

Stochastic variation in reproductive success of a rare frog, *Rana sevosa*: implications for conservation and for monitoring amphibian populations

Stephen C. Richter^{a,*}, Jeanne E. Young^{a,1}, Glen N. Johnson^b, Richard A. Seigel^{a,2}

^aDepartment of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402-0736, USA

^bUSDA Forest Service, Southern Research Station, Southern Institute of Forest Genetics, 23332 Highway 67, Saucier, MS 39574, USA

Received 19 September 2001; received in revised form 15 April 2002; accepted 22 August 2002

Abstract

Although amphibian populations are thought to be declining in many parts of the world, detailed information on populations in decline are often not available. From 1988 to 2001, we studied temporal variation in the reproductive biology of the only known population of dusky gopher frogs, *Rana sevosa* Goin and Netting. We found high annual variation in reproductive effort, mortality at the egg and larval stages, and hydroperiod length. No overall trends were apparent in terms of either number of egg masses deposited or in reproductive success, as we found extensive variation among years in the number of egg masses deposited, a high rate of reproductive failure, and no consistent relationship between the number of females present, the number of eggs deposited, and the number of metamorphs emerging. Given the complete isolation of this population from other gopher frogs and the high rate of reproductive failure, the probability of extinction of this population appears to be quite high (0.125–0.316).

© 2003 Elsevier Science Ltd. All rights reserved.

Keywords: Variation in reproduction; Population viability; Egg mass counts; Monitoring; Reproductive success; Amphibian; Anuran; Ranidae

1. Introduction

Although the debate over the extent and causes of the widespread decline in amphibian populations continues (cf. Pounds et al., 1997; Alford and Richards, 1999), attention has increasingly been focused on a critical question: why do some amphibian populations persist for long periods of time whereas others do not (Pechmann et al., 1991; Blaustein et al., 1994; Beebe, 1997; Skelly et al., 1999; Marsh and Trenham, 2001)? Answering this question requires comprehensive information on both reproductive and population ecology, data that are often difficult to obtain for declining species.

One extreme case of a species in decline is the dusky gopher frog, *Rana sevosa*. This sister species to the more

widespread *R. capito* was once abundant in Mississippi and Louisiana (Allen, 1932), but only one population (Glen's Pond) is now known. Despite numerous surveys for calls, egg masses, and sites, no other breeding population of *R. sevosa* has been found in Louisiana, Mississippi, or Alabama in over 10 years. In December 2001, *R. sevosa* was listed under the US Endangered Species Act as endangered (LaClaire, 2001). Elsewhere we have presented data on the demography of this population (Richter and Seigel, 2002). Here, we present data on the reproductive biology of this isolated population, with special attention to how variation in reproductive success and recruitment affect population persistence when no immigration from other sites is possible.

2. Methods

2.1. Study site and period

We studied gopher frogs from 1988 to 2001 at Glen's Pond, an ephemeral pond located in De Soto National Forest in Harrison County, Mississippi, USA. Glen's

* Corresponding author. Present address: Department of Zoology and Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, 2401 Chautauqua, Norman, OK 73072, USA.

E-mail address: richter@ou.edu (S.C. Richter).

¹ Present address: Faculty of Science, Information, and Technology, Northern Territory University, Casuarina Campus, NT 0909, Australia.

² Present address: Department of Biological Sciences, Towson University, 8000 York Road, Towson, Maryland 21252, USA.

Pond is approximately 440 m in circumference and fills to a maximum depth of about 1.1 m. The pond typically fills in midwinter, dries during the summer, and has high annual variation in hydroperiod length (see Results), although it has held water beginning as early as September (following a tropical storm) and has dried as late as September (Fig. 1). We identify breeding seasons (winter to summer) as the later year of the season (e.g. September 1993–August 1994 = 1994).

2.2. Study species

The historic range of *Rana sevosa* extended throughout the upland longleaf pine, (*Pinus palustris*) forests of western Alabama, Mississippi, and Louisiana (Goin and Netting, 1940). Even as recently as 14 years ago, isolated males were heard calling at sites within 8 km of Glen's Pond; however, none has been heard since. Both *Rana sevosa* and the related *R. capito* breed in ephemeral ponds from late autumn to early spring and spend the remainder of the year in adjacent upland habitat. *Rana sevosa* in Mississippi takes refuge in small mammal burrows and holes associated with dead trees (though historically in gopher tortoise burrows) up to 300 m from the breeding site (Richter et al., 2001). Age at maturity of gopher frogs ranges from less than 1 year for males to ≥ 2 years for females (Palis, 1998; Richter and Seigel, 2002). Among-year survival ranges from 15 to 17% between consecutive years. So, most adults do not return to breed in multiple years and longevity appears to be low for most individuals, though a small proportion of individuals were found to breed for 4–5 years (Richter and Seigel, 2002). For example, of 68 adults that bred in 2001, only seven were adults tagged during previous breeding years (Richter and Seigel, 2002).

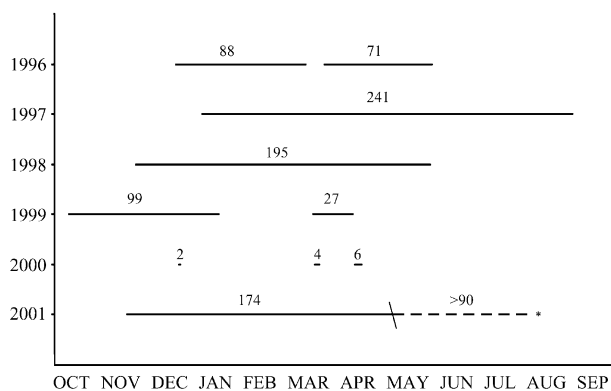


Fig. 1. Hydroperiods for 1996–2001 at Glen's Pond. Slash followed by dashed line in 2001 represents when the pond would have dried without human intervention. * = Pond held water through April 2002.

2.3. Egg mass counts and hatching success

In all years, Glen's Pond was systematically searched 1–5 times per week (depending on rainfall and frog breeding activity) for newly deposited egg masses. *Rana sevosa* egg masses could be distinguished from those of southern leopard frogs (*R. sphenoccephala*) by the larger size of the ova and the roundness and firmness of the mass. Given the small size of Glen's Pond and the distinctive nature of *R. sevosa* egg masses, we believe we found all egg masses deposited. During 1996 and 1997, clutch size was estimated using a water displacement technique similar to Davis and Folkerts (1986). See Richter (1998) for complete clutch size data. A subsample of eggs was used to determine how many eggs were required to displace 1 ml of water in a graduated cylinder, and by extrapolation, the number of eggs in each mass was calculated. From 1996 to 1998 egg masses were checked several times per week (sometimes daily) to determine hatching date and to measure hatching success. After hatching and when tadpoles were no longer clinging to the egg mass, the number of undeveloped eggs was counted for each mass. We compared embryo mortality among years by using the average number of undeveloped eggs per mass.

2.4. Counts of adults and metamorphs

From 1996–2001, a 525-m drift fence completely enclosing Glen's Pond was used to sample adults and metamorphs entering and exiting the pond. The fence was approximately 90 cm high and composed of fine-woven, Department of Transportation grade, black plastic mesh ("silt" fencing). It was installed such that 8–10 cm of the fence was beneath the soil and was equipped with 68 pairs of 25-l buckets serving as pitfall traps (one on each 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. We thus believe we were 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. Each pitfall trap was equipped with a large, moist sponge to minimize the desiccation of amphibians.

During periods when the fence was operational, the pitfall traps and fence were checked for animals daily. The fence was checked multiple times daily during rainy periods, often at night from 2100 to 0600 h. During non-rainy periods, the fence was checked daily between 0700 and 1000 h. Adults were individually marked using unique toe-clips from 1994 to 1996 and PIT tags (passive integrated transponders; AVID[®]) from 1997–2001. Metamorphs were too small for PIT tagging and were

given an annual cohort mark by clipping the same toe on every individual within a given year.

2.5. Statistical methods

Statistical analyses were performed using SYSTAT (SPSS, Inc.). All means are followed by ± 1 standard error. For statistical testing, alpha was set at 0.05.

3. Results

3.1. Yearly variation in hydroperiod

Dates for onset of the pond filling ranged from 13 September (1999 season) to 5 January (1997 season; Fig. 1). Total hydroperiod (date of first filling to drying) ranged from 27 to 241 days. In 2 years (1996 and 2000), there was a bimodal hydroperiod, where the pond filled, dried, and then filled again. Intervals between the first and second hydroperiod were 11 and 61 d, respectively, in those years (Fig. 1).

3.2. Egg mass counts

Egg masses were deposited as early as October (following tropical storms) but more typically from December through early April (Table 1). The widest variation of egg deposition dates in any single breeding season was from 4 December 1994 to 15 March 1995. Egg masses were deposited in 12 of 14 years (85.7%). Numbers of egg masses varied markedly, from zero in two years (due to low water levels from severe drought) to a maximum of 130 (Fig. 2; mean = 42 ± 10.6).

3.3. Egg mortality

Egg mortality was relatively low in 1996 (53.5 ± 10.55 eggs/mass), high in 1997 (423.5 ± 49.15 eggs/mass), and intermediate in 1998 (286.9 ± 48.80 eggs/mass), which based on an average clutch size (1134.2, see Section 4.1) translates to proportions of 4.7, 37.3, and 25.3%, respectively. At least some of the egg mortality was due to the attachment of caddisfly larvae (Order Trichoptera, Family Phryganeidae) to egg masses, which were found on 100% of the egg masses in 1997 and 1998, but were not seen in 1996 (Richter, 2000). Any damage caused by caddisfly larvae to *Rana sphenoccephala* eggs always resulted in death to the developing embryo in the laboratory (Richter, 2000).

3.4. Developmental periods

We determined minimum developmental periods (i.e. the number of days between egg deposition and metamorphosis) for 1997 and 1998, the only 2 years that the drift fence was operational when there was natural reproductive success. We estimated developmental period by calculating the number of days between the deposition of the first egg mass and the emergence of the first and last metamorph. The minimum to maximum range of development was 81–179 d in 1997 and 139–155 d in 1998 (Fig. 3).

3.5. Reproductive success

We define reproductive success as the appearance of at least one metamorph either at the pond (prior to fence construction) or at the drift fence. Prior to construction of the drift fence in 1996, we were able to

Table 1

Summary of reproductive patterns at Glen's Pond from 1988 to 2001, including timing of reproduction, number of egg masses, numbers of adults, and extent of juvenile recruitment (if known)

Breeding season	Egg mass deposition period	# Of egg masses	# Of females	Reproductive success?	# Of metamorphs
1988	3 Feb–30 Mar	86	–	–	–
1989	No breeding	0 (Drought)	–	No	0
1990	22 Jan–3 Mar	71	–	–	–
1991	16 Jan–20 Feb	55	–	–	–
1992	27 Jan–29 Feb	29	–	–	–
1993	24 Jan–25 Mar	30	–	–	–
1994	11 Mar	3 (Drought)	–	No	0
1995	4 Dec–15 Mar	130	–	Yes	–
1996	26 Jan–19 Apr	37	50	No	0
1997	1 Feb–22 Mar	58	58	Yes	221
1998	7 Jan–30 Mar	37	37	Yes	2488
1999	3–11 Oct	5	5	No	0
2000	No breeding	0 (Drought)	1	No	0
2001	5 Feb–16 Mar	36	68	No ^a	0

^a Metamorphs emerged from the pond; however, because this was due to human intervention (see text), we do not consider this a naturally successful year.

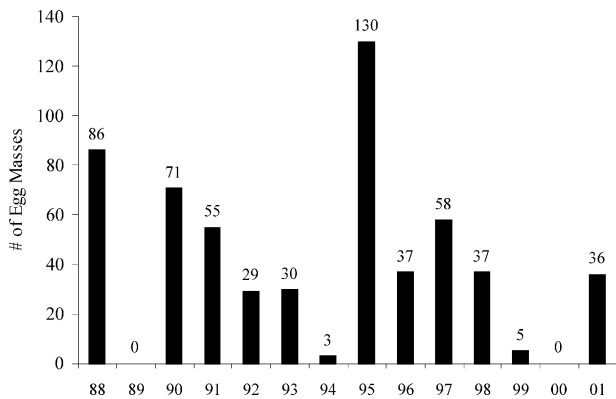


Fig. 2. Variation in number of egg masses deposited each year at Glen's Pond from 1988–2001.

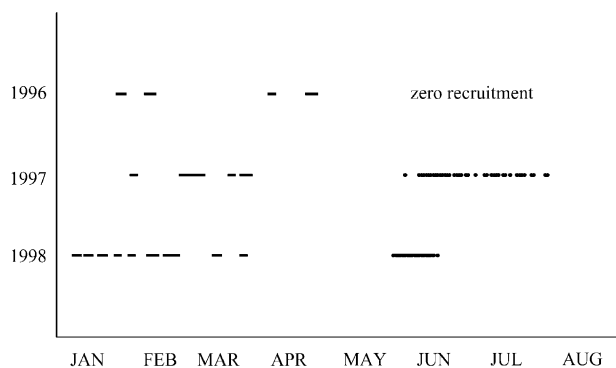


Fig. 3. Timing of egg mass deposition (rectangular symbols) and metamorphic frog emergence (circular symbols) for 1996–1998.

determine whether reproductive success occurred in only three years, when either no egg masses were laid (1989), when tadpoles were stranded by low water levels and died (1994), or small males were captured in the following year as seen in 1998 (1995). Of the seven breeding seasons for which we have data sufficient to determine whether metamorphs were produced (1995 through 2001), successful production of metamorphs occurred in only three of these (43%): 1995, 1997, and 1998 (Table 1). No natural metamorphosis occurred for three consecutive breeding seasons (1999 through 2001). Because of human intervention to prevent pond drying in 2001, metamorphs successfully emerged from the pond, but we do not consider this year as successful in our analysis of population persistence. The overall probability of successful recruitment was thus 0.37 (if

we include all years where we could make a definite assessment) or 0.43 (if we include only the 7 years for which we have consecutive data).

3.6. Egg mass counts and reproductive success

There was a close relationship between the number of egg masses laid and the number of females known to be in the pond in 1997 (58 egg masses: 60 females) and 1998 (37 egg masses: 38 females). This contrasts strongly to 1996, when we found 37 egg masses and 50 females (Table 2). There was a significant difference among years in the ratio of females to egg masses (contingency table analysis, $\chi^2 = 18.080$, $df = 2$, $P < 0.001$). We also found no consistent relationship between the number of egg masses deposited and reproductive success (Table 2). A total of 37 egg masses in 1996 resulted in zero metamorphs, 58 egg masses in 1997 resulted in 221 metamorphs, and 37 egg masses in 1998 resulted in 2248 metamorphs, which demonstrates high variation in production ratios (# metamorph: # egg masses) of 0.0, 3.81, and 60.76, respectively. Therefore, reproductive success could not be simply estimated by measuring the number of females entering the pond or by counting egg masses, at least not with a high degree of certainty.

4. Discussion

4.1. Juvenile recruitment

Timing and length of the hydroperiod frequently play a significant role in metamorphic success and body size in anurans (Wilbur and Collins, 1973; Semlitsch, 1987; Pechmann et al., 1989, 1991; Rowe and Dunson, 1995). This was evident at Glen's Pond. We found natural reproductive success in only 2 years for which we knew hydroperiod length: 1997 (hydroperiod of 241 days) and 1998 (195 days). Given the minimum developmental period for *R. sevosia* of 81 days, this relationship between hydroperiod and reproductive success is not surprising. Such a long developmental period/short hydroperiod also explains the high rate of reproductive failure seen in our study, since few years had the lengthy continuous hydroperiod required to allow successful metamorphosis (Fig. 1). As discussed below, such a small hydroperiod to developmental period ratio may

Table 2
Summary of gopher frog reproductive output for 1996–1998 (M = male, F = female)

Year	# M	# F	# Egg masses	Estimated # of eggs	# Metamorphs	Eggs/F	Production (metamorphs/ egg mass)	Survival to metamorphosis	Hydroperiod length (d)
1996	47	50	37	43,801	0	876	0/37 = 0.0	0.00%	88 and 71
1997	50	60	58	63,947	221	1065.8	221/58 = 3.81	0.35%	241
1998	29	38	37	41,965	2248	1104.3	2248/37 = 60.76	5.36%	195

suggest that the long-term viability of this isolated population is low.

The only year in which we have both clutch size estimates and when reproductive success occurred is 1997. Based on the estimated number of eggs laid in 1997 (63,947) and the number of metamorphs (221), 0.35% of eggs resulted in metamorphs. We estimated the number of eggs produced during 1998 by taking the average clutch size from the combined data of 1996 and 1997 (1134.2; $n=95$ clutches) and multiplying this average by the number of egg masses for 1998 (37). Based on the estimated number of eggs produced (41,965) and the number of emerging metamorphs (2248), the overall estimated recruitment rate for 1998 was 5.36%. There are no previous data on recruitment rate for this species as a basis of comparison, but studies of other amphibians suggest that the rate in 1997 was very low (Anderson et al., 1971; Shoop, 1974; Semlitsch, 1987; Stangel, 1988 and references therein). Conversely, the estimates for 1998 were comparable to other *Rana* species: *R. pretiosa*—4.3% (Turner, 1960); *R. aurora*—5% (Calef, 1973); *R. sylvatica*—3.7% (Herreid and Kinney, 1966).

4.2. Egg mass mortality

Mortality rates for egg masses were higher in 1997 than in other years, suggesting a change in the source or intensity of the factors that determine egg survival. We observed a much higher rate of caddisfly infestations on egg masses in 1997 compared to 1996 (Richter, 2000), and caddisfly larvae have been reported as a factor causing egg mortality (often severe) in *R. sevosia*, other ranid frogs, and many other amphibians (reviewed in Richter, 2000). Other environmental variables (temperature, pH, etc.) were not measured between years, so cannot be addressed. Other possibilities include differential fertilization, fungal infection, and developmental abnormalities.

4.3. Developmental periods

The developmental periods for the first and last egg masses define the possible range of time that all other egg masses developed in a given season (81–179 in 1997 and 139–155 in 1998). These developmental periods are similar to those found for *R. sevosia* in the laboratory at an average temperature of 20 ± 3 °C (141–155 d; Volpe, 1958) and to estimates by Semlitsch et al. (1995) of *R. capito* in South Carolina (87–113 d). However, our developmental-period estimates differ strongly from those of a Florida population of *R. capito* (210 d; Palis, 1998). This difference is probably due to the overwintering of Florida tadpoles, whose development took place from October to May (assuming these individuals survived the winter to metamorphosis).

4.4. Patterns in reproduction and implications for monitoring amphibian populations

Concern for amphibian declines has resulted in development of standardized methodologies for monitoring and measuring amphibian populations (Heyer et al., 1994). Many studies of amphibian ecology have relied on indirect measures (e.g. egg mass counts) to estimate demographic variables such as population size and reproductive success (e.g. Corn and Livo, 1989; Gilbert et al., 1994). The use of egg mass counts to determine population status or reproductive success requires that two assumptions be validated: (1) There must be a close correlation between the number of breeding adult females in the population and the number of egg masses observed, and (2) there must be a close correlation between the number of egg masses observed and reproductive success.

We question the validity of both assumptions. In our study, the ratio of egg masses to adult females was close to 1:1 in 1997 and 1998 but not in 1996, when egg mass counts substantially underestimated the number of females known to be in the pond (a ratio of egg masses to females of 0.74). Why some females entered the pond but did not lay eggs is unknown. At least four gravid females left the pond, and 14 females never left the pond. We also found no association between egg mass counts and reproductive success. A total of 37 egg masses in 1996 resulted in zero metamorphs, whereas 58 egg masses in 1997 resulted in 221 metamorphs and 37 egg masses in 1998 resulted in 2248 metamorphs. We thus found no predictable relationship between numbers of egg masses and the numbers of metamorphs. Because the ratio of egg masses to both adults and recruitment was not stable or predictable among years, we feel that validations must be performed at the population level before this measure is used to assess population status.

4.5. Population persistence and stochastic variation in reproduction

Gopher frogs were consistent in depositing egg masses in almost every year of our study (12 of 14 years), but otherwise showed highly variable patterns of both reproductive output (3–130 egg masses produced) and reproductive success (0–2488 metamorphs, with a probability of successful reproduction ranging from 0.37 to 0.43 per year). Furthermore, gopher frogs at our site were exposed to highly variable hydroperiods of 27 to 241 days (Fig. 1), which contributed to the high degree of variation in numbers of metamorphs produced and yearly variation in the size of those metamorphs.

Although no other data for *R. sevosia* are available, information for the sister taxon, *R. capito*, suggests the level of variation in reproductive output we have seen at Glen's Pond is not atypical. For example, the number of

egg masses laid per year ranged from 0 to 183 at a pond in the Conecuh National Forest in Alabama, with some level of reproduction in seven of eight years (87.5%; M. Bailey and E. Blankenship, personal communication). Frequency of breeding in South Carolina ranged from 0.06 to 0.67/year, but no data on numbers of egg masses were available (Semlitsch et al., 1995).

What perhaps distinguishes the Glen's Pond population from other localities is the low frequency of reproductive success. In the only long-term study of gopher frogs existing at multiple ponds, Greenberg (2001) found that *R. capito* breeding in a complex of eight ponds in north-central Florida had some level of recruitment in all 5 years of her study but that variation in recruitment among ponds was extremely high. Some ponds had apparent recruitment in all five years (e.g. Pond #8) whereas others (e.g. Pond # 2) had metamorphs in only 2 of 5 years. Even in a "good year," the number of metamorphs among ponds varied from less than 10 to more than 120 per pond. Interestingly, Greenberg found "an abundance of unmarked juveniles entering most ponds in high-recruitment years . . . suggesting that many originated at untrapped ponds within the vicinity," indicating the presence of a metapopulation [at least in the sense of "ponds as patches" (Marsh and Trenham, 2001)]. Thus, while variation was high in reproductive success for any given pond in Greenberg's (2001) study, the probability of failure for all ponds taken as a unit was effectively zero, and immigration among ponds was highly feasible at this site, albeit not proven.

Semlitsch et al. (1995) suggested that gopher frogs in South Carolina were subject to rapid local extinction due to small population sizes and infrequent recruitment of metamorphs. We concur with this assessment, especially when populations are isolated, as is true in Mississippi. Such isolation means that the so-called "rescue effect" (where a population nearing extinction is "rescued" via recruitment from a nearby source; Stacey et al., 1997; Skelly et al., 1999; Marsh and Trenham, 2001) cannot occur at Glen's Pond. Under this scenario, amphibian breeding sites that are part of a larger metapopulation complex would be less likely to go extinct than would isolated populations where no recruitment from outside sources is possible. Given this extreme stochasticity in reproductive success at Glen's Pond and the fact that immigration from other sites is impossible for this species, what is the likelihood of continued population persistence at this site?

One way of examining population persistence uses the known variation in reproductive success combined with available demographic data. Mark-recapture data of this population indicated that only a small proportion of adults returned for multiple breeding events and that most adults entering the pond in a given year were first-time breeders, presumably the most recent group of metamorphs from the last successful breeding season

(Richter and Seigel, 2002). In 2001, which was the first large-scale breeding event since 1998 (Table 1), only seven of 68 adults (10.3%) were recaptures from previous years (Richter and Seigel, 2002). Thus, the vast majority of adults in 2001 represented metamorphs from 1997 and 1998, and possibly 1995.

Because few adults appear to breed more than once or twice, we conclude that, in the absence of recruitment from another site, Glen's Pond must experience some degree of successful reproduction (metamorphs) at least once every 4–5 years. A lack of reproduction for at least 4 or 5 consecutive years means that the apparent average longevity (3–4 years) of remaining adults would be exceeded. Thus, the key issue for this case of extreme isolation is "what is the probability of four or five consecutive years of reproductive failure?" Based on the 7 consecutive years and 8 total years of known reproductive success, 66–75% of years results in reproductive failure; based on a simple binomial, the range of probabilities of four consecutive years of reproductive failure is 0.189–0.316; for 5 years it is 0.125–0.237. Thus, there is a minimal probability of extinction of this population of 0.125 and a maximum probability of 0.316, even in the absence of other threats such as introduced diseases, collecting, or introduced predators. Given that the Glen's Pond site apparently represents the last breeding site for the entire species, this extremely high rate of possible extinction warrants special attention.

Based on reproductive data of salamanders collected in multiple years at three ponds, Semlitsch (1987) concluded that periodic years of complete reproductive failure would not eliminate a population of a long-lived (> 6 years) amphibian but would cause fluctuations in adult population size structure. This may be the case in relatively undisturbed areas in which habitat fragmentation and disturbance are minimal and the potential for metapopulation dynamics exists. Shifts in population size structure following years of reproductive failure (1996, 1999, 2000), primarily through a loss of smaller-bodied individuals, were observed for this population (Richter and Seigel, 2002). However, due to the isolation of this population and that there has been, and will probably continue to be, human-induced stressors (e.g. two clearcuts on adjacent property during the past seven years and the construction of a retirement community, both approx. 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 rate of extinction probabilities at this site, a detailed recovery plan defining critical habitat is essential, and the management agencies responsible for this species (US Fish and Wildlife Service and USDA Forest Service) should consider one or more of the following options. First, use of well water to artificially extend the hydroperiod when necessary would increase reproductive success and possibly

lower the probability of extinction. Second, some tadpoles should be raised in nearby wading pools or cattle tanks to insure some metamorphs are produced each year. Third, the absence of a metapopulation structure appears to severely increase the chances for extinction of *R. sevosus*. Thus, serious consideration should be given to increasing the number of populations via construction of new ponds or rehabilitation of older, abandoned breeding sites nearby (i.e. within 1000 m). The first of these options was tested experimentally during 2001 and found to be moderately successful (R. Seigel, personal observation). The second option is scheduled for implementation during 2002, and the third during 2003.

Acknowledgements

We are grateful to L. LaClaire, R. Jones, and T. Mann, for financial assistance, support and encouragement. We also thank S. Doody, M. Pilgrim, J. Demuth, B. Horne, L. Richter, M. Moore, C. Kennedy, N. Anderson, T. Lorenz, A. Dinsmore, and J. Lee and others who helped in the field; R. Doudrick, F. Bridgewater, and others at the Harrison Experimental Forest for the use facilities; R. Glasgow, D. Tyrone, and R. Smith for logistical support; and J. Caldwell and anonymous reviewers for comments on earlier drafts. This research was supported by the US Fish and Wildlife Service, the Mississippi Department of Wildlife, Fisheries, and Parks; the USDA Forest Service and the Department of Biological Sciences of Southeastern Louisiana University.

References

- Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30, 133–165.
- Allen, M.J., 1932. A survey of the amphibians and reptiles of Harrison County, Mississippi. *American Museum Novitates* 542, 1–20.
- Anderson, J.D., Hassinger, D.D., Dalrymple, G.H., 1971. Natural mortality of eggs and larvae of *Ambystoma t. tigrinum*. *Ecology* 52, 1107–1112.
- Beebee, T.J.C., 1997. Changes in dewpond numbers and amphibian diversity over 20 years on chalk downland in Sussex, England. *Biological Conservation* 81, 215–219.
- Blaustein, A.R., Wake, D.B., Sousa, W.P., 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8, 60–71.
- Calef, G.W., 1973. Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology* 54, 741–758.
- Corn, P.S., Livo, L.J., 1989. Leopard frog and wood frog reproduction in Colorado and Wyoming. *Northwestern Naturalist* 70, 1–9.
- Davis, M.S., Folkerts, G.W., 1986. Life history of the wood frog *Rana sylvatica* LeConte (Amphibia: Ranidae) in Alabama. *Brimleyana* 12, 29–50.
- Gilbert, M., LeClair jr, R., Fortin, R., 1994. Reproduction of the northern leopard frog (*Rana pipiens*) in floodplain habitat in the Richelieu River, P. Quebec, Canada. *Journal of Herpetology* 28, 465–470.
- Goin, C.J., Netting, M.G., 1940. A new gopher frog from the Gulf Coast, with comments upon the *Rana areolata* group. *Annals of Carnegie Museum* 28, 137–169.
- Greenberg, C.H., 2001. Spatio-temporal dynamics of pond use and recruitment in Florida gopher frogs (*Rana capito aesopus*). *Journal of Herpetology* 35, 74–85.
- Herreid, C.F., Kinney, S., 1966. Survival of Alaskan woodfrog (*Rana sylvatica*) larvae. *Ecology* 47, 1039–1041.
- Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S. (Eds.), 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington DC.
- LaClaire, L.V., 2001. Endangered and threatened wildlife and plants; final rule to list the Mississippi gopher frog distinct population segment of dusky gopher frog as endangered. *Federal Register* 66, 62993–63001.
- Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15, 40–49.
- Palis, J.G., 1998. Breeding biology of the gopher frog, *Rana capito*, in western Florida. *Journal of Herpetology* 32, 217–223.
- Pechmann, J.H.K., Scott, D.E., Gibbons, J.W., Semlitsch, R.D., 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology and Management* 1, 3–11.
- Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253, 892–895.
- Pounds, J.A., Fogden, M.P.L., Savage, J.M., Gorman, G.C., 1997. Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology* 11, 1307–1322.
- Richter, S.C., 1998. The demography and reproductive biology of gopher frogs, *Rana capito*, in Mississippi. Unpublished MS thesis, Southeastern Louisiana University, Hammond.
- Richter, S.C., 2000. Larval caddisfly predation on the eggs and embryos of *Rana capito* and *Rana sphenoccephala*. *Journal of Herpetology* 34, 590–593.
- Richter, S.C., Seigel, R.A., 2002. Annual variation in the population ecology of the endangered gopher frog, *Rana sevosus* Goin and Netting. *Copeia* 962–972.
- Richter, S.C., Young, J.E., Seigel, R.A., Johnson, G.N., 2001. Post-breeding movements of the dark gopher frog, *Rana sevosus* Goin and Netting: implications for conservation and management. *Journal of Herpetology* 35, 316–321.
- Rowe, C.L., Dunson, W.A., 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of Central Pennsylvania, USA. *Oecologia* 102, 397–403.
- Semlitsch, R.D., 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. *Copeia* 61–69.
- Semlitsch, R.D., Gibbons, J.W., Tuberville, T.D., 1995. Timing of reproduction and metamorphosis in the Carolina gopher frog (*Rana capito capito*) in South Carolina. *Journal of Herpetology* 29, 612–614.
- Shoop, C.R., 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55, 440–444.
- Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80, 2326–2337.
- Stacey, P.B., Taper, M.L., Johnson, V.A., 1997. Migration within populations. The impact upon local population dynamics. In: Hanski, I., Gilpin, M.E. (Eds.), *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, pp. 267–291.
- Stangel, P.W., 1988. Premetamorphic survival of the salamander *Ambystoma maculatum*, in eastern Massachusetts. *Journal of Herpetology* 22, 345–347.
- Turner, F.B., 1960. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird and Girard, in Yellowstone Park, Wyoming. *Ecological Monographs* 30, 251–278.
- Volpe, E.P., 1958. The early development of *Rana capito sevosus*. *Tulane Studies in Zoology* 5, 207–225.
- Wilbur, H.M., Collins, J.P., 1973. Ecological aspects of amphibian metamorphosis. *Science* 182, 1305–1314.