FACTORS AFFECTING POPULATION FLUCTUATIONS IN LARVAL AND ADULT STAGES OF THE WOOD FROG (*RANA SYLVATICA*)[1]

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Abstract. During a 7-yr population study on the wood frog, *Rana sylvatica,* the breeding population size fluctuated by a factor of 10 and juvenile production by a factor of 100. Variation in the adult population among years was largely due to variation in juvenile recruitment. Annual net replacement rates (R_0) varied from 0.009 to 7.49. Survivorship curves (calculated using the number of eggs deposited as the initial point) showed that most variation in the proportion of individuals surviving to adulthood was due to variation in larval survival; juvenile and adult survival was relatively constant among years. Male and female survival did not differ. Because females matured a year later than males, on average 2.3 times as many males as females from a given clutch survived to breed. This difference accounted for the observed male-biased sex ratio in breeding choruses. Pre-metamorphic survival and size at metamorphosis were negatively correlated with the number of eggs deposited. Length of larval period was positively correlated with number of eggs deposited. Survival was higher among juveniles that metamorphosed early and were large at metamorphosis. Larger juveniles matured earlier and were also larger as adults. The population appeared to be regulated through density-dependent factors affecting larval survival, larval size, and time of metamorphosis. Adult population size also negatively affected total clutch volume. Mean monthly rainfall positively affected adult survival.

Key words: amphibian; body size; density dependent; fitness; life table; metamorphosis; population dynamics; Rana sylvatica; reproduction; survival.

INTRODUCTION

Identifying the factors regulating populations of most organisms remains a challenge for ecologists. Population regulation in vertebrates, particularly birds and mammals, has received much discussion (see Krebs 1985). Many amphibians differ from other vertebrates in having life cycles with a larval stage adapted for rapid growth, and a terrestrial phase adapted for dispersal (Wilbur 1980). Metamorphosis, the transition between these two phases, is associated with an abrupt ontogenetic change in morphology, physiology, behavior, and habitat (Wassersug 1974, 1975). For organisms with complex life cycles, such as amphibians, understanding population regulation is challenging since it may occur in any combination of life history stages (Wilbur 1980).

Although the effect of larval developmental patterns on larval fitness components, population persistence, and community organization is well documented, relatively little is known about population dynamics after metamorphosis (Turner 1962, Wilbur 1980). In addition, the relative importance for population regulation of biotic and abiotic factors is not well understood nor is the extent that density dependence operates in each stage. Finally, with the exception of a few studies

(Berven and Gill 1983, Smith 1987, Semlitsch et al. 1988) little is known concerning how variation in larval traits (such as size and time of metamorphosis) affects postmetamorphic growth, survival, adult reproductive fitness, and population dynamics.

The present study summarizes the results of a 7-yr population study of two populations of the wood frog, *Rana sylvatica,* in Maryland. Life tables are constructed and used to examine population regulation and the relationship between larval traits, juvenile survival, and adult reproductive success.

METHODS AND MATERIALS

Natural history.—The wood frog is widely distributed throughout eastern North America, ranging from the mesic forests of the southern Appalachians to the tundra within the Arctic Circle. The life cycle includes an aquatic larval stage and a terrestrial juvenile and adult stage. Relative duration of each stage varies considerably throughout their geographic range (Martof and Humphries 1959, Berven 1982*a, b*). The frogs commonly breed in small temporary ponds during the first warm rains of spring. In Maryland all eggs are deposited in late February. The egg-laying period lasts for only ≈1 wk. Larvae metamorphose in early June and begin their terrestrial phase. Males and females mature sexually 1–2 yr following metamorphosis. More details on reproductive characteristics of wood frogs can be found elsewhere (Berven 1982*a,* 1988).

Field sampling and marking techniques. — This study was conducted at two ponds, Beltsville I (BVI) and Beltsville II (BVII), located on the Beltsville Agricultural Research Station, Prince Georges County, Maryland (see Berven 1982a for exact locations). The ponds, 50 m apart, are surrounded by mixed hardwoods and evergreens. BVII pond is larger (30 vs. 20 m in diameter), and deeper (1.5 vs. 5 m) than BVI and generally persists throughout the year. BVI dries by early July.

I surrounded each pond by a 0.75 m tall drift fence constructed of aluminum window screening supported by wooden stakes. I buried cans (18 and 36 L) every 3 m along the inside and the outside of the fence to catch adult and recently metamorphosed juveniles entering and leaving the ponds.

Adult frogs collected from the cans in spring were returned to the laboratory and stored in water in 4°C walk-in cold rooms, marked, and then returned to the ponds. I marked all captured frogs by removing toes. Adult and juvenile frogs got a "pond clip" (removal of a single pond-specific toe from the left front foot) to indicate the pond where they were first captured, or, in the case of metamorphosing juveniles, the pond in which they underwent larval development. Metamorphosing juveniles got a "year clip" (a year-specific toe from the right front foot) indicating year of metamorphosis. In addition, unmarked adults and marked juveniles recaptured as breeding adults got an individual number by removing a unique combination of toes from the other three feet (see Berven 1982a), or else an adult year clip by removing a single toe from a rear foot (which was unique to each year). This species does not regenerate cut toes.

I measured body length of adults and juveniles from the tip of the snout to the caudal end of the ischium (SI) to the nearest 0.5 mm, and measured wet mass to the nearest 0.1 g on a Mettler balance.

Survivorship curves. — I calculated survivorship curves from egg to adult. Initial point for each year was number of eggs deposited. I estimated total number of eggs using regressions of egg number and female body size for each age class of females together with the size distribution and numbers of females breeding each year (see Berven 1988). I calculated premetamorphic survival as the proportion of the estimated number of eggs captured at the fence as metamorphosing juveniles. I estimated juvenile and adult survival from recaptures of marked individuals in subsequent years (summarized in Table 1). Juveniles and adults not recaptured were assumed to be dead. The lack of suitable breeding sites within 2 km and low dispersal rates of wood frogs (K. A. Berven, *personal observation*) supports this assumption.

During 1980 a sample of emerging juveniles was collected from the pitfall traps. The frogs were returned to the laboratory, size was measured (see preceding section), and sex determined by cutting the animal open

TABLE 1. Data used in survivorship calculations for wood frogs from two Maryland ponds for the years 1976–1980.

Year	Pond	Estimated number of eggs deposited	No. of marked juveniles	Proportion recaptured as adults	
				Males	Females
1976	BVI	245 712	445	.112	.058
1977	BVI	206 646	16	...	...
1977	BVII	819 973	521	.061	.035
1978	BVI	51 251	3370	.256	.141
1978	BVII	120 869	1163	.048	.021
1979	BVI	13 400	579	.321	.089
1979	BVII	51 513	388*	...	...
1980	BVI	274 858	20 262	.116	.039
1980	BVII	156 325	401	.314	.164

* This cohort of juveniles was not marked.

and examining its reproductive organs (Rugh 1951). Sex ratios of recently metamorphosed juveniles did not depart significantly from unity ($\chi^2 = 0.76$; $N = 112$; $P = .85$). Based on these results and similar results from five other ponds that year, which differed in sun exposure, size, species composition, and population density, I assumed a sex ratio of marked juveniles in all years to be 1:1.

The number of nonbreeding, 1-yr-old males was unknown since only breeding males were recaptured at the fence each spring. To estimate this group, I assumed that survival of 1-yr-old breeding males from year 1 to year 2 equaled survival of 1-yr-old nonbreeding males for the same period. To estimate the total number of 1-yr-old nonbreeding males, I divided the survival rate of 1-yr-old breeding males into the number of males breeding for the first time as 2 yr olds. This method may underestimate the number of nonbreeding males since breeding may negatively influence survival. Since so few females that bred as 1 yr olds were recaptured, I was not able to estimate the survival of 1-yr-old nonbreeding females.

Statistical procedures. — I used Spearman's rank correlations to test the hypothesis that number of eggs deposited negatively affected larval survival, length of the larval period, and/or size at metamorphic climax. The correlation matrices were calculated for each pond separately, using the number of eggs deposited, the proportion of eggs surviving to metamorphosis (premetamorphic survival), the mean length of larval period, and mean length at metamorphic climax for each larval cohort between 1976 and 1982.

To test the hypothesis that juvenile size and day of year on which metamorphosis occurred affected juvenile survival and male and female age and size at first reproduction, I used Spearman's rank correlation. I also used Spearman's rank correlation to test for associations among juvenile survival, age and size at first reproduction, population size, and rainfall. Population size was the total number of juveniles and adults for the period of survival. Mean monthly rainfall was obtained from a United States weather station 1 km west

of the study site. All correlations used the mean values for each juvenile cohort from BVI and BVII between 1976 and 1982.

Product-moment and Spearman's rank correlations tested the hypothesis that adult survival and fecundity were affected by population size and mean monthly rainfall between 1976 and 1982. All statistical analyses used SPSS statistical software. Standard deviations of the mean are reported unless otherwise noted.

RESULTS

Population size of breeding adults. —Breeding populations at BVI and BVII fluctuated greatly among years (Fig. 1). Both ponds had their greatest decline (86% in both ponds) between 1977 and 1978. Although BVI eventually recovered to its 1977 levels, the population of BVII never did. The sex ratio (males : females) averaged 3.1 and ranged from 12.3 to 1.02. Variation in breeding population size among years was largely due to variation in juvenile production. Increases in breeding adult males always followed years of high juvenile output, whereas increases in females (which bred 2 yr following metamorphosis) occurred 2 yr following metamorphosis (Fig. 2). The close relationship between juvenile production and breeding population sizes accounted for the gradual decline in breeding sizes of BVII, which produced relatively few juveniles during the period of this study. In fact, in 1981 46% of the males and 38% of the females in 1982 breeding in BVII were juveniles that emerged from BVI pond in 1980.

Larval, juvenile, and adult survival. —Survivorship curves for wood frogs from BVI and BVII using pooled data for 1976–1982 are shown in Fig. 3. The survivorship curves represent three phases: (1) premetamorphic survival, (2) survival from metamorphosis to reproductive age (juvenile survival), and (3) adult sur-
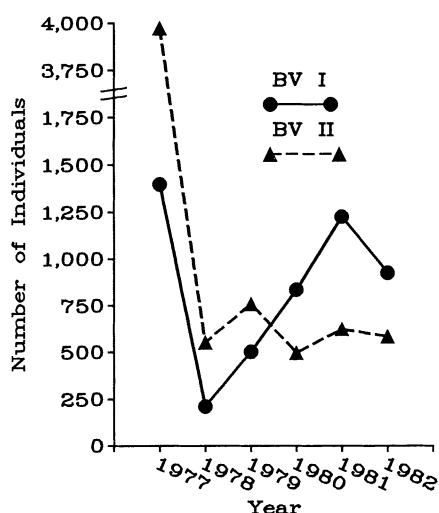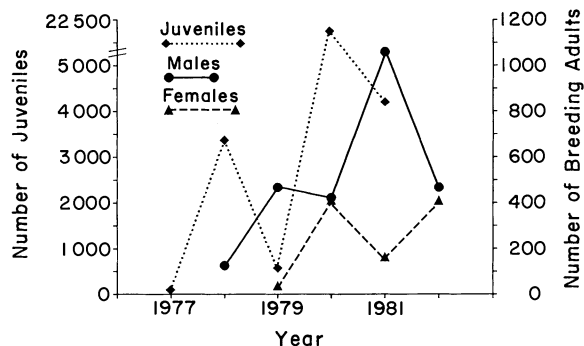

FIG. 2. Relationship between juvenile recruitment and adult population size in subsequent years. Data shown are from BVI pond.

vival (1–3 yr). Number of eggs deposited each year and premetamorphic survival varied widely among years and between ponds (Table 1). Premetamorphic survival averaged 4.5 ± 2.8% (range: 0.36–8.0%; $N = 6$; $cv = 55.5\%$) in BVI, compared to 0.95 ± 0.71% in BVII (range: 0.09–1.7%; $N = 6$; $cv = 79.7\%$). Although both ponds normally persisted until well after metamorphosis was completed, BVI dried prematurely on 27 May 1977, after only 16 individuals metamorphosed. BVII pond, which normally was permanent, dried by late June.

The proportion of adult male and female frogs alive 1, 2, and 3 yr following metamorphosis varied annually by as much as two orders of magnitude (Fig. 3). Most of the variation in number of individuals surviving to become adults was due to annual variation in premetamorphic survival. Juvenile and adult survival was relatively constant among years (Fig. 3). On average, 76% of the males (limits: 56–96%) first bred when 1 yr old (first spring following metamorphosis) and the remainder (24%) when 2 yr old (see Berven 1982a). Average survival of males from metamorphosis to age 1 (8-mo period) was 37.9 ± 12% (limits: 25.9–59.8%; $N = 7$) or 24.0 ± 11.6%/yr. Adult survival declined with age; on average 17.7 ± 0.07% of 1-yr-old males (limits: 12.0–24%) survived their 2nd yr and 10.8 ± 0.02% (limits: 0–12.5%) survived their 3 yr. Approximately 84% of the males bred once, 14% twice, and only 2% three times. No males from any marked juvenile cohort lived >3 yr.

Females from the 1976 and 1977 cohorts all reproduced for the first time when 2 yr old; however, in some years 1.6–19% of the females bred for the first time as 1 yr olds. Among the juvenile cohorts, 86.8% of the females bred once, and 14.2% bred twice. Since so few individuals that bred as 1 yr olds survived to breed a second time, it was not possible to reliably estimate female survival during that 1st yr. However, on average 7.8% ± 0.05 ($N = 7$) of the females from a juvenile cohort survived to breed at age 2. This corresponded to an annualized rate of survival of 21.6 ±

FIG. 1. Breeding adult (male and female) population sizes in BVI and BVII ponds.
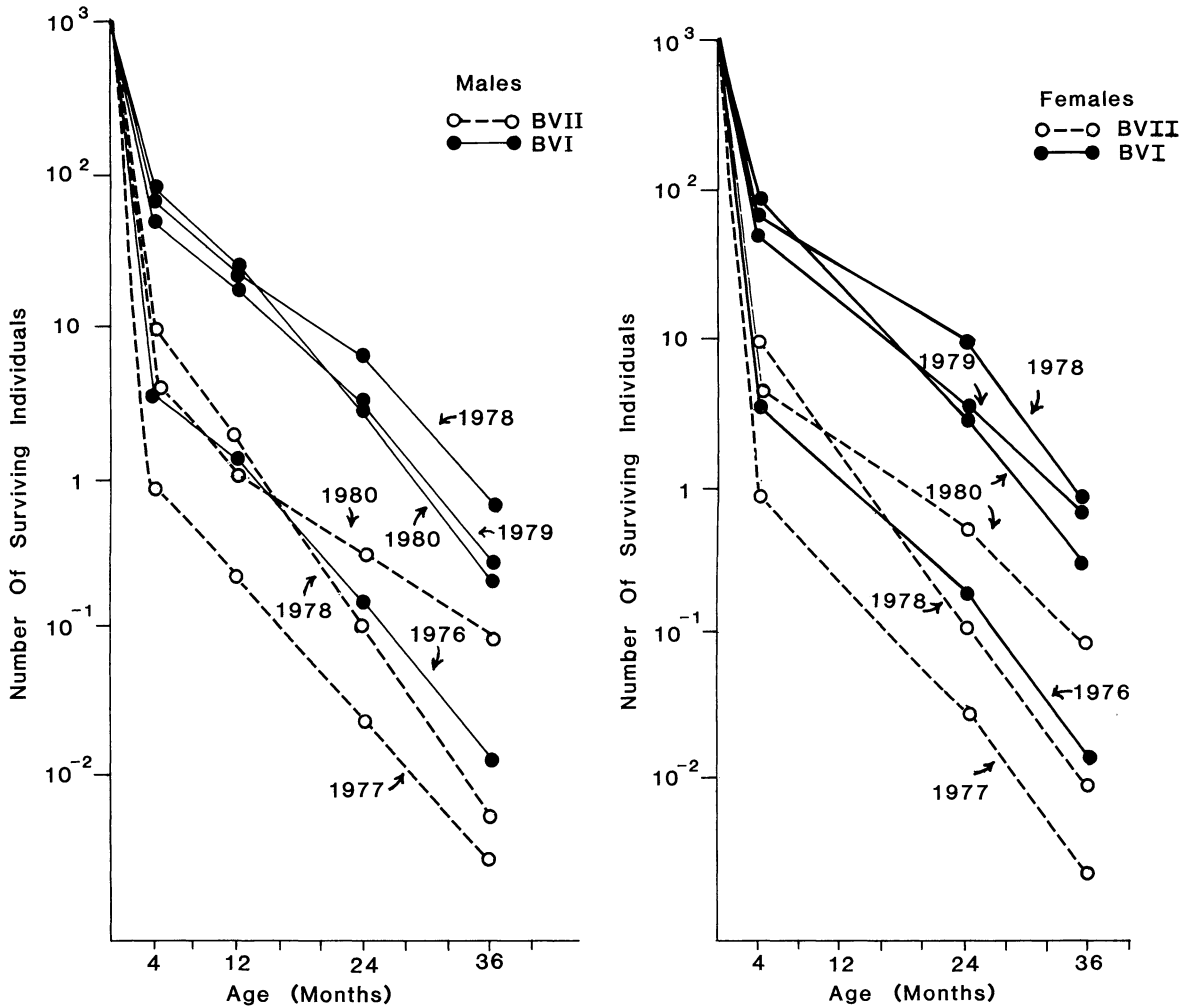
FIG. 3. Survivorship curves for males and females (1976–1980).

8.4% vs. 24.0% for males. On average 12.6% (limits: 7.6–23.8%; $N = 7$) of the females survived to breed again as 3 yr olds (a value comparable to that of similar aged males, i.e., 10.8%). No female from a juvenile cohort was observed to live >3 yr.

Survivorship curves based on individuals of uncertain age that were initially marked as breeding adults are shown in Fig. 4. Assuming most marked males were 1 yr olds and females 2 yr olds, males had a per annum survival rate of 14.0% compared to 12.8% for females. These values are in agreement with those based on marked juvenile cohorts (Fig. 3). In contrast to the data for frogs of known age, a small number of males initially marked in 1977 were recovered three times and a few females were recovered two times, indicating some individuals lived up to 4 yr. The lack of any 4-yr-old frogs among the marked juvenile cohorts was probably due to the smaller number of juveniles marked and higher mortality during the juvenile period (Fig. 3).

Replacement rate. — I have previously reported the pattern of egg production in females for this population (Berven 1988). Clutch size increases positively with female body size, is higher for younger females, and varies from year to year (Berven 1988). Combining fecundity data with survivorship data reported here, it is possible to construct a life table for each juvenile cohort and estimate several demographic parameters (Table 2). Replacement rates for BVI correlated very well with the observed changes in population size. Low values in 1976 and lack of reproduction in 1977 coincided with an 86% drop in population size (Fig. 1), while replacement values of 7.5 and 1.66 in 1978 and 1979 were followed by a six-fold increase in population size. Between 1980 and 1982 the population replacement rate was 1.06 (Fig. 1), and the population changed little.

Correlates of larval survival. — Annual premetamorphic survival was negatively correlated with total number of eggs deposited each year in BVII, but not
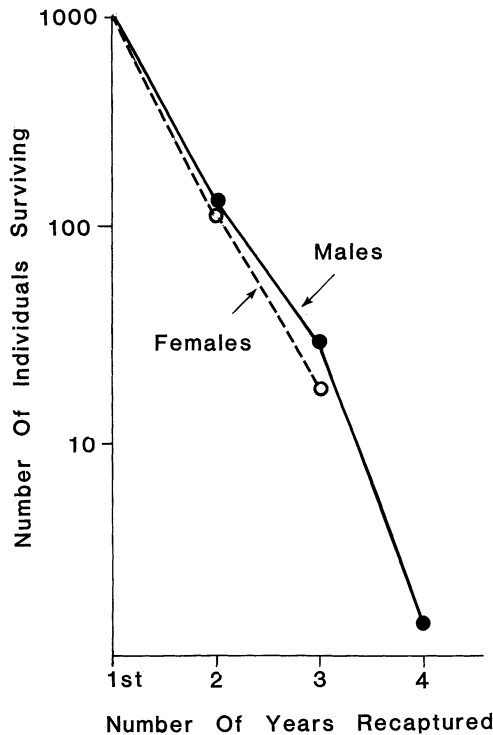
FIG. 4. Survivorship curves based on individuals initially marked as adults. Each point represents the mean number of males and females surviving from BVI and BVII ponds for the period 1977–1982, standardized to an initial number of 1000.

TABLE 2. Life table analysis including measures of net replacement rates (R_0), and generation times (G) for wood frogs from BVI and BVII pond for 1976–1980. Fecundity data (number of eggs per female) are taken from Berven 1988.

Year	Age	l_x	m_x	$l_x m_x$	R_0	G
1976	0	1.0000	0	0.000		
	1	0.0012	0	0.000		
	2	0.000212	287	0.061		
	3	0.000016	390	0.006	0.067	2.09
1977*	0	1.0000	0	0.0000		
	1	0.00024	0	0.0000		
	2	0.000032	289	0.0092		
	3	0.00000035	371	0.0001	0.0093	2.01
1978	0	1.0000	0	0.0000		
	1	0.0298	3.34	0.0998		
	2	0.0183	373	6.8408		
	3	0.0016	344	0.5504	7.49	2.06
1979	0	1.0000	0	0.0000		
	1	0.0163	15.8	0.2574		
	2	0.0035	333	1.1655		
	3	0.0008	301	0.2408	1.66	2.11
1980	0	1.0000	0	0.0000		
	1	0.02197	1.04	0.0229		
	2	0.00314	286	0.8983		
	3	0.00039	352	0.1375	1.06	2.10
1980*	0	1.0000	0	0.0000		
	1	0.00177	21.7	0.0384		
	2	0.00053	325	0.1722		
	3	0.00008	352	0.0275	0.238	1.96

* BVII pond.

in BVI (Table 3, Fig. 5). However, the low correlation in BVI is primarily due to one year (1980). If that point is eliminated the correlation is -0.90 and significant, suggesting environmental factors (independent of annual egg production) such as water level, food availability, etc. may alter the otherwise negative relationship between larval density and survival.

Average length of the larval period varied from 73 to 113 d and did not differ between ponds (BVI: $\bar{X} = 90.7 \pm 9.5$ d vs. BVII: $\bar{X} = 94.0 \pm 11.7$ d; $t = 0.53$; $N = 12$; $P = .46$). The date wood frogs initially breed in this population can vary up to 6 wk (Berven 1982b). However, correlation between mean day of year on which breeding occurred and mean length of larval period each year was low and not significant ($r_s = 0.12$; $N = 12$; $P = .55$), indicating that early breeding did not result in early metamorphosis. Initial number of eggs deposited was positively correlated with the mean duration of the larval period in both ponds (Table 3).

Size at metamorphosis varied from 14.2 to 18.1 mm, and again did not differ between ponds (BVI: $\bar{X} = 15.6 \pm 1.3$ mm vs. BVII: $\bar{X} = 16.2 \pm 1.2$ mm; $t = 0.9$; $N = 12$; $P = .45$). Mean size at metamorphic climax was negatively correlated with the mean length of the larval period in BVI but not in BVII (Table 3). Total number of eggs deposited also was correlated negatively with mean size at metamorphosis (Table 3). Thus, increased

egg numbers were associated with reduced survival, decreased size at metamorphosis, and prolongation of the larval stage.

Factors affecting juvenile survival. —Several factors including body size, population density, precipitation levels, and predator abundance are thought to influence amphibian survival during their terrestrial phase. In this study, juvenile survival was positively correlated with mean juvenile size at metamorphosis (Table 4, Fig. 6). The estimated survival of nonbreeding 1-yr-old males was also positively correlated with mean juvenile size ($r_s = 0.77$; $N = 6$; $P < .05$). In addition larger juveniles also tended to be larger as adults (Table

TABLE 3. Tests for the relationship among number of eggs deposited (PS); premetamorphic survival (LS); duration of larval period (LP); and size at metamorphosis (SM) using Spearman's rank correlation. Upper value for BVI pond ($N = 6$); lower value for BVII pond ($N = 6$).

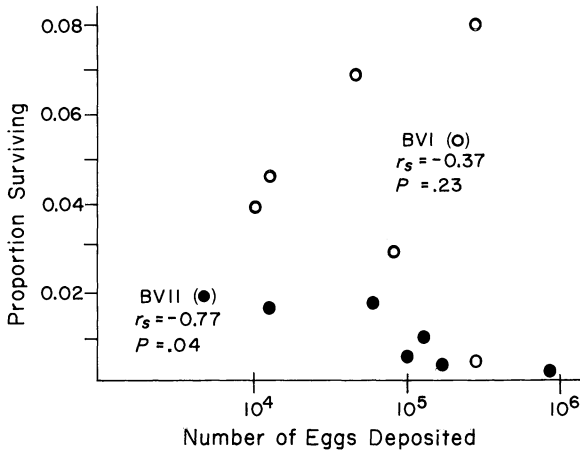|	PS	LS		LP		SM	
		r_s	P	r_s	P	r_s	P
PS	⋯	−.37	(.23)	.83	(.02)	−.94	(.002)
		−.77	(.04)	.77	(.04)	−.77	(.04)
LS		⋯		−.37	(.23)	.26	(.31)
				−.31	(.27)	.54	(.13)
LP				⋯		−.77	(.04)
						−.49	(.19)
SM						⋯	

FIG. 5. Relationship between initial number of eggs and the proportion of individuals that successfully metamorphosed for BVI and BVII ponds, for the period 1976–1982.
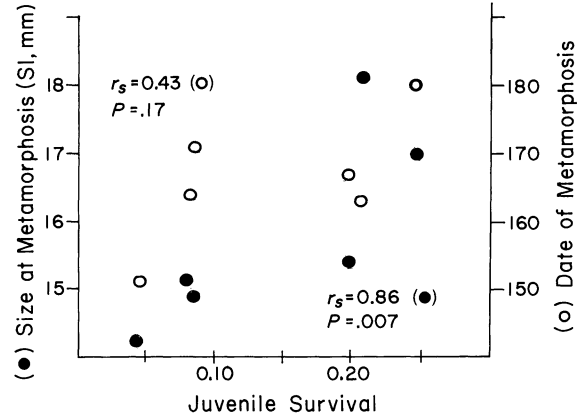

FIG. 6. The relationship between mean juvenile size, the mean day of year on which metamorphosis occurred (juvenile emergence date), and proportion of individuals (males and females) surviving to maturity. SI = length from tip of snout to caudal end of ischium.

4, Fig. 7). Mean juvenile size was negatively correlated with age of males and females at first reproduction (Table 4). In contrast, the mean day of year on which metamorphosis occurred (emigration from the pond) was not correlated with survival, age at first reproduction, or adult body size (Table 4).

Population size (total number of adults and juveniles) was not correlated with juvenile survival or adult body size, or male and female age at first reproduction (Table 4). Mean monthly rainfall was not correlated with juvenile survival or adult body size, but was negatively correlated with male age at first reproduction (Table 4). Female age at first reproduction was independent of rainfall (Table 4).

Factors affecting adult survival. —While some yearly variation in adult survival was present, the linear relationship between survival (log scale) and age indicated that adult survival was largely independent of

age. Since size is also correlated with age (Berven 1982*a*) the pattern of survival suggests that adult survival is also independent of size. To test for the relationship between size and adult survival, for each cohort I compared the mean size of adults that were recaptured a second or third time with the mean size of those that did not breed again. In every case, there was no significant difference in the mean or variance of these two groups.

Adult survival was, however, positively correlated with mean monthly rainfall but not with population size (Table 5, Fig. 8). Population size and rainfall were significantly negatively correlated (Table 5). Fecundity (total clutch volume adjusted for body size) of 2- and 3-yr-old females was negatively correlated with population size but not rainfall (Table 6, Fig. 9).

The importance of juvenile traits on survival and

TABLE 4. Tests for the relationship among date of metamorphosis (DM, day of year on which metamorphosis occurred); juvenile length (JL); juvenile survival (JS); male age at first reproduction (MA); female age at first reproduction (FA); male length at maturity (ML); female length at maturity (FL); mean monthly rainfall (MR) and population size (PS, number of adults and juveniles) using Spearman's rank correlation. Sample size = 7; P values in parentheses.

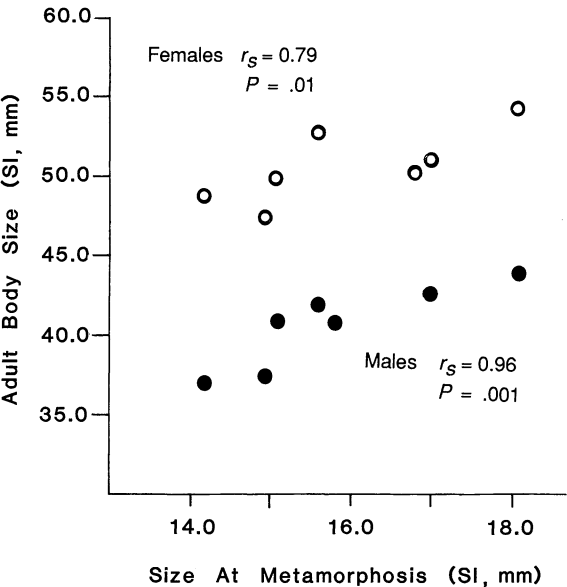|	DM	JL	JS	MA	FA	ML	FL	MR	PS
DM	⋯	.36	.43	.04	−.27	.25	−.18	.26	.37
		(.21)	(.17)	(.47)	(.28)	(.29)	(.35)	(.29)	(.22)
JL		⋯	.86	−.82	−.81	.96	.79	.56	−.22
			(.007)	(.01)	(.01)	(.001)	(.01)	(.10)	(.32)
JS			⋯	−.75	−.79	.93	.75	.52	−.11
				(.03)	(.01)	(.001)	(.03)	(.11)	(.41)
MA				⋯	.63	−.89	−.86	−.70	.37
					(.06)	(.003)	(.007)	(.04)	(.21)
FA					⋯	−.85	−.61	−.07	−.24
						(.008)	(.07)	(.44)	(.30)
ML						⋯	.86	.56	−.22
							(.007)	(.10)	(.32)
FL							⋯	.48	−.52
								(.14)	(.12)
MR								⋯	−.58
									(.09)
PS									⋯

FIG. 7. The relationship between mean juvenile size and mean adult age at first reproduction. SI = length from tip of snout to caudal end of ischium.

adult reproductive success was also determined from a "natural experiment." During the summer of 1980, 20 262 juveniles emerged from BVI pond, which held an estimated 245 086 eggs. This 1980 cohort emerged in two nonoverlapping groups separated by 2 wk (early: $\bar{X} = 90 \pm 1.3$ d; late: $\bar{X} = 102 \pm 6.9$ d). The early metamorphosing juveniles were given one identification mark and the later group another distinctive mark. Size at metamorphosis for these two cohorts did not differ (early: $\bar{X} = 15.1 \pm 0.9$ mm vs. late: $\bar{X} = 15.3 \pm 0.8$ mm; $t = 0.7$; $N = 205$; $P = .42$). In addition to this group, 401 juveniles emerged from neighboring BVII pond, which held 156 325 eggs. This group metamorphosed significantly later than either cohort from BVI ($\bar{X} = 113 \pm 7.0$ d; $t = 30.5$; $N = 12\,203$; $P < .001$) and at a significantly larger size ($\bar{X} = 17.0 \pm 0.9$ mm; $F_{(2,337)} = 158$; $P < .001$). Thus, three uniquely identifiable cohorts of juvenile frogs: early-small, late-small, and late-large were available for study.

Since these ponds were located so close to one another, it is presumed that each juvenile cohort experienced identical growing conditions in the neighboring forests after metamorphosis. Therefore, any differences in re-

TABLE 5. Tests for the relationship among adult survival (AS); population size (PS, number of adults and juveniles); and mean monthly rainfall (MR), using Spearman's rank correlation. Sample size = 18. P values in parentheses.

	AS	PS	MR
AS	$\cdots$	−.32 (.09)	.54 (.01)
PS		$\cdots$	−.83 (.001)
MR			$\cdots$

TABLE 6. Tests for the relationship among population size (PS, number of adults and juveniles); clutch volume (CV, adjusted for body length); and mean monthly rainfall (MR). Sample size = 9. P values in parentheses.

	PS	CV	MR
PS	$\cdots$	−.83 (.003)	.54 (.071)
CV		$\cdots$	.52 (.08)
MR			$\cdots$

productive traits among these cohorts can be assumed to result, at least indirectly, from conditions experienced during the larval period or produced by variation in larval population size (timing and size at metamorphosis).

Juvenile survival differed markedly among the three cohorts (males: $\chi^2 = 184.5$; $N = 3$; $P < .001$; females: $\chi^2 = 131.3$; $N = 3$; $P < .001$). Number of males and females surviving was higher among the late-large cohort, and lowest for the late-small cohort (Table 7). Proportion of males breeding the 1st yr following metamorphosis differed among the three cohorts (early-small: 0.82; late-small: 0.73; late-large: 0.81; contingency chi-square on data shown in Table 7; $\chi^2 = 13.5$, df = 2, $P < .005$). Proportion of females breeding as 1 yr olds also differed (early-small: 0.03; late-small: 0.02; late-large: 0.18; contingency $\chi^2 = 19.3$, df = 2, $P < .005$; Table 7). The initial differences in metamorphic size also persisted at maturation (Table 8).

DISCUSSION

The present study provides the first attempt to identify the degree of population regulation that occurs in the larval vs. the adult stage, and the relative importance of density-independent and density-dependent factors for an amphibian. Wilbur (1980) proposed three
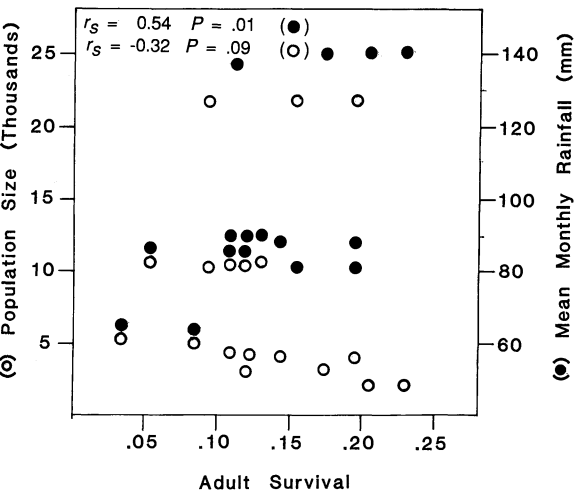

FIG. 8. The relationship between mean adult survival, population size, and mean monthly rainfall.

TABLE 7. The effect of variation in larval developmental patterns on juvenile survival in wood frogs.

| | | Adult survival to year 1 and year 2 | | | | | |
| | | Males | | | Females | | |
	Number marked	1 yr	2 yr	Survivorship	1 yr	2 yr	Survivorship
Early–Small	8460	520	114	.150	7	218	.053
Late–Small	11 802	385	141	.089	4	162	.028
Late–Large	401	51	12	.314	6	27	.155

possible scenarios for population regulation in amphibians. For species with restricted habitats or short-lived adults, regulation should occur during the larval stage. In this case adult population size may be sufficient to saturate the larval habitat, however larval success may not be sufficient to saturate the adult habitat. Larval density would determine larval success, while adult population sizes would vary independently of larval population size. In contrast, for long-lived species, or those in which adults live in a habitat that is less productive than the larval habitat, the number of adults may be too low to saturate the larval habitat, but a sufficient number of juveniles may be produced each year to saturate the adult habitat. In this case, larval survival may be largely determined by random events, while adult fecundity and survival would be determined by adult density. Finally, if adult population density is sufficient to saturate the larval habitat, and the productivity of the larval habitat is sufficient to saturate the adult habitat, populations may be regulated in both stages.

Wood frogs appear to most closely resemble the two-stage population regulation scenario involving both density-dependent and density-independent factors. Between 92 and 99% of the mortality in wood frogs occurred among premetamorphic individuals. Assuming that the number of eggs deposited each year was a good predictor of larval density, premetamorphic survival is primarily determined by density-dependent factors. Not only was the number of successful metamorphs each year a function of the number of eggs deposited, but, in addition, the time of metamorphosis and particularly size at metamorphosis were also strongly correlated with number of eggs deposited. The negative effects of density on time of metamorphosis and metamorphic size carried over into juvenile success. Larger juveniles and those metamorphosing early enjoyed higher survival, earlier age at first reproduc-
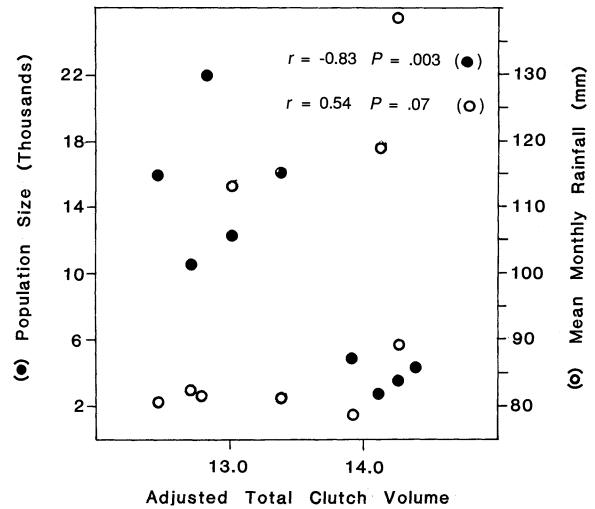

FIG. 9. The relationship between total clutch volume (adjusted for body size and cube-root transformed), population size, and mean monthly rainfall. Fecundity data taken from Berven 1988.

tion, and were larger as adults. Juvenile survival and growth rates did not appear to depend on adult population size.

The importance for larval survival of density-independent factors such as water level, productivity, and persistence cannot be discounted. In 1977, a particularly dry year, the entire larval population in BVI pond died when the pond dried early. However, larval density may still exert an influence on larval survival by slowing development beyond that needed for most larvae to successfully complete metamorphosis. This would be particularly important for species such as wood frogs that typically breed in temporary ponds.

Adult survival in this study was very consistent not only among age classes and sex, but also among years, despite wide fluctuations in population size, rainfall, and adult size. Among these variables, rainfall was the only factor that significantly correlated with adult survival. Population size did, however, negatively affect fecundity in females. Increases in population size were correlated with nearly a 33% drop in total egg volume among 2 yr olds and a 30% drop among 3-yr-old females, independent of body size. Thus adult population size, while apparently not affecting survival, did strongly affect fecundity.

In summary, it is clear that chance climatic conditions, such as prolonged dry weather, may reduce adult population sizes either directly or by limiting juvenile

TABLE 8. Comparison of the adult size at first reproduction ($\bar{X} \pm$ SD) among the three larval cohorts in 1980. Common superscripts indicate means that do not differ at $P = .05$ using a Student-Newman-Keuls multiple-range test.

| Size* | Larval cohort | | | Results of ANOVA | |
	Early–Small	Late–Small	Late–Large	F	P
Male (SI, mm)	40.5 ± 2.2^a	40.5 ± 2.2^a	42.4 ± 2.4^b	8.5	<.01
Female (SI, mm)	50.5 ± 1.3^b	48.8 ± 1.4^b	51.3 ± 1.6^b	3.2	<.05

* SI = length from tip of snout to caudal end of ischium.

recruitment, such that adult population sizes are insufficient to saturate the larval habitat (1977–1978 in this study). In the absence of competition, both adults and larvae experience increased survival, growth, and fecundity. Under these conditions the high reproductive capacities of wood frogs quickly increase the adult population size (1979–1980 in this study). At that point density-dependent factors acting in both the larval and adult stage stabilize population size by reducing larval survival and fitness, and reducing female fecundity (1980–1982 in this study).

Although this study clearly demonstrated the importance of density-dependent regulation in wood frogs, the underlying explanations are not clear. Generally, density-dependent influences on populations are thought to result from biotic factors such as competition, predation, or pathogens (Krebs 1985). The density effects on premetamorphic survival and development were identical to many other studies on amphibians that have demonstrated density-dependent survival, growth, and development time, by manipulating larval densities in field enclosures or laboratory aquaria (Richards 1958, 1962, Licht 1967, Brockelman 1969, Wilbur 1972, 1976, Dash and Hota 1980, Semlitsch and Caldwell 1982, Berven and Chadra 1988). Explanations for this phenomenon include competition for food (Wilbur 1972, 1977, Travis 1984, Petranka and Sih 1986), production of growth inhibitors (Rose 1960, Richards 1962, Licht 1974), and hormonally-mediated behavioral interactions (Gromko et al. 1973).

Licht (1974) dismissed the importance of food as a limiting factor for larval *Rana pretiosa* and *Rana aurora*. Since tadpoles are able to feed on a variety of algal species and detritus, he argued that food shortages were not relevant as a mortality factor. Laboratory studies, however, have shown that food availability can have significant effects on larval developmental patterns (Wilbur 1977, Berven and Chadra 1988). Although vernal ponds are considered to be one of the most productive habitats, food may become limiting due to the tremendous larval densities possible (as high as 1160 larvae/m² in this study). Anecdotally, it is interesting to note that in experiments using field enclosures conducted in these ponds (Berven 1982b) that as long as tadpoles were in the cages, the water in the cages remained clear. If tadpoles were removed, the water quickly became choked with algae, suggesting that food may indeed by limiting under high population densities.

Predation on amphibian larvae has been well documented (Heyer et al. 1975, Walters 1975), and the potential role of predators as population regulators has been well established under seminatural (Morin 1983, Wilbur et al. 1983) and natural field conditions (Licht 1974, Smith 1983). Predator levels were not monitored in this study so it is not known to what degree year-to-year variation in survival can be attributed to variation in predator densities. Smith (1983) demonstrated

that predation was more important in regulating larval number of *Pseudacris triseriata* in permanent ponds, than in temporary ponds. The lower average survival of wood frog larvae in BVII pond is consistent with his findings. BVII pond dried only once during this study, and supported larger populations of the predatory salamander *A. maculatum*. In addition, the BVII pond also supported populations of spotted turtles, painted turtles, and red-spotted newts, all potential predators that did not occur in BVI pond.

The factors contributing to adult and juvenile mortality are poorly understood. Martof (1956) and Licht (1974) argued that predation was the main source of mortality on green frogs, *Rana clamitans*, and two western ranids, *R. aurora* and *R. pretiosa*. Numerous predators including birds, snakes, raccoons, and skunks inflict a high toll on juvenile and adult wood frogs. However, since survival in adult wood frogs is largely independent of age, sex, and size, the predators involved must not be size limited, and must exert a constant predation pressure. Bellis (1962) concluded that humidity and rainfall were the most important factors affecting terrestrial activity and foraging time of wood frogs. Rainfall was strongly correlated with adult survival in this study. The higher mortality during years with low rainfall could increase the chances of desiccation and starvation. The negative correlation between female fecundity and population density also suggests that food availability can become limiting in the terrestrial environment. Fraser (1980) found food availability to limit clutch size in a plethodontid salamander. Disease and parasitism may also affect adult and juvenile survival.

This study supports the hypothesis that male survival is higher for individuals that metamorphose early in the season, or at large size. Female survival was higher for larger juveniles, but was not affected by time of metamorphosis. The effect of large juvenile size on male survival to reproduction occurred in two ways: first, by directly reducing mortality in the 1st yr, and secondly, by decreasing age at first reproduction. Among cohorts of large-sized juveniles, a significantly higher proportion of both breeding and nonbreeding males were alive the 1st yr following metamorphosis. Since mortality is relatively constant with respect to age, those individuals unable to breed the 1st yr incurred a 2nd yr of mortality, reducing their chances of surviving until the next breeding season. Fewer subadults from smaller sized juvenile cohorts, together with their delayed maturity, resulted in a lower proportion reaching sexual maturity.

This study also supports the hypothesis that large juvenile size results in larger adults with higher fitness. For wood frogs, larger adult size directly affects fitness by increasing the probability that a male will mate (Berven 1981, Howard and Kluge 1985), and by increasing the number and size of eggs produced by females (Berven 1982b).

The results of this study differ somewhat from the

only other field study of an anuran that examined the effects of body size and larval period on juvenile survival and adult body size (Smith 1987). For the chorus frog *Pseudacris triseriata* juvenile size affected the proportion of individuals able to breed the 1st yr following metamorphosis, but not survival. Individuals metamorphosing at a large body size maintained their size advantage at maturity. In another study, Semlitsch et al. (1988) showed that both time and size at metamorphosis in the salamander *Ambystoma talpodium* affected survival and age and size at first reproduction, as reported for wood frogs. More studies of this nature are required before any general conclusions can be drawn; however, all suggest that adult fitness may be strongly affected by larval environment.

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