1998 (Tables 1–2; Fig. 3). Male SVL was significantly smaller than female SVL for 1996–1998 (Table 2; Fig. 3), but the degree of sexual dimorphism fluctuated considerably among years. Using the sexual dimorphism index (SDI) of

TABLE 1. SEX RATIO, MEAN BODY SIZE, AND MEAN RESIDENCY LENGTH OF ADULT GOPHER FROGS FOR EACH BREEDING SEASON.

	SEX RATIO (M:F)	MEAN SVL (MM) \pm 1 SE		MEAN MASS (G) \pm 1 SE		MEAN RESIDENCY LENGTH (D) \pm 1 SE	
		M	F	M	F	M	F
1996	47:50	63.2 \pm 1.18	82.7 \pm 0.81	26.3 \pm 1.64	60.0 \pm 1.55	36 \pm 7.7	16 \pm 2.6
1997	50:60	70.2 \pm 0.64	78.0 \pm 0.80	38.0 \pm 0.94	55.8 \pm 1.70	31 \pm 3.8	15 \pm 2.3
1998	29:38	67.7 \pm 1.82	79.3 \pm 0.62	38.0 \pm 3.16	56.6 \pm 1.44	76 \pm 6.0	18 \pm 2.6

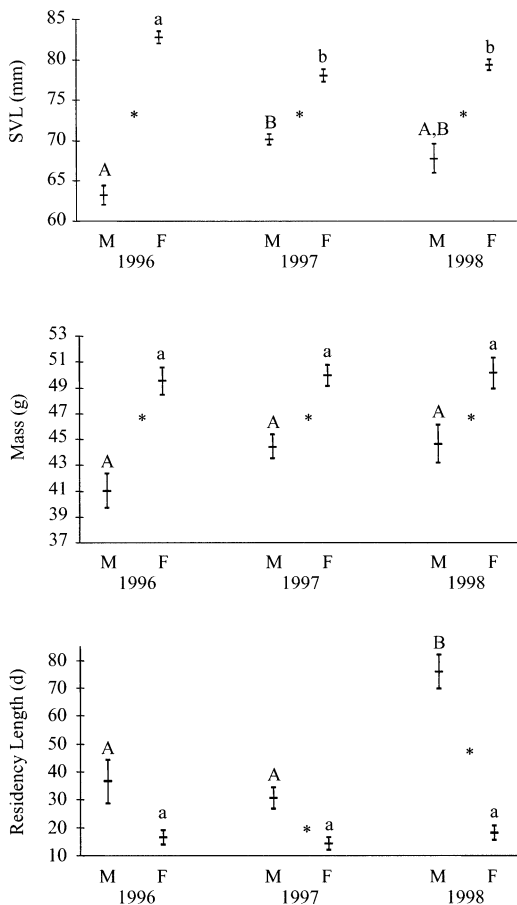


Fig. 3. Average (± 1 SE) SVL, body mass, and residency length of male and female *Rana sevensa* during 1996, 1997, and 1998. Letters and asterisks depict differences found using Games-Howell multiple comparisons following AN(C)OVA analyses (see Table 2 and Materials and Methods for details). An asterisk indicates a significant within-year difference between the sexes. Upper case letters represent among-year comparisons for males, and lower case letters represent among-year comparisons for females. In both cases, a different letter indicates a significant difference among years.

Gibbons and Lovich (1990), which is positive for a species with larger females and negative for those with larger males, SDI varied from 0.31 in 1996, 0.11 in 1997, and 0.17 in 1998. After removing the effects of SVL, body mass did not differ within each sex among years but did differ between the sexes for each year (Tables 1–2; Fig. 3).

Residency within the pond.—We defined residency length as the amount of time a frog remained within the pond, beginning when the frog was captured entering the fenced area and ending

when it was captured exiting. Therefore, length of residency was not available for every individual because not every frog that was captured entering the pond was captured exiting. The absence of residency data for some frogs could be caused by individuals remaining in the pond beyond the study period or to within-season mortality.

Males typically entered the pond before females and stayed within the perimeter of the drift fence for longer periods in all years. All intersexual differences in residency length were significant except in 1996 because of wide variation in male residency length (Tables 1–2; Fig. 3). All terms in the model (sex, year, and sex \times year) were significant; thus not only were there significant differences between the sexes among years, but because the interaction was significant, these differences were not constant across years (Table 2). Male residency length was significantly different between 1996 and 1998 and between 1997 and 1998, but female residency length did not differ among years (Table 2; Fig. 3).

Within-season survival.—Within-season survival was estimated by comparing the number of individuals that were captured entering the pond with those that were also captured exiting. These data should be considered as minimum estimates of within-season survival because they are exact only if all frogs that failed to exit the pond died during the breeding season. Some frogs that entered the pond to reproduce may have become residents within the fence and so may not have exited during the study period. For example in 1997, four burrows, apparently constructed by small mammals, were found within the fenced area where frogs had taken residence. Two of these four frogs were not known to have left the fence before it was taken down in August 1997. Therefore, our survivorship data may underestimate the number of frogs that survived the breeding season.

Of 93 adult frogs that entered the pond in 1996, 67 eventually emerged (72.0%), compared with 90 of 106 (84.9%) in 1997, and 36 of 52 (69.2%) in 1998. There was no significant difference in within-season survivorship between the sexes in 1996 (Table 3, contingency table analysis, $\chi^2 = 0.252$, $df = 1$, $P = 0.615$) or 1998 ($\chi^2 = 0.099$, $df = 1$, $P = 0.753$); however, there was a significant sexual difference in 1997 ($\chi^2 = 4.931$, $df = 1$, $P = 0.026$). Male within-season survivorship did not vary significantly among years (contingency table analysis, $\chi^2 = 1.398$, $df = 2$, $P = 0.497$), but the opposite was

TABLE 3. WITHIN-SEASON SURVIVORSHIP OF MALE AND FEMALE GOPHER FROGS FOR 1996–1997. Male survivorship was lower than female survivorship, although the difference was only significant for 1997 (see text).

	Male	Female
1996	65.1% (<i>n</i> = 43)	70.0% (<i>n</i> = 50)
1997	76.1% (<i>n</i> = 46)	91.7% (<i>n</i> = 60)
1998	66.7% (<i>n</i> = 18)	71.0% (<i>n</i> = 31)

true for females (contingency table analysis, $\chi^2 = 9.580$, *df* = 2, *P* = 0.008).

Metamorph emergence.—Metamorphs emerged from the pond naturally (i.e., no artificial manipulation of hydroperiod) in 1997 and 1998. In 2001, the hydroperiod was artificially extended to allow metamorphosis (see Richter et al., in press). The mean SVL and body mass of metamorphs was 35.7 ± 0.09 mm and 5.04 ± 0.042 g in 1997 (*n* = 213), 29.8 ± 0.05 mm and 2.58 ± 0.013 g in 1998 (*n* = 813), and 34.1 ± 0.25 mm and 4.47 ± 0.112 g in 2001 (*n* = 113). Metamorph SVL significantly differed among years (*F* = 1487.07, *df* = 2,1136, *P* < 0.0001) with 1997 > 2001 > 1998 (GH multiple comparison procedure, *P* < 0.05). After removing the effects of SVL, metamorph body mass also significantly differed among years (*F* = 4950.82, *df* = 2,1133, *P* < 0.0001); however, 1997 and 2001 did not differ significantly but were both significantly larger than 1998 (GH multiple comparison procedure, *P* < 0.05). Overall, metamorphs were significantly larger in 1997 and 2001 as compared to 1998.

We found that metamorphic frogs emerged from the pond and exited through specific migratory corridors (see Dodd and Cade, 1998). The pattern of emergence of metamorphs was significantly different from random in all years: 1997 ($\chi^2 = 39.36$, *df* = 7, *P* < 0.001), 1998 ($\chi^2 = 266.96$, *df* = 7, *P* < 0.001), and 2001 ($\chi^2 = 14.51$, *df* = 7, *P* = 0.04). Orientation of emergence for all years was toward the north and east in the direction of a recent clearcut (Fig. 2; Richter et al., 2001: fig. 1).

Minimum age and size at maturity.—Of the 29 males found at Glen’s Pond in 1998, 11 were metamorphs originally marked in 1997. The timing of emergence of metamorphs in 1997 was between 30 May and 30 July, and the first 1997 metamorph returning to breed was captured on 30 November 1997. Therefore, assum-

TABLE 4. SUMMARY OF RECAPTURE DATA FOR ALL GOPHER FROGS RECAPTURED FROM 1996 TO 2001. Numbers represent the number of individuals recaptured per year and are separated by sex and year of original capture.

Original capture year	Sex	1997	1998	1999	2000	2001
1996	M	8	2	1	0	1
1996	F	8	1	0	0	0
1997	M	—	9	2	0	2*
1997	F	—	13	0	0	3
1998	M	—	—	1**	0	0
1998	F	—	—	1	0	1*

* One of which skipped 1999.

** Originally captured as a metamorph in 1997; PIT tagged in 1998.

ing these individuals were attempting to breed, the minimum age at maturity of males was between 123 and 184 days (4–6 months). The average SVL of these 11 recaptures was 56.3 ± 1.13 mm (an average growth of 20.6 ± 1.13 mm) and the mean body mass was 18.8 ± 1.31 g (an average weight gain of 13.8 ± 1.31 g). Thus, males that returned to breed increased in SVL by a magnitude of 1.6 and in mass by 3.7. No females originally marked as metamorphs were recaptured, so the minimum age at maturity for females was at least 2–3 yr.

Rate of return of adults.—Recapture data of 1996 adults are only considered for 1997 because of the high incidence of natural loss of toes and rapid regeneration observed (i.e., many frogs captured had toes missing that did not coincide with previous marks and toes that had obviously regenerated). Also, no toe-clip markings found on frogs from 1998 onward matched previous captures, indicating that either additional toes had been lost naturally or regenerated or that the frogs were never recaptured.

Of all frogs marked (*n* = 301), only 41 (13.6%) were captured in more than one season. Of these, 32 (78.1%) were captured in two seasons, seven (17.1%) in three seasons, one (2.4%) in four seasons, and one in five seasons (2.4%; Table 4). The average number of breeding seasons in which adults bred was 1.18 ± 0.029 .

Of 98 adults originally toe-clipped in 1996, 16 individuals returned to breed in 1997 (16.3%). Of the 110 adults originally PIT-tagged in 1997, 25 were recaptured in 1998 (21.8%), three (2.7%) of which were recaptures from 1996. Of the 68 frogs captured in 2001, seven were recaptures from previous years (of 185 previously PIT tagged; 3.8%). Therefore, the rate of return

of adults from one breeding season to the next varied from 16.3–21.8%. The percent recaptures (i.e., number of recaptures from any previous year/number of total captures for that year) varied widely among years; 14.5% in 1997 (16 of 110), 37.3% in 1998 (25 of 67), 62.5% in 1999 (5 of 8), 0.0% in 2000 (no frogs captured), and 10.3% in 2001 (7 of 68; $\chi^2 = 26.6$, $df = 3$, $P < 0.001$). Based on years with large numbers of captures (i.e., excluding 1999 and 2000), rate of return among breeding seasons was low.

DISCUSSION

Differences among years.—We found major differences among years in adult body size structure, within-year survival, rate of return of adults, residency length, and metamorph body size. Some of these differences are likely because of variation in the timing and length of the hydroperiod, especially residency length and metamorph size, which increased with hydroperiod length (Richter et al., in press) similar to other studies (Semlitsch, 1987; Pechmann et al., 1989). Other differences were more difficult to explain as a direct result of hydroperiod and are discussed below.

Population body size structure.—We found shifts in both mean body size and the degree of sexual dimorphism among years (Fig. 3). Although sexual dimorphism always favored females, these shifts illustrate that indices of body size (such as SDI), although viewed as a constant in the literature (Fairbairn, 1997), are subject to considerable among-year variation.

Dodd (1994) found that *Bufo quercicus* and *Bufo terrestris* exhibited changes in population body size structure similar to what we found (i.e., significant differences among years in SVL and body mass within and between the sexes). However, Dodd (1994) gave no explanation of this occurrence and stated that there were no trends or patterns evident in the relative frequencies of various size classes. Population size structure is indirectly related to hydroperiod in that differential recruitment rate (numbers per year) and body sizes of metamorphs contribute to among-year variation in population size structure (Fig. 4; Semlitsch, 1987; Berven, 1990; Richter et al., in press). Population size structure was directly affected by years with zero reproductive success, differential age at maturity between the sexes, and differential adult mortality among years.

Within-season survivorship.—Because we have no data on the exact sources of mortality for go-

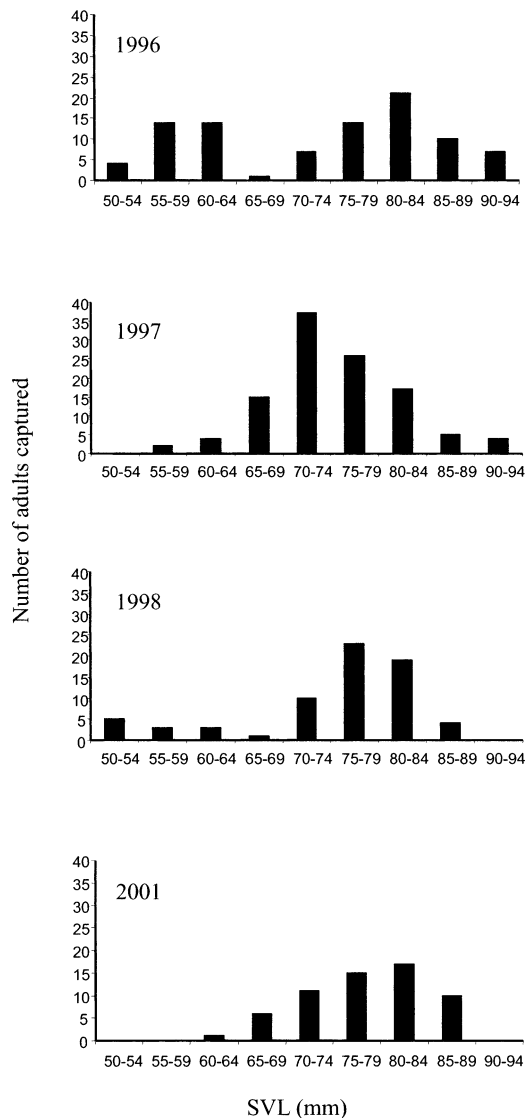


Fig. 4. Body size (SVL) distribution of adult *Rana sevosa* at Glen's Pond 1996–2001 depicting temporal shifts in population size structure.

pher frogs, we cannot determine why within-season survival differed among years in females but not in males. It does not appear that this is a result of length of time in the pond because female residency length was invariant among years, whereas male residency varied (Fig. 3). In addition to these intrasexual differences, male survival was lower than females for each year (Table 3), although these differences were significant only in 1997. Such a sexual difference in survival is not unexpected, because males spend a longer period in the pond than females and vocalization by males may lower energy re-

serves and attract predators (Tuttle and Ryan, 1981; Given, 1988). Other studies of ranid frogs found no difference between the sexes in within-year survivorship (e.g., Gibbons and McCarthy, 1984; Berven, 1990; Elmberg, 1990).

Although our estimates of within-year survivorship must be considered as minimum values (because some frogs possibly remained inside the fence beyond the study period), the error is likely small. All frogs recaptured in years following initial capture were captured both entering and exiting the fence during the first year. That is, no frogs thought to have died during a breeding season were ever recaptured in following years.

Recruitment of metamorphs.—Recruitment and body size of metamorphs was variable among years (0–2488 individuals; 29.8–35.7 mm), which is presumably a result of differing hydroperiod lengths in different years (Semlitsch, 1987; Richter et al., in press). The range of metamorph body size was below that found for *R. capito* in South Carolina (41–43 mm; Semlitsch et al., 1995) and peninsular Florida (Greenberg, 2001; 37–43 mm) but similar to those in Alabama (Braid et al., 2000; 32.3–37.5) and western Florida (Palis, 1998; 31–38 mm).

Minimum age and size at maturity.—Males had a minimum age at maturity of 4 to 6 months and were apparently capable of returning to breed during the year of emergence, whereas females required a much longer time to reach maturity. Palis (1998) estimated age at maturity of *R. capito* based on the application of an average constant rate of growth for adults developed for *R. capito* by Franz (1986), in which the rate of growth was determined by averaging the growth of male and female frogs over a 16-month period. Palis (1998) estimated that female *R. capito* mature at 29 months (compared to our 24–36 months for *R. sevosa*) and males mature at 18 months (compared to our 4–6 months). Although our estimate of female age at maturity was similar to Palis's estimate for *R. capito*, our estimate for males was much lower. The estimations of Palis (1998) assumed (1) that males and females do not differ in rate of growth and (2) that the growth rate of metamorphic frogs and adults are equal. Our data for *R. sevosa* suggest that the first assumption may be incorrect, and Franz (1986) found that small *R. capito*, adult or metamorphic, grow faster than large gopher frogs. Thus, although we do not discount the use of Franz's (1986) equations to estimate growth trajectories of adult frogs, we question using them to estimate age at maturity.

Rate of return of adults among years.—We found a low rate of return for adults among years 1996–2001 (maximum between-year rate = 21.8%); that is, only a small fraction of individuals returned to breed in more than one year (Table 4). Our average number of breeding seasons for adults found (1.18 yr) is similar for that of *Rana temporaria* (1.45 yr; Elmberg, 1990). Aside from sampling error (loss of PIT tags or bypassing the fence, both of which we feel are unlikely for this population), there are three possible explanations for this low rate of return: adults use alternate breeding sites, adults have a low frequency of reproduction (i.e., skip years between reproductive events), and adults have low annual survival.

Do adult frogs use alternate breeding sites? Survival rates may be underestimated if dispersal contributes to apparent mortality. Newly captured adult frogs may emigrate from nearby ponds (Dole, 1971; Caldwell, 1987; Berven, 1990). This cannot explain our findings because there are no other known breeding sites for gopher frogs in Mississippi, and there are definitely no other breeding ponds within 3–5 km of Glen's Pond that support gopher frogs. Also, total distances of postbreeding movements for 11 radio-telemetered individuals of this population did not exceed 300 m (Richter et al., 2001).

Do frogs skip years between reproductive events? Some anurans reproduce biennially, such as *Bufo cognatus* and *Rana pretiosa* (Bragg, 1940; Turner, 1960). To some degree, this clearly was the case for *R. sevosa* since there was no breeding in 2000; however, this was because the pond did not fill. Five individuals skipped years (other than 2000) between reproductive events (Table 4). However, biennial reproduction cannot fully explain the low among-year recapture rate. For example, of the 110 adults PIT-tagged in 1997, only 23 were ever seen again, and almost all (17) of those were only found the next year. Although the possibility exists that these individuals have skipped the intervening three breeding seasons (or two, if 2000 is discounted), the absence of these individuals for three consecutive breeding seasons suggests a breeding cycle of four years or longer, which seems unlikely. Finally, the literature suggests that in species where females have a low frequency of reproduction, males breed yearly (e.g., *R. pretiosa*—Turner, 1960; *Ascaphus truei*—Metter, 1964). If the low rate of return in this population is caused by individuals exhibiting a low frequency of reproduction, it is not just the females but also the males that are exhibiting an extremely low rate of reproduction.

Do adults experience low among-year surviv-

TABLE 5. AMONG-YEAR SURVIVORSHIP OF *Rana* SPECIES.

Species	Sex	% Survival	Reference
<i>Rana aurora</i>	M, F	69	Licht (1974)
<i>R. cascadae</i>	M	59	Briggs and Storm (1970)
<i>R. cascadae</i>	F	46	Briggs and Storm (1970)
<i>R. erythraea</i>	M, F	2–5	Brown and Alcalá (1970)
<i>R. esculenta</i>	M, F	53–70	Holenweg Peter (2001)
<i>R. lessonae</i>	M, F	72–84	Holenweg Peter (2001)
<i>R. pretiosa</i>	M	45	Licht (1974)
<i>R. pretiosa</i>	F	67	Licht (1974)
<i>R. sevoosa</i>	M, F	16–22	This study
<i>R. sylvatica</i>	M, F	4–24	Berven (1990)
<i>R. temporaria</i>	M, F	25–38	Gibbons and McCarthy (1984)
<i>R. temporaria</i>	M, F	36	Loman (1984)
<i>R. temporaria</i>	M	16–51	Elmberg (1990)
<i>R. temporaria</i>	F	5–33	Elmberg (1990)

al? This question is difficult to address, and data appear contradictory. Low among-year survival seems implausible based on four factors. First, within-season survivorship for all years was high (65–93%). Second, data for many other species (although not all) of *Rana* suggest a much higher among-year survivorship than 16–22% (Table 5). Third, data on longevity of many *Rana* species (6–10 yr) suggest such low survivorship is improbable (Martof, 1953; Briggs and Storm, 1970; Shirose and Brooks, 1995). Fourth, every frog monitored by radio-telemetry over a two-month period survived migration to its non-breeding habitat, which is potentially a time when vulnerability to predators is increased (Richer et al., 2001).

However, our data of capture rate of unmarked individuals indicate that the majority of annual captures are first-time breeders and that adults have low among-year survival. The other explanation for capturing unmarked adults is that they bred in seasons prior to the study and skipped years during the study. This seems unlikely, and in years following reproductive failure (which occurred in all but two years of our study), the number of adults captured decreased, especially after two years of reproductive failure (2001; Fig. 4).

Preliminary indications based on the annual capture rate of unmarked adults and annual trends in population body size (thus age) structure are that adults are short-lived and that few individuals return to breed in more than one breeding season (see Table 4). Because of this and the isolation of the pond (thus no metapopulation dynamic), the viability of the population is contingent on consistent recruitment with a low frequency of total reproductive failure.

Conservation status.—In relatively undisturbed habitats, periodic years of complete reproductive failure will not likely eliminate a population of long-lived (> 6 yr) amphibian but might cause fluctuations in adult population size structure (e.g., Semlitsch, 1987). For areas where habitat fragmentation and disturbance occur and the potential for metapopulation dynamics does not occur, the effects of years without juvenile recruitment would be more profound, especially if the frequency of failure was high. We observed shifts in population size structure following years of reproductive failure (1996, 1999, 2000), primarily through a loss of smaller-bodied individuals. Because this population is isolated and has been and will probably continue to be exposed to human-induced stressors (e.g., two clearcuts on adjacent property during the past seven years and the construction of a retirement community, both approximately 250 m from pond), we feel that periodic years of reproductive failure impact it more severely and increase the likelihood of extinction. Given the apparently high likelihood of extinction at this site (also see Richter et al., in press), a detailed recovery plan defining critical habitat is essential.

ACKNOWLEDGMENTS

We thank the many people who helped in the field, especially G. Johnson, M. Pilgrim, J. Demuth, B. Horne, L. Richter, M. Moore, C. Kennedy, N. Anderson, T. Lorenz, A. Dinsmore, and J. Lee. We also thank R. Doudrick, G. Johnson, and K. Mansfield at the Harrison Experimental Forest for the very gracious use of their cabin and laboratory facilities. Thanks to J. Caldwell for helpful comments on an early version of this

manuscript. We are grateful to the U.S. Fish and Wildlife Service, USDA Forest Service, and the Mississippi Department of Wildlife, Fisheries, and Parks, especially B. Jones, T. Mann, B. Glasgow, and L. LaClaire. This research was supported primarily through funding from the Section 6 Program of the Endangered Species Act. Additional funding was provided by the USDA Forest Service and the Department of Biological Sciences of Southeastern Louisiana University, through the cooperation of G. Childers and N. Norton.

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