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REGULATION OF STRUCTURE IN COMPLEX SYSTEMS: EXPERIMENTAL TEMPORARY POND COMMUNITIES¹

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Abstract. Interactions among competition, predation, and disturbance in determining the abundances of four species of anurans were studied in a factorial experiment using 36 replicated experimental ponds. Hatchlings of the four species (*Rana utricularia*, *Scaphiopus holbrooki*, *Bufo americanus*, and *Hyla chrysoscelis*) were introduced at the same relative abundances at a low or a high initial density. Competition determined survival, body size at metamorphosis, and length of larval period in high-density communities, which were food-limited. The predatory salamander *Notophthalmus viridescens* did not alter either the total number of metamorphs or their combined biomass in the high-density communities, but the relative abundance of metamorphs was shifted as *Scaphiopus holbrooki*, the competitive dominant, was selectively eaten. In low-density communities, predation decreased survival and biomass production of tadpoles, often to zero, in all species. For each of the four combinations of tadpole density and presence or absence of predators, ponds were drained at three rates to simulate different drying regimes. Competition slowed growth and thus increased the risk of desiccation in high-density populations in drying ponds. Predation ameliorated the effects of competition, allowing survivors to grow rapidly enough to metamorphose before ponds dried.

Survival of tadpoles to metamorphosis, body size at metamorphosis, and the timing of metamorphosis were determined in a complex way by interactions among all of the treatment effects and the life history characteristics of the four species studied. *Scaphiopus* was the species least sensitive to tadpole density and was the competitive dominant in ponds without newts. It has a rapid growth rate and metamorphosed soon enough to escape desiccation. It suffered the greatest risk of predation and was eliminated from even some of the high-density communities. *Rana* was most successful in low-density communities without predators. No *Rana* survived in rapidly drying (50-d) ponds because of insufficient time to obtain a minimum size for metamorphosis. *Rana* were also eliminated from most populations exposed to predation. The effect of competition on *Bufo* in high-density populations, few or no survivors, was reversed by predation as newts selectively fed on *Scaphiopus* and *Rana*. This result was most striking in the tanks that dried most rapidly. *Hyla* did very poorly in all slowly drying (100-d) tanks compared with controls because of intense competition. It had moderate success in high-density communities where newts had removed most competitors.

These results show that biological and environmental factors interact to determine the structure of anuran communities. Neither competition nor predation is the single unifying force, but rather they interact to determine the different consequences of the date of drying of a pond to the success of each species.

Key words: amphibian; *Bufo*; competition; disturbance; environmental uncertainty; experimental field study; food web; *Hyla*; *Notophthalmus*; predation; *Rana*; *Scaphiopus*.

INTRODUCTION

A general answer to the classic question in community ecology of what regulates the distribution and abundance of species remains elusive (Strong et al. 1984, Diamond and Case 1986, Pickett and White 1985, Slobodkin 1986). The importance of competition, predation, disturbance, and historical effects have all had their champions and moments of uncritical acceptance. As in most such controversies, the answer is likely to involve all of these competing mechanisms with the mixture dependent on the habitats and or-

ganisms being studied. Factorial experiments can evaluate the roles of each mechanism and possible interactions among them; however, even with a well-designed experiment the argument can be settled only for the range of conditions actually manipulated. I experimentally controlled the levels of competition, predation, and disturbance in a factorial design involving five manipulated species to study how these three processes interact to determine the structure of complex communities under controlled field conditions.

My experimental system of amphibians in replicated mesocosms was designed to capture important elements of natural temporary pond ecosystems. When a temporary habitat first becomes available, colonization

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may follow a predictable sequence of species, but each species may exploit the changing habitat for only a portion of its life cycle. Between years, the dynamics of populations associated with ponds may be described by Caswell's (1978) notion of an open, nonequilibrium system with each pond being a cell where species interactions may occur and from which colonists move to other cells. Within a season, each pond may be crudely treated as a closed system tending toward an equilibrium. In my experiment, communities were started with different initial conditions and then the outputs of metamorphs were compared.

The suitability of a particular pond as a breeding site for amphibians depends on its hydrologic cycle, which sets the length of time available for the larval period of potential colonists and their risks of predation. The surrounding terrestrial habitats and the life histories of individual species determine the ensemble of species that breed in a particular pond. The level of biological interactions among the species depends on the structure of the food web (predators may preclude competition among their prey) and the level of disturbance in the habitat (a pond may dry so rapidly that competition and predation may be trivial sources of mortality compared with desiccation). Temporary ponds may have high productivity and provide an opportunity for rapid growth, but they may also harbor efficient predators and have an uncertain period before they dry. The advantages of high larval growth rate can be offset by a high risk of mortality through competition, predation, or desiccation (Wilbur 1980, 1984). The length of time a species of frog larva remains in the pond is thought to reflect genetic adjustments to interactions between the relative growth rates and mortality risks as an aquatic larva compared to what it would be as a terrestrial juvenile (Werner 1986).

My hypothesis is that, in the absence of predation, competition slows growth and increases the likelihood of death by desiccation. Moderate levels of predation could reduce the effective density of tadpoles, allowing the survivors to grow rapidly enough to escape ponds that dry early in the summer. This hypothesis was tested by manipulating all three processes in a replicated factorial design. The length of time that experimental ponds held water was directly controlled as an experimental factor by draining them at three different regulated rates. Within each of these treatments, four species of anuran larvae were raised at two densities in the presence or absence of a predator. This design allowed a direct analysis of the interaction between competition, predation, and length of a pond's life on the structure of a guild of tadpoles.

Field experiments using enclosures in ponds have been used to study the population regulation of tadpoles (Brockelman 1969, Wilbur and Collins 1973, Wilbur 1977), competition between pairs of species (DeBenedictis 1974, Wilbur 1976), and interactions between competition and predation (Wilbur 1972).

Small artificial ponds permit more highly replicated experiments with more complex designs than are practical in heterogeneous ponds. The experiments we have accomplished using such mesocosms have demonstrated that realistic densities of the newt *Notophthalmus viridescens* can preclude competition within communities of larval anurans (Morin 1981, Morin et al. 1983, Wilbur et al. 1983). Newts are size-limited predators that are effective mortality agents only for the first few weeks of tadpole growth. Anuran species that co-occur in natural ponds have different vulnerabilities to predation by newts; Morin (1983) found that *Scaphiopus* was more vulnerable than the other five species used in his experiment. Even after tadpoles have grown too large to be killed by newts, they may suffer tail damage in failed predation attempts (Morin 1985). In the absence of newts, tadpoles compete vigorously via both exploitation mechanisms of competition (food limitation) and interference mechanisms (growth inhibitors) (Wilbur 1977, Steinwascher 1978). Competition is also sensitive to the relative arrival time at the pond of the interacting species. Differences as small as 6 d can have persistent effects on the community for several months (Alford and Wilbur 1985, Wilbur and Alford 1985).

METHODS

The experimental units were 36 galvanized steel tanks, painted with epoxy enamel. Each tank was 1.8 m² in surface area and had a volume of \approx 1000 L. Fiber glass screen (1.5-mm mesh) lids prevented unwanted colonization by insects and frogs and retained metamorphs of experimental animals until they were collected. Tanks were arranged \approx 1 m apart in a hexagonal array to minimize the area used for the experiment. This array was divided into three interlocking blocks as insurance against possible environmental gradients in three directions in an open field at the Zoology Field Station adjacent to the Duke Campus in Durham, North Carolina. Treatments were assigned randomly to ponds within blocks.

The advantages of using small artificial ponds, rather than enclosures in a larger pond, as experimental units was that all components of the ecosystem could be controlled and each unit was a truly independent estimate of an experimental effect. The use of containers allowed us to clean the ponds and start fresh communities with very little initial variation in physical, chemical, or biological properties. The use of physically separate ponds was obviously required for the study of the effects of draining rate on community structure.

All tanks were filled to 50 cm deep on 17–19 March 1984. On 19 March, 500 g of litter raked from the margin of a temporary pond in the Sandhills Region of North Carolina, along with 50 g of laboratory rabbit fodder, were added to each pond for structural complexity and as a source of nutrients and dormant stages

of microorganisms. On 20 March, plankton was collected from 15 temporary or small fish-free, permanent ponds in the Sandhills. All samples were pooled and thoroughly mixed. Eight 100-mL subsamples were taken from this pooled mixture and were assigned randomly to each tank to insure uniformity of the original inoculum of microorganisms. On 29 March, a second collection was made, this time from 36 ponds, and three stratified subsamples (two of 300 mL and one of 1000 mL) were assigned randomly to each tank. On 12 April, a third collection was made from four ponds; and four stratified subsamples of 200 mL each were added at random to each tank. These multiple introductions insured that diverse communities of microorganisms (e.g., ≈ 10 common species of microcrustacea: Kaiser 1985) had a chance to become established and serve as the base of a complex food web.

Temperature of the water at the bottom of each tank was measured shortly after dawn on 31 March (when the experiment was started), and on 11 and 29 April. There were significant differences among the three blocks on two dates ($P = .034$ on 31 March; $P = .13$ on 11 April; $P = .0025$ on 29 April; MANOVA, $P = .004$, simultaneously considering temperatures on all three dates), but the ranking of blocks was not concordant between dates. There were no differences in temperature among tanks receiving different treatments on any of the dates, confirming that the randomization of treatments among tanks avoided confounding temperature with treatment effects during the 1st 4 wk of the experiment.

Sixteen treatments were applied to these uniform communities. Two experiments with overlapping treatments were randomized together over each of the three blocks of 16 tanks each. One experiment is reported by Alford (1986). My experiment was a $3 \times 2 \times 2$ factorial design of 12 treatments, each represented once in a random position of each block (Table 1).

The first factor included three rates of pond draining: 50 d, 100 d, or control tanks kept at 50 cm deep. Each tank had a drain fitted with an L-shaped standpipe, which could be rotated to lower the water level at a predetermined schedule to simulate loss of water to groundwater and to evaporation. The ponds were drained according to the expression $D_j = 1 - (j/t)^a P$, where D_j is the desired depth on day j , j is the time in days since the start of the experiment, t is the target date for the depth to reach zero, P is the maximum depth (50 cm) at the start of the experiment, and a is a shape parameter ($a = 2$) for the curves. The treatment levels were $t = \infty$, 100, and 50 d. The ponds were dried in 5-cm increments to follow the design within 2.5 cm. Since precipitation exceeds evaporation in most 2-wk periods in North Carolina (Clay et al. 1975), the water level never dropped > 5 cm below its regulated depth. Standpipes were enclosed in a cage of plankton netting during the draining episodes and were covered by 1.5

mm mesh fiber glass screening at other times. When tanks were within 1 d of their target drying date, the entire contents of each tank was carefully searched for newts, newt larvae, and tadpoles, which were preserved for later identification and enumeration. The litter was air-dried in full sun for 2 d then returned to the 50-d tanks, which were then refilled to 50 cm depth. Four newts were reintroduced to appropriate communities, and then these ponds were drawn down on the same schedule as during the 1st 50 d.

The second factor was the presence or absence of four adult newts, two males and two females, randomly assigned to each tank. Newts (*Notophthalmus viridescens dorsalis*, Caudata: Salamandridae) were collected in the Sandhills on 22 March and introduced on 23 March. At the beginning of the experiment, there was no difference in sizes of newts introduced into different treatments (ANOVA, $P \gg .10$). The experimental density of four newts per tank was 2.2 newts/m², which was above the mean (1.0) but within the range (0.2–4.2) of densities observed in April and May during a 3-yr sampling program of a natural pond (R. Harris, R. Alford, and H. Wilbur, *personal observations*).

The third factor was either a high or low density of four species of anuran larvae. Relative abundances of the four species were the same at the two densities but their total abundances in high-density treatments were four times those at low densities. The base abundance, X , of each species was a function of the clutch size and number of females that typically oviposit in temporary ponds (H. Wilbur, *personal observation*). The high density was less than the typical clutch size for each species.

Eggs were collected from natural ponds and held in the laboratory until they were just about to hatch, then they were counted into groups of 10, and these groups were randomly assigned to larger containers for each tank. This stratified sampling procedure was repeated until sufficient eggs were pooled to make up treatments. Groups of eggs for each initial density were then randomly assigned to blocks.

On 23 March, hatchling *Rana utricularia* (= *R. sphenoccephala*: Ranidae) with $X = 50$ ($4X = 200$) were introduced into tanks. This species is primarily a scraper of periphyton off the litter and sides of the tank, although they will also filter phytoplankton from the water column and will rapidly aggregate around carrion. On 4 April, hatchling *Scaphiopus holbrookii* (Pelobatidae) were added ($X = 65$, $4X = 260$). By this date, most *Rana* tadpoles had been eaten by newts in tanks with newts. *Scaphiopus* is an explosive breeder that exploits temporary ponds by having a rapid growth rate and short larval period. *Scaphiopus* tadpoles are very active swimmers that filterfeed and scrape periphyton. They do not have a well-developed escape response, in contrast to *Rana*, but they do form dense schools in the presence of newts (H. Wilbur, *personal observation*). On 19 April, *Bufo americanus* (Bufonidae) were added to all tanks ($X = 200$, $4X = 800$). At

TABLE 1. Experimental design and mean response of each species.

Treatments	0	0	0	0	0	0	4
Adult newts	low	low	low	high	high	high	low
Tadpole density	never	100	50	never	100	50	never
Drying time (days)							
Responses*							
<i>Bufo</i> populations	3	3	3	3	3	3	3
Number of metamorphs	97.3	161.0	121.3	168.7	56.0	0	32.0
Mass of metamorphs (g)	0.080	0.093	0.083	0.046	0.037	...	0.158
Larval period (days)	42.1	39.2	32.9	98.8	69.2	...	36.6
Biomass of metamorphs (g)	7.860	14.993	10.084	7.867	2.169	0	5.070
<i>Hyla</i> populations	3	0	1	3	0	1	3
Number of metamorphs	48.0	0	2.0	7.7	0	1.0	12.7
Mass of metamorphs (g)	0.264	0.186	...	0.159	0.583
Larval period (days)	56.2	...	38.0	103.4	...	146	29.1
Biomass of metamorphs (g)	11.557	0	...	1.427	0	0.159	7.344
<i>Rana</i> populations	3	3	0	3	3	0	1
Number of metamorphs	37.0	34.7	0	18.3	6.3	0	3
Mass of metamorphs (g)	1.341	0.974	...	0.994	0.676
Larval period (days)	83.9	87.1	...	123.6	90.3	...	83
Biomass of metamorphs (g)	49.102	33.6	0	17.612	4.341	0	...
<i>Scaphiopus</i> populations	3	3	3	3	3	3	1
Number of metamorphs	58.7	54.0	54.3	200.7	208.7	221.3	1
Mass of metamorphs (g)	0.597	0.604	0.501	0.243	0.260	0.225	0.114
Larval period (days)	36.6	38.2	35.3	54.1	40.4	38.1	46.0
Biomass of metamorphs (g)	34.879	32.894	28.253	48.850	54.310	49.768	0.114

* Number of the three replicate populations with at least one metamorph.

"Number of metamorphs" and "biomass of metamorphs" are the means of the three replicate populations for the number of metamorphs and the combined total biomass of each. If no individuals metamorphosed in a population these two variables had values of zero. "Mass of metamorphs" and "larval period" are the means of population means. Population means were computed only for replicates with at least one metamorph.

this time, the *Scaphiopus* were near their maximum size but had not yet begun to metamorphose. Most *Rana* and *Scaphiopus* tadpoles had been eliminated in tanks with adult newts. *Bufo* are primarily bottom-feeders that grow rapidly but metamorphose at a small size. On 31 May, 6 d after the 50-d tanks had been drained and refilled, *Hyla chrysoscelis* (Hylidae) were added to all tanks ($X = 125$, $4X = 500$). *Hyla* is a summer-breeding species that feeds on phytoplankton in midwater and scrapes periphyton from the sides of the tanks. It can have a larval period as short as 3 wk (Wilbur and Alford 1985).

Tanks were searched daily for metamorphs (defined by forelimb emergence) from late April until the end of July, and then every second night until the experiment was terminated on 27 November. All wintering *Rana* tadpoles and larval and adult newts were then collected. The only tanks with overwintering *Rana* tadpoles were the three replicates of the control tanks with no newts and high initial densities. These few tadpoles ($N = 18$, 8, 18) were not included in the analyses of metamorphs. All metamorphs were weighed to 0.001 g precision, then released at the site of egg collection.

STATISTICAL ANALYSIS

Individual responses were the mass at metamorphosis and length of larval period. A linear growth rate can be approximated by dividing mass at metamorphosis by the length of the larval period. Individuals

within a tank cannot be treated as statistically independent observations because they may be competing with one another resulting in a negative covariance in the response variables among members of a population. That is, if resources are limited, a large metamorph will be associated with a small metamorph, on average. A positive covariance among members of a population can occur if some tanks are, on average, better environments than others, in spite of our attempt to equalize initial conditions. For both these reasons tests are based on population means rather than individual values.

Experimental blocks (spatial groups of tanks that are each a replicate of all experimental treatments) are treated as random effects, which implies that the blocks can be treated as random samples from a larger population of similar blocks. The three experimental factors (drying rate, newt occurrences, and tadpole density) were treated as fixed effects. The effects of the experimental factors and their interactions (fixed effects) were tested over their interactions with block effects (random effects). This is tantamount to testing population means rather than individual responses. The full analyses are presented because there is useful information contained in the term describing variation within populations (contra Hurlbert 1984).

Multivariate analysis of variance (MANOVA) was used to analyze body mass at metamorphosis and date of metamorphosis, because these two responses are

TABLE 1. Continued.

4 low 100	4 low 50	4 high never	4 high 100	4 high 50
1	3	3	3	0
4.0	84.7	294.0	234.0	0
0.069	0.054	0.073	0.098	...
35.2	32.6	43.0	42.6	...
0.278	4.831	22.590	24.471	0
0	0	3	3	0
0	0	43.3	24.3	0
...	...	0.393	0.293	...
...	...	33.9	29.4	...
0	0	16.677	6.048	0
0	0	1	0	0
0	0	17	0	0
...	...	1.853
...	...	104.1
0	0	31.493	0	0
0	0	2	3	1
0	0	81.5	15.0	73.0
...	...	0.357	0.275	0.438
...	...	39.5	37.4	35.9
0	0	29.542	4.755	31.940

often correlated within populations. Both variables were logarithmically transformed to uncouple means and variances within treatments. Survival and population biomass were analyzed by univariate analyses of variance (ANOVA). Relative abundance was analyzed by MANOVA of the relative frequency of *Bufo*, *Rana*, and *Scaphiopus*. *Hyla* was omitted since knowing the proportion of three species fixes the proportion of the fourth.

Sixty of the 144 anuran populations were eliminated by the experimental treatments; no populations were lost by uncontrolled misfortunes. In the tanks in which all four anuran species were eliminated (Table 1), the relative abundances were set to zero to preserve the balance of the experimental design. The elimination of some populations required that only subsets of the full design were used for the analysis of the length of larval period and body size at metamorphosis.

RESULTS

The initial densities were 65 *Scaphiopus*, 50 *Rana*, 200 *Bufo*, and 125 *Hyla* or four times these densities (260, 200, 800, and 500, respectively) so that initial relative abundances were the same at each density. As initial relative abundances were thus fixed in all treatments, the final relative abundances could be analyzed as a response vector representing the species composition of the cohort of metamorphs from each pond. If mortality among the species was random, then no change in community structure from the initial to the final relative abundances would be expected. This null hypothesis was clearly rejected, as all MANOVA effects except the three-way interaction term (draining rate ×

predation × density) were significant (Table 2). The dominant effects were the presence of newts and the density of tadpoles. There was a clear reduction in the number of species that successfully metamorphosed as experimental treatments became harsher, with 11 of the 16 possible 0-, 1-, 2-, 3-, and 4-species communities actually observed among the final outcomes. The five combinations not observed all included *Rana*, which metamorphosed only in 4-species assemblages with a single exception, a tank in which only three *Rana* and eight *Hyla* escaped predation by newts.

Competition in tanks that did not dry and had no newts

The most benign environments for tadpoles were in the tanks that did not have newts and never dried. At low tadpole densities, *Rana* and *Bufo* metamorphs had nearly the same relative abundances as they did when they were hatchlings (Fig. 1). The relative abundance of *Scaphiopus* increased to 167% of its initial value and *Hyla* decreased 76%. At high densities the increase in relative abundance of *Scaphiopus* was more marked (a 353% increase over the initial abundance); *Rana* had a 60% decrease, and *Hyla* had a strong 93% reduction. *Bufo* showed little change. In summary, relative abundances changed with density in a pattern that suggests *Scaphiopus* is a competitive dominant and *Hyla* is a competitive subordinate.

Only a design that includes several relative initial abundances can rigorously test for competition. The data from my experiment can be used to make inferences about competition because newt predation generated such a variety of early abundances of the anuran species. I compared the mean growth rate of individuals in each population with the number of potential competitors, including conspecifics, that metamorphosed (Table 3). The simple correlation coefficient measures the strength of the association between the growth of the focal species and the number of metamorphs of each species. It measures the maximum strength of the interaction. The partial correlation coefficient removes variation caused by the abundances of all species except the competitor being examined. It measures the minimum strength of the interaction. Negative values imply competition; positive values imply facilitation. There was no evidence for predation or cannibalism within the tadpole guild. Only data from tanks that never dried were used, to avoid confounding effects of competition with effects of draining the tanks. The number of *Hyla* metamorphs was not used in the analysis of the growth of *Bufo* and *Scaphiopus* because these species had completed metamorphosis before *Hyla* were introduced. However, all species were included in the analysis of *Hyla* because early species can have indirect persistent effects on a late species by removing nutrients or altering the structure of the food web early in the season (Wilbur and Alford 1985).

TABLE 2. MANOVA of relative abundance of metamorphs (arcsine transformation).*

Source	df	Wilks' criterion	F ratio	P
Drying	6,36	1.0281	6.70	<.0001
Newts	3,18	0.1095	48.82	<.0001
Density	3,18	0.2280	20.32	<.0001
Dry × newts	6,36	0.2346	6.39	<.0001
Dry × density	6,36	0.2839	5.26	.0006
Density × newts	3,18	0.6110	3.82	.0280
Dry × density × newts	3,18	0.7290	2.23	.1197

Sums of squares and cross-product matrices							
Error			Drying time				
	<i>Bufo</i>	<i>Rana</i>	<i>Scaphiopus</i>		<i>Bufo</i>	<i>Rana</i>	<i>Scaphiopus</i>
<i>Bufo</i>	1.000	-0.3918	-0.4285	<i>Bufo</i>	0.6446	-0.2022	0.1163
<i>Rana</i>	-0.3918	1.0000	0.1118	<i>Rana</i>	-0.2022	0.2454	-0.1657
<i>Scap</i>	-0.4285	0.1118	1.0000	<i>Scap</i>	0.1163	-0.1657	0.1127

Presence of newts			Tadpole density			Drying time × newts		
1.8009	-0.5850	-2.4749	0.2895	0.1227	-0.6082	1.3219	0.0608	-0.6755
-0.5850	0.1891	0.7999	0.1227	0.0520	-0.2578	0.0608	0.0306	-0.0853
-2.4748	0.7999	3.3840	-0.6082	-0.2578	1.2777	-0.6755	-0.0853	0.4511

Drying time × density			Newts × tadpole density			Dry × newts × density		
1.3543	-0.1786	-0.5362	0.2308	0.0783	-0.1191	0.1239	-0.0318	0.0599
-0.1786	0.0369	0.1027	0.0783	0.0266	-0.0404	-0.0318	0.0081	-0.0154
-0.5362	0.1027	0.2893	-0.1191	-0.0404	0.0615	0.0599	-0.0154	0.0290

* *Hyla* not included, as knowing the relative abundance of three species fixes the value of the fourth.

The role of *Scaphiopus* as a competitive dominant was confirmed by the correlation analysis (Table 3). The number of *Scaphiopus* metamorphs had a negative effect on the growth rate of all species including itself. It even had a strong negative effect on *Hyla*, with which it did not overlap in time. The number of *Rana* metamorphs also had a strong negative effect on the growth rate of *Hyla*. *Bufo* did not have a strong negative effect

on any species, including itself. The moderate positive associations between the number of metamorphs of *Bufo* and growth rates of *Scaphiopus* and *Rana* were probably because these species grew well at low densities caused by predation, which was correlated with high numbers of *Bufo* metamorphs as discussed below. *Hyla* had a moderate negative effect on itself.

The number of *Rana* metamorphs had a strong positive effect on the growth rate of *Scaphiopus*, which grew most rapidly in low-density populations without newts where *Rana* also did well. The correlation remained high when the numbers of *Bufo* and *Scaphiopus* were removed by partial correlation analysis. This suggests a biological facilitation of *Scaphiopus* by *Rana* rather than a correlation mediated by one of the other species. *Rana* may have facilitated *Scaphiopus* growth by scraping periphyton from the sides of the tank and releasing nutrients that enhanced production of suspended phytoplankton. Filamentous periphyton is a low-quality resource for *Scaphiopus* (Wilbur et al. 1983). The number of metamorphs of *Scaphiopus* had a strong negative relationship with the growth rate of *Rana* indicating an amensal rather than a mutualistic relationship. The positive effect of *Rana* on *Scaphiopus* makes *Rana* an indirect competitor of all species in the community.

Certainly some of the negative effects of *Rana* and *Scaphiopus* are attributed to their being the first species added to the communities, but the order of addition was not the sole determinant of competitive relationships. *Scaphiopus* was introduced 12 d after *Rana* but still had a strong competitive effect on it. *Hyla* was

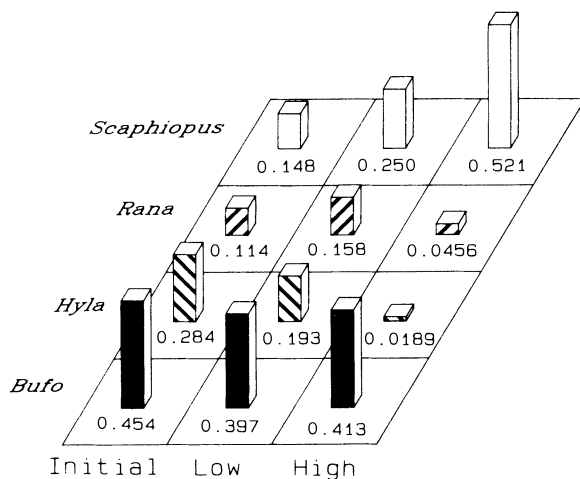


FIG. 1. The relative abundances of hatchlings of each of the four anuran species introduced into ponds (initial) and the relative abundances of metamorphs in communities started at low and high initial densities. All populations were in the control ponds that had no newts and never dried. The numbers are the means of the proportional abundances of metamorphs in the three replicates.

TABLE 3. Correlation coefficients of growth rate of each species vs. the number of metamorphs of potential competitors.

	Number of metamorphs			
	<i>Scaphiopus</i>	<i>Bufo</i>	<i>Rana</i>	<i>Hyla</i>
<i>Bufo</i> growth rate (<i>N</i> = 10)				
Simple correlation	-0.7945	-0.2610	-0.5528	...*
Partial correlation	-0.6486	-0.1997	-0.2865	...
Regression coeff. × 10 ⁻⁵	-0.9484	-0.1253	-1.4899	...
<i>Scaphiopus</i> growth rate (<i>N</i> = 9)				
Simple correlation	-0.3417	-0.0743	+0.7336	...
Partial correlation	-0.7503	+0.4202	+0.7798	...
Regression coeff. × 10 ⁻⁵	-5.6057	+1.2706	+28.9316	...
<i>Rana</i> growth rate (<i>N</i> = 7)				
Simple correlation	-0.8166	+0.0802	-0.2032	+0.5285
Partial correlation	-0.8300	+0.3974	-0.4564	-0.1760
Regression coeff. × 10 ⁻⁵	-7.0045	+0.8670	-11.0615	-2.5996
<i>Hyla</i> growth rate (<i>N</i> = 12)				
Simple correlation	-0.7831	-0.3529	-0.7200	-0.0715
Partial correlation	-0.7135	+0.1065	-0.7139	-0.6046
Regression coeff. × 10 ⁻⁵	-6.0312	+0.2917	-6.0312	-9.7799

* *Bufo* and *Scaphiopus* had completed metamorphosis before *Hyla* were introduced.

introduced 57 d after *Scaphiopus*, 2 wk after all *Scaphiopus* had metamorphosed, yet still suffered from its lingering effects. The correlation between the growth rate of *Hyla* and the number of *Scaphiopus* metamorphs remained strong even after removing the effects of all other species, including *Hyla*, by partial correlation analysis.

The effects of drying time

Although competition appears to have determined survival and growth rates, it did not drive any of the four species to extinction in the tanks that never dried. In the 100-d tanks, *Hyla* were eliminated, leaving a three-species community at both high and low initial tadpole densities (Fig. 2). *Hyla* was introduced into the 100-d tanks when they were already crowded due to low water levels. As the tanks still had 40 d before they dried, this was clearly a case of death due to direct competition; *Hyla* can metamorphose in 20 d under similar field conditions (Wilbur and Alford 1985). In the low-density tanks that dried in 100 d, all surviving *Scaphiopus* (mean = 54) and *Bufo* (mean = 161) metamorphosed before the tanks dried; no larvae died of desiccation. Most *Rana* (mean of 69%) also metamorphosed (only 13% on average died of desiccation). In the high-density 100-d tanks, only *Scaphiopus* completed metamorphosis without population losses; many *Rana* larvae (mean = 47%) and most *Bufo* (mean = 63%) were killed by desiccation, with only a few metamorphs (3% of *Rana* and 7% of *Bufo*) successfully escaping.

In 50-d tanks, a *Scaphiopus*-*Bufo* community dominated all replicates with low initial densities. Only two *Scaphiopus*, but all *Rana*, tadpoles died of desiccation. Most *Bufo* (60.5%) completed metamorphosis with an average of only 15 larvae (7.5%) dying of desiccation.

At high densities, *Rana* and *Bufo* were eliminated by competition-mediated desiccation, whereby density reduced growth rate and increased the risk of desiccation. No *Scaphiopus* died of desiccation, and survival to metamorphosis was high (80%). As *Hyla* were introduced after the 50-d tanks were dried and refilled, their low survival at both densities was due to a shortage of resources and intrusion by predatory dragonflies (10 naiads in one tank, 2 in another), rather than to

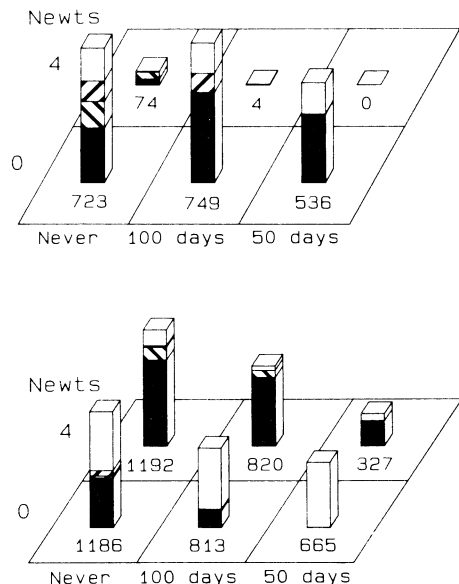


FIG. 2. The number of metamorphs of the four anuran species (■ *Bufo*, ▨ *Hyla*, ▩ *Rana*, □ *Scaphiopus*) from low-density (upper panel) and high-density (lower panel) populations, as a function of the number of adult newts and rate of pond drying (never, 100 d, or 50 d). Data are the sums of the numbers of metamorphs in the three replicates.

TABLE 4. The estimated fate of all tadpoles (%). Data are means of three replicates. See Results: The Effect of Newts for computational assumptions for partitioning deaths between predation, competition, and unknown causes.

	No newts				Four adult newts			
	<i>Rana</i>	<i>Scaphiopus</i>	<i>Bufo</i>	<i>Hyla</i>	<i>Rana</i>	<i>Scaphiopus</i>	<i>Bufo</i>	<i>Hyla</i>
100-d tanks—Low density								
Desiccation	12.6	0	0	58.2	0	0	0	0
Metamorphosis	69.3	83.1	80.5	0	0	0	0.3	0
Predation	82.0	83.1	80.2	58.1
Competition	18.0	16.9	19.5	41.8	18.0	16.9	19.5	41.9
Initial number	50	65	200	125	50	65	200	125
100-d tanks—High density								
Desiccation	47.0	0	62.6	27.9	0	0	0.04	11.9
Metamorphosis	3.2	80.3	7.0	0	0	5.8	29.3	4.9
Predation	50.2	74.5	40.3	11.2
Competition	49.8	19.7	30.4	72.1	49.8	19.7	30.4	72.1
Initial number	200	260	800	500	200	260	800	500
50-d tanks—Low density								
Desiccation	82.6	0	7.3	6.2	0	0	0	0
Metamorphosis	0	86.7	60.5	0.5	0	0	0	0
Predation	83.3	86.7	67.8	6.6
Competition	17.4	13.2	32.2	93.3	16.6	13.3	32.2	93.3
Initial number	50	65	200	125	50	65	200	125
50-d tanks—High density								
Desiccation	80.7	0.3	64.0	0.3	0	0	17.5	0
Metamorphosis	0	85.0	0	0	0	9.3	10.6	0
Predation	80.7	75.9	35.9	0.3
Competition	19.3	14.7	36.0	99.7	19.3	14.7	36.0	99.7
Initial number	200	260	800	500	200	260	800	500

direct competition with the other three species of tadpoles.

The effect of newts

Searching of tanks just before they dried provided a count of all larvae that escaped predation but were destined to die of desiccation. The numbers of metamorphs and remaining larvae in tanks without newts were used to estimate the minimum mortality due to desiccation and the sum of competition and unknown sources. This estimate was used to partition deaths in tanks with newts between predation and other causes under the assumption that mortality risks were not interacting. A separate analysis of mortality was possible for 50-d and 100-d tanks with high initial densities (Table 4). The estimated total number of tadpoles eaten by newts in these high-density populations of 1760 hatchlings was nearly the same (673 in 100-d tanks and 647 in 50-d tanks). The difference was due to 35 more *Bufo* and 55 more *Hyla*, but 61 fewer *Rana* and 4 fewer *Scaphiopus* being eaten in 100-d tanks. This was expected because *Bufo* and *Hyla* were still small enough to be captured by newts in the period between day 50 and day 100.

The most hostile environment for tadpoles was the treatment combination of low tadpole density, newts present, and 50-d tanks. None of the species metamorphosed in any of the replicates of this treatment; there were no survivors of predation found when the tanks were searched just before they dried. Newts could

be satiated, however, by high tadpole densities. Some *Bufo* escaped both predation and desiccation in all three replicates of the high-density 50-d tanks; *Scaphiopus* escaped in only one replicate. The *Bufo* had an average survival of 64% before desiccation in 50-d tanks without newts; these all died by desiccation (Fig. 3). With newts, only 28% survived newt predation, but 44% of these were able to metamorphose before the ponds dried.

In the 100-d tanks with newts present and low tadpole density, there were no survivors of any species in two replicates; the other replicate produced only four *Bufo*. In the 100-d tanks with newts but high tadpole densities, *Rana* were eliminated by predation leaving a three-species community. The few *Scaphiopus* (mean = 15) that survived were able to metamorphose. Many *Bufo* (mean = 234, 29.25%) survived and were able to metamorphose before the 100-d tanks dried.

In the tanks with newts, that never dried, survival was low, but at least one individual of each species survived in at least one replicate at low initial tadpole densities. Only *Hyla* in the control tanks consistently produced metamorphs from low-density populations. When the *Hyla* were introduced late in the season, zooplankton populations may have been dense enough to be a preferred food for newts. Newts were satiated by high tadpole densities of some species. At high initial densities *Bufo* and *Hyla* were successful in all three replicates, *Scaphiopus* survived in two replicates, and *Rana* in only one. *Rana* was the first species introduced

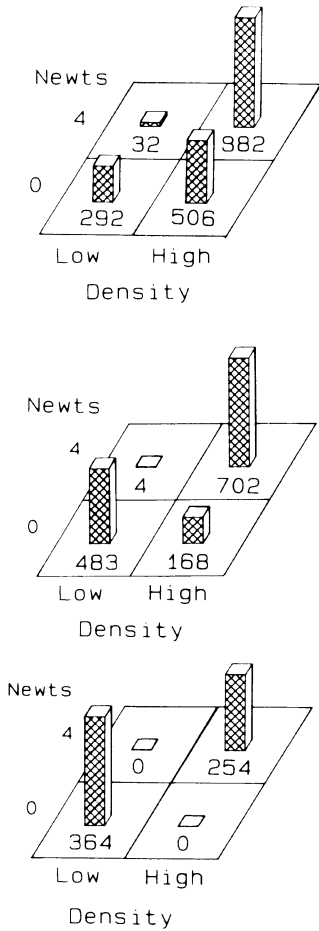


FIG. 3. The number of *Bufo* metamorphs as a function of initial tadpole density (low or high) and the presence of adult newts (0 or 4) in control tanks that never dried (upper panel), tanks that dried in 100 d (middle panel), and tanks that dried in 50 d (lower panel). Data are the sums of the numbers of metamorphs in the three replicates.

and was vulnerable to predation at a time before the zooplankton had reached high densities (H. Wilbur, *personal observation*). *Rana* also had the lowest initial density (50 or 200) of all species. Preferences of newts for the species cannot be inferred from these data (Table 4), because tadpoles were introduced at different times when zooplankton had different abundances. Morin (1983) experimentally demonstrated, using choice tests in the laboratory, that the order of preference for tadpoles by newts was *Scaphiopus* then *Bufo* then *Rana*, with *Hyla* and *Rana* being about equal as the least preferred genera.

The effect of treatments on limnological characteristics of the ponds

The draining of tanks at controlled rates was designed to simulate different levels of environmental uncertainty. Many environmental factors other than crowding change simultaneously as ponds dry. Al-

though the summation of temperatures (degree-days) did not change, temperatures became more variable as the total volume of the pond shrank (Fig. 4). In natural ponds, surface area and volume change concordantly, but in the artificial ponds with straight sides, volume, but not surface area, decreased as the tanks were drained. Even as late as 29 April, there were no differences in early morning temperatures among the tanks of different depths (ANOVA, $P \gg .10$). There were significant differences in conductivity of the water in the tanks on 29 April, but not near the start of the experiment on 31 March. At the end of April, the 50-d tanks had lower conductivities (mean 44 $\mu\text{S}/\text{cm}$) than either the 100-d or control tanks, which both had 82 $\mu\text{S}/\text{cm}$ (ANOVA effect of drying time, $P = .0006$). This effect probably was primarily due to the dilution of the water by rain concordant with the draining. By this date, conductivities in tanks with newts were 6% higher than in tanks without newts ($P < .0001$), and tanks with high initial tadpole density had 2.5% lower conductivities ($P = .039$) than tanks with low initial densities. All three effects were additive; the treatments with the most dissolved material were ones with few tadpoles. All treatments had a significant effect on water trans-

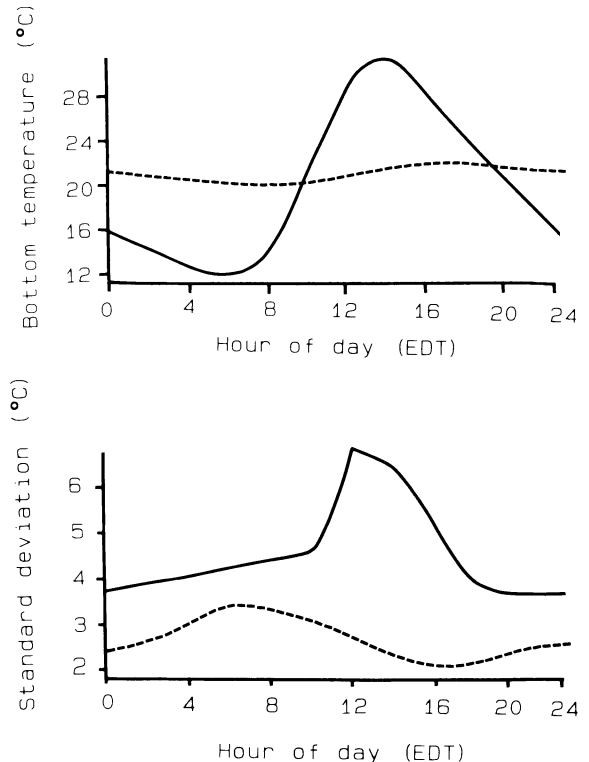


FIG. 4. (Top) The mean water temperature at each hour at the bottom of --- a control (50 cm deep) pond and — an adjacent pond that dried in 50 d, during the period from day 30 to day 50. (Bottom) The standard deviations of the hourly temperatures at the bottoms of — the control and --- drying tanks during same period.

TABLE 5. ANOVA of total biomass of metamorphs produced by all anurans.

Source	df	ss	F	P
Model	11	37 130	12.84	<.0001
Drying time	2	8355	15.89	<.0001
Newts	1	19 022	72.37	<.0001
Density	1	1263	4.81	.0383
Dry × newts	2	449	0.85	.4381
Dry × density	2	119	0.23	.7983
Newts × density	1	5379	20.47	<.0001
Dry × newts × density	2	2540	4.83	.0172
Error	24	6308		
Total	35	43 438		

parency (measured with a 9 cm Secchi disk mounted on a metre stick) on both 25 and 29 April. Differences in transparency were due to the density of phytoplankton because all tanks had the same initial water quality; a low transparency reflects dense phytoplankton populations, usually a diatom of the genus *Scenedesmus* (Kaiser 1985). The effect of the draining treatment on phytoplankton density was additive (MANOVA, $P = .0004$), but the effects of newts ($P = .013$) and initial tadpole densities ($P = .0003$) interacted ($P = .025$). The tanks with low initial tadpole densities had high transparencies regardless of the presence or absence of newts. Tanks with high initial tadpole densities and no newts had transparencies about half of the value of tanks with few tadpoles. Tanks with high initial tadpole densities

with newts present had intermediate transparencies. These data suggest that tadpoles facilitate the population growth of small species of phytoplankton as tadpoles graze periphyton and macrophytes, making nutrients available for phytoplankton in the water column.

Total biomass of metamorphs

The total biomass of metamorphs was computed as the sum of all metamorph masses of all species without regard to date of metamorphosis. The effects of differences among blocks were pooled as the error term in the analysis, yielding a conservative test of the importance of manipulated factors. The full model (Table 5) accounted for 85% of the variance in anuran biomass. The effects of newts dominated the analysis in part because newts caused the extinction of many populations (Fig. 5). In only one treatment (4 newts, low tadpole density, and pond drying in 50 d) did the newts eliminate all four species of anurans in all three blocks, resulting in zero biomass. The maximum biomass was obtained in the treatment with no newts, a low density of tadpoles, and the pond never drying. The second strongest effect was the interaction between newt density and tadpole density. This was largely due to the different effects of newts at high and low tadpole densities in the tanks that did not dry. At high tadpole densities, newts caused only an 8% reduction in biomass, whereas at low tadpole densities, newts caused a 91% reduction. The main effect of rate of drying of the pond was also highly significant. Within each combination of newt density and tadpole density, more rapidly drying ponds always produced less total anuran biomass than longer lasting ponds, largely due to the loss of *Rana* tadpoles by desiccation. In the absence of newts, an increase in tadpole density resulted in a reduction of biomass in the long-lasting tanks and a slight increase in biomass in the short-lived tanks. In the presence of newts, an increase in tadpole density always resulted in an increase in biomass of metamorphs.

The analysis of total biomass suggests that, in long-lasting ponds without newts, the tadpoles, as a guild, are food-limited by a mechanism of scramble competition (Wilbur 1976, 1980). Many individuals consume some of the resource but are unable to reach the lower size threshold required for metamorphosis; as density is reduced, a higher fraction of the population is able to metamorphose and the total biomass of metamorphs increases. In high-density populations, newt predation does not have a strong negative impact on biomass production by the anuran guild, but it does have a dramatic effect on the distribution of biomass among the species. In the tanks that never dried, the effect of newts on high-density populations was to alter the biomass composition from domination by *Scaphiopus* (67%) to codominance by *Scaphiopus* (25%), *Bufo* (33%), and *Hyla* (24%). Four adult newts are not sufficient to reduce the high density of tadpoles to a

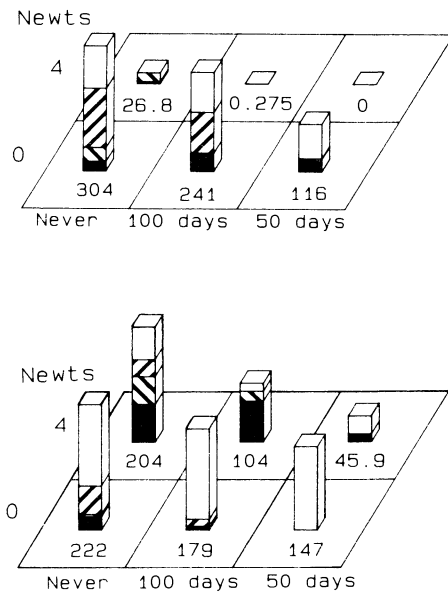


FIG. 5. The total biomass of metamorphs (g) as a function of the presence of adult newts (0 or 4) and the rate of pond drying (never, 100 d, or 50 d) in communities with low (upper panel) and high (lower panel) initial tadpole densities. The data are sums of the biomasses of all metamorphs in the three replicates. The contributions of each species (■ *Bufo*, ▨ *Hyla*, ▩ *Rana*, □ *Scaphiopus*) to the biomass in each treatment are indicated.

level at which the guild as a whole is not food-limited. In low-density communities, newt predation reduces the biomass of metamorphs to well below its potential value. *Rana* dominated the biomass composition (47%) in tanks that had no newts and low densities of tadpoles, and that dried slowly or not at all. That is, in the best environment for tadpole growth, *Rana* dominated production. In the rapidly drying 50-d tanks, *Scaphiopus* was the strong dominant. In the presence of newts, *Bufo* dominated or codominated with *Scaphiopus*, with *Bufo* having slightly higher biomass in long-lived tanks and *Scaphiopus* having higher biomass in 50-d tanks.

Responses of individual species

Bufo.—*Bufo* survival declines slowly with increases in initial density. This tolerance to density is expected in species, such as *Bufo*, with large clutch sizes that breed explosively. *Bufo* had at least four metamorphs in 26 of the 36 communities, the broadest success of any species. Survival was highest in low-density tanks without newts (80.5% in 100-d tanks, 60.6% in 50-d tanks, and 48.6% in the permanent tanks). The analysis of survival showed a highly significant interaction (ANOVA, $P \ll .01$) between the occurrence of newts and the density of tadpoles. Survival was reduced by newts in low-density populations and increased by newts in high-density populations (Fig. 3). This effect was repeated at all three drying times. This paradox, enhancement of survival at high density by predation, appears to be due to release from competition with *Scaphiopus* and *Rana* when newts were present.

The 10 communities from which no *Bufo* metamorphosed preclude a full analysis of variance of body size and length of larval period, but the effects of each treatment and most two-way interactions can be studied by the analysis of subsets of the full design. At low density without newts, there were some metamorphs from all tanks that had the three drying treatments. The univariate effect of drying was significant on larval period ($F_{2,4} = 10.18, P = .027$) but not on mass ($P = .23$). Metamorphosis was accelerated by drying of the ponds (Fig. 6). Tadpoles from 50-d tanks metamorphosed, on average, 10 d sooner (a 4% decrease), and the earliest metamorph was 6.6 d earlier than in control tanks. There was some truncation of the distribution (an average of 7% of tadpoles died of desiccation). Tadpoles from the 100-d tanks metamorphosed an average of 3 d before the controls and the first metamorph was 1.3 d earlier than the first metamorph in the control populations. There was no truncation of the distribution of lengths of larval periods as all *Bufo* metamorphosed before the 100-d tanks dried. At high density, there were metamorphs from only the control and the 100-d tanks; all surviving tadpoles desiccated in the 50-d tanks. Metamorphosis was accelerated in the 100-d tanks (mean 29 d, which is a reduction to 70% compared with the controls, ANOVA $F_{1,2} = 32.19, P =$

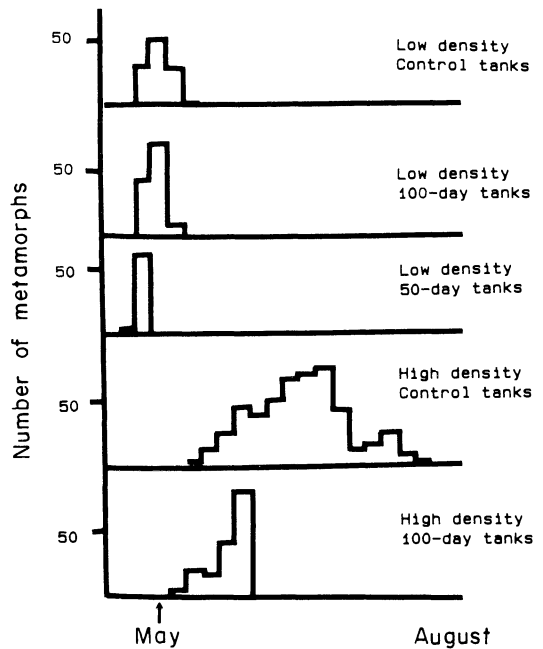


FIG. 6. The distributions of dates of metamorphosis of all *Bufo* in tanks without newts. All panels have the same scale on the abscissa (2-d intervals) to demonstrate the acceleration of metamorphosis in drying ponds. Labels indicate the initial tadpole density (low or high) and the drying time (50 or 100 d, or never). The arrow indicates the date when the 50-d ponds dried. Counts from all three replicates are pooled.

.030) with the earliest metamorph 5.3 d earlier than in the control population. This acceleration of metamorphosis was accompanied by a weak ($F_{1,2} = 21.26, P = .044$) effect of drying treatments on mass at metamorphosis. The MANOVA test was not significant ($F_{2,1} = 25.86, P = .15$). The acceleration was also accompanied by a truncation in the distribution of larval periods due to the desiccation of an average of 501 tadpoles (63%) in the drying tanks.

The main effect of tadpole density was studied in the permanent tanks without newts. There was not a significant MANOVA effect of tadpole density ($F_{2,1} = 14.75, P = .18$, main effect of density tested over the density \times block interaction) even though the ANOVAs for each response were significant (mass: $F_{1,2} = 54.59, P = .018$; larval period: $F_{1,2} = 50.26, P = .019$). Metamorphosis in high-density populations occurred an average of 56 d later and at 58% of the body mass of low-density populations. The total biomasses of *Bufo* were nearly identical (7.860 g in low-density populations, 7.867 in high-density populations) as body size and number of metamorphs were compensatory.

The interaction between the effects of newts and the rate of pond drying on growth was studied using only the 100-d and control ponds with 800 initial *Bufo*. The main effect of newts in the MANOVA was not significant ($P = .19$) nor was the effect of drying time ($P =$

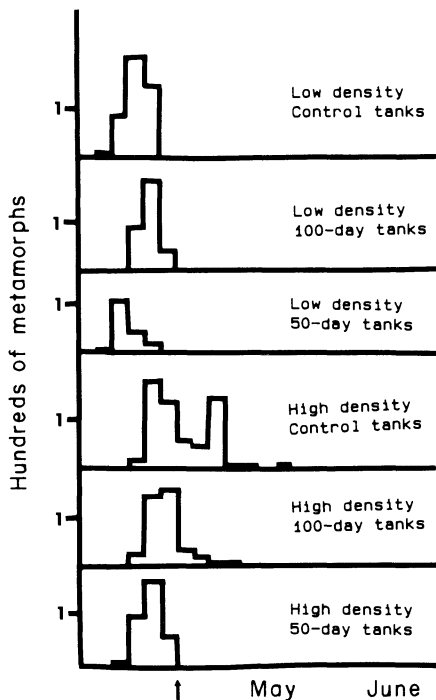


FIG. 7. The distribution of dates of metamorphosis of all *Scaphiopus* in tanks without newts. All panels have the same scale (weekly intervals on the abscissa and the 100 tic on the ordinate). Labels indicate the initial tadpole density (low or high) and the drying treatment (50 or 100 d, or never). The arrow indicates the date when the 50-d tanks dried. Counts from all three replicates are pooled. There is no clear evidence that this species accelerated metamorphosis in drying ponds.

.37), but their interaction was ($F_{2,1} = 1728, P = .017$ with the newt \times drying time interaction tested over the newt \times dry \times block error matrix). This significance was more due to the effect on mass than on length of larval period. Newts, by lowering densities of competitors, caused an increase in the mass at metamorphosis of *Bufo*. This enhancement was more pronounced in the 100-d tanks than in the control tanks (Table 1). The extreme interaction occurred in the 50-d tanks in which the interaction between competition and predation resulted in no metamorphs in two treatments (Fig. 3).

Scaphiopus.—Like *Bufo*, *Scaphiopus* is an explosive breeder with density-tolerant larvae. It is a competitively dominant species but is highly vulnerable to predation by newts. Only a single metamorph was produced in the nine tanks with newts and low tadpole density (three replicates of each of three treatments). Sampling of ponds just before they dried demonstrated that this was due to efficient predation by newts (Table 4, Fig. 2). *Scaphiopus* metamorphosed (73 survivors) in only one of the 50-d tanks with a high initial tadpole density and newts. *Scaphiopus* had a very high survival (75–92%) in the nine tanks with no newts and low initial density. The maximum output of metamorphs

(mean 221 or 85%) was from the 50-d tanks with high initial density and no newts. The rapidly drying tanks enhanced survival of *Scaphiopus* presumably due to reduced competition with other anurans.

The interaction between tadpole density and rate of drying of the pond was studied using the 18 tanks without newts, which all had at least 49 *Scaphiopus* metamorphs. In the MANOVA, there was a weak main effect of tadpole density ($F_{2,1} = 260, P = .044$, density tested over the density \times block interaction) and a weak main effect of rate of drying ($F_{4,6} = 4.69, P = .046$, with the drying effect tested over the drying \times block interaction). The interaction between density and rate of drying was not significant ($P = .77$). The density effect was strongest on mass at metamorphosis; mass was smaller in high-density populations in all drying treatments. The drying treatment had no demonstrable effect on mass, but rapidly drying ponds resulted in reduced larval periods when *Scaphiopus* were at high density (Table 1, Fig. 7). There was no evidence that metamorphosis of individuals was actually accelerated; the reduction in the mean was due to truncation of the size distribution by desiccation of slowly growing larvae.

The effect of newts was primarily on survival; some *Scaphiopus* survived to metamorphosis in all three replicates in only the high-density 100-d tanks with newts. These were compared with the high-density 100-d tanks without newts. There was no demonstrable MANOVA effect of newts ($P = .25$), or, in the ANOVA, effect of newts on the logarithm of mass ($P = .92$) or on the logarithm of length of larval period ($P = .11$) in spite of the vast difference in the number of metamorphs (mean = 208.7 without newts and 15.0 with newts). This result is probably explained by competition with other species.

Rana.—*Rana* responded strongly to all experimental treatments. No tadpoles metamorphosed in any of the 50-d tanks. In the 100-d tanks no *Rana* escaped newt predation. Without newts, survival was high (69%) in the low-density populations but low (3%) in the high-density populations due to competition-mediated desiccation. In the tanks that never dried, survival was higher in the low-density populations (74%) than in the high-density populations (9%) without newts, but there were no significant effects on mass or larval period. Newts exterminated all *Rana* in two replicates of each density in the tanks that never dried. The few *Rana* that survived in one replicate had large body sizes and short larval periods (Table 1). The most successful *Rana* populations in terms of number of metamorphs (mean = 37) and total biomass (mean = 49.101 g) were the low-density populations without newts in ponds that never dried. High-density control populations produced fewer metamorphs (mean = 18.3) that were smaller (0.994 g vs. 1.341 g) and had larval periods that averaged 40 d longer, yielding a total biomass of 17.611 g.

TABLE 6. ANOVA of *Hyla* responses in control ponds that never dried.

Source	df	Individual responses						
		Log(mass in grams)				Log(larval period)		
		Type III ss	Test MS	F	P	ss	F	P
Model	11	43.070						
Newts	1	11.602	N × B	69.18	.0141	1355 × 10 ⁻⁶	33.85	.0283
Density	1	2.439	B × B	33.22	.0288	540 × 10 ⁻⁶	12.67	.0706
Block	2	1.843				159 × 10 ⁻⁶		
Newts × density	1	0.062	N × D × B	0.21	.6916	4 × 10 ⁻⁶	10.25	.0853
Newts × block	2	0.335				116 × 10 ⁻⁶		
Density × block	2	0.147				32 × 10 ⁻⁶		
Newts × density × block	2	0.589				23 × 10 ⁻⁶		
Within populations	254	9.253				274 × 10 ⁻⁶		
Total	265	52.323				1629 × 10 ⁻⁶		
Source	df	Population responses						
		Biomass			Survival			
		ss	F	P	ss	F	P	
Model	3	3407			2.257			
Newts	1	1820	7.62	.0084	1.399	27.77	<.0001	
Density	1	185	0.78	.3832	1.559	3.10	.0855	
Newts × density	1	1402	5.87	.0196	0.702	13.94	.0005	
Error	44	10 507			2.2164			
Total	47	13 914			4.4737			

Hyla.—*Hyla* had only sporadic survival in the 50-d tanks after they were refilled (4 survivors from 3 of the 12 tanks) and in the 100-d tanks (mean = 24.3 survivors from high-density populations exposed to newts). Some *Hyla* metamorphosed from all of the control tanks. In the control tanks, there was an interesting interaction between the effects of tadpole density and the presence of newts (Table 6). In the tanks without newts, there were more survivors (48 vs. 7.7) that metamorphosed at a larger size (0.265 vs. 0.186 g) after a larval period that was 47 d less at low than at high initial densities. In the presence of newts, the effect of density on survival was reversed. The low-density populations produced an average of only 12.7 survivors but they were large (0.583 g). The high-density populations produced an average of 43 small metamorphs with a mean mass of 0.293 g. The mean larval period was identical in the two treatments. Biomass also showed the interaction, being large when newts were present and initial densities were high or when newts were absent and initial densities were low.

Hyla did very poorly in the 50-d tanks that were drained and refilled, even though all competitors had been removed by the draining treatment. There was contamination by libellulid dragonfly naiads in some tanks, but *Hyla* did poorly in all replicates. My explanation is that the treatment removed nutrients during the initial draining regime both through water loss and through removal of tadpoles as the pond dried. No new nutrients were added when the tanks were refilled. Natural ponds would lose some nutrients to ground water, but the death of tadpoles by desiccation might leave nutrients for the next cycle of filling, if it occurred soon

enough. The current result complements the results of Wilbur and Alford (1985) in which recently filled ponds were much better for *Hyla* (500 hatchings, the same as the high density in the present experiment) than ponds that had been filled for 65 d but had never had tadpoles in them. These two studies support the contention (Wilbur 1980) that tadpoles exploit recently filled ponds that have a flush of primary productivity as nutrients are imported by runoff or released from the decomposition of litter in the basin.

DISCUSSION

The primary conclusion of this study is that three dominant causes of mortality interacted with each other and with the life histories of the four species to determine the structures of 36 experimental communities, which had the same initial relative abundances. Desiccation had a great impact on *Rana*, but little effect on *Scaphiopus*. Predation fell heavily on *Scaphiopus*, but actually improved the success of *Bufo*. Competition was felt strongly by *Hyla*, but not very much by *Scaphiopus*. The answer to the question, what regulates the dynamics of tadpole populations, depends on the tadpole species and the specific environment in which it occurs.

This experiment suggests that in nature competition probably dominates simple habitats of short duration, such as overflow pools along streams and on rock outcrops and very temporary rainpools. Species that exploit such ephemeral habitats, such as *Scaphiopus* and *Bufo*, breed synchronously, have high fecundities, and appear to have evolved a tolerance to high density. The experimental increase in population density reduced

the growth rate of all species causing a prolongation of the larval period and smaller sizes at metamorphosis. This growth response, together with the reduction in biomass output as initial density was increased, is evidence for food limitation in the high-density populations without predators. Over 90% of the mortality in the tanks without predation or desiccation was due to density effects that were felt evenly over all replicates, which suggests that epidemic disease or parasitism were less likely proximal causes than food limitation. The reduction to the concentration of dissolved solids and the switch from large standing crops of periphyton to high concentrations of small phytoplankters also support this interpretation.

A short larval period is a necessary prerequisite for a species to use temporary ponds. The ability of a larva to sense the deterioration of its habitat and initiate metamorphosis, even at the cost of a small juvenile size, is an obvious adaptation for the use of ephemeral habitats (Wilbur and Collins 1973). There was evidence that *Bufo* was able to accelerate metamorphosis in the rapidly drying ponds. In contrast, desiccation eliminated all but a single *Rana* from the 50-d tanks. The long larval period of *Rana* precludes its use of temporary ponds. At the opposite extreme is *Scaphiopus*, which was affected very little by even rapidly drying ponds. This explosive breeder rapidly colonizes new temporary ponds where the risk of competition and predation are low.

Predation becomes increasingly important in ponds that retain water for longer periods, permitting the establishment of larger predators. For example, permanent ponds that are occupied by fish have very low amphibian diversities in the Southeast. Many predators of tadpoles, such as newts, some fish, and many insects, are size-limited and can be satiated by species that have synchronized breeding and high fecundities. The tadpoles in this experiment grew rapidly enough to escape predation by newts in a week or two. Nevertheless, predation eliminated 9 of the 24 populations (four species \times two densities \times three replicates) in the tanks that did not dry. Newts were satiated by high total densities of tadpoles, but even in these communities they had a strong effect on the relative abundance of metamorphs. Differential predation was due to species-specific vulnerabilities, rather than prey choice by the predator, because the species were introduced at different times so that pairs of species were generally not vulnerable at the same time. Different risks of predation were likely due to true differences in behavior and palatability of the tadpoles as well as environmental effects correlated to the time of species introductions. Early in the season, zooplankton populations, an alternative prey for newts, were at low densities, temperatures were low, and macrophytes and filamentous algae provided less cover than later in the season.

The primary goal of the experiment was to study the

interactions between these three primary mortality sources. The interaction between predation and competition in ponds that did not dry resulted in rapid growth among the survivors of predation in ponds that had high initial densities. These tadpoles were able to metamorphose at a large size and after a short larval period, a result that duplicated our previous work (Wilbur et al. 1983). The high initial densities that often result from the synchronized breeding and high fecundities of many anurans that breed in ponds suggest that moderate levels of predation may be an important ingredient of larval success in many communities (Heyer et al. 1975). Predation is a benefit to the survivors. The high initial densities apparently satiated the four newts so that the total number of metamorphs and their combined biomass were not strongly affected by predation. The species composition, however, was greatly altered. *Bufo* and *Hyla* benefited from predation at the expense of *Rana* and *Scaphiopus*. Morin (1983, 1986) found a similar indirect facilitation by newts using a guild of three of the same species (*Rana sphenoccephala*, *Scaphiopus holbrooki*, *Hyla chrysoscelis*), a very closely related toad, *Bufo terrestris*, and two additional species of treefrogs, *Hyla crucifer* and *H. gratiosa*. Both *H. crucifer* and *H. gratiosa* benefited from newt predation on the other anurans. Morin did not independently manipulate tadpole density and the intensity of predation. His interpretation of indirect effects is supported by my study, the experiment we did jointly (Wilbur et al. 1983), and his own recent experiment (Morin 1986).

The interaction between competition and desiccation was also striking. Desiccation was a much higher risk for individuals in high-density populations than in low-density populations. *Bufo* had the most striking response with no survivors from high-density tanks that dried in 50 d, but good success in low-density tanks. Species differed in both their ability to accelerate metamorphosis in response to drying ponds and in their sensitivity to density. It is not known if the acceleration of metamorphosis is a direct effect of the thermal regime in drying ponds or if density or growth rate per se is directly assayed by tadpoles.

The interaction between predation and desiccation was not as obvious as the three-way interaction involving these two factors and competition. Predation reduced competition by *Rana* and *Scaphiopus* permitting *Bufo* to grow rapidly enough to escape drying ponds. This effect was very strong in the 50-d tanks and less obvious in the 100-d tanks.

This experiment has demonstrated the complexity of interactions between biological and environmental factors in determining the distribution and abundance of species. Species interactions via competition and predation may also result in indirect mutualisms in complex food webs (e.g., Levine 1976, Vandermeer and Boucher 1978, Vandermeer 1980, Boucher et al. 1982, Holt 1984, Boucher 1985). *Bufo* clearly benefited

from the presence of newts, which reduced competition, allowing *Bufo* to escape drying ponds. Another indirect effect was the positive effect of *Rana* on *Scaphiopus*, the dominant competitor, which resulted in *Rana* being an important species beyond its direct competitive effect on the other anurans.

These results show the futility of arguments between proponents of predation and competition as the single unifying force structuring communities. They also demonstrate that chance effects, such as the time it takes a pond to dry, are not environmental noise obscuring biological interactions, but rather they set the stage for different biological mechanisms having different importances in structuring communities. Such mechanisms include species interactions as well as physiological and life history adaptations to different kinds of habitats. I am very much in agreement with Connell's (1975) view that communities will be structured by different processes in habitats with different levels of disturbance. Only a replicated experiment in which disturbance is an explicit treatment allows partitioning the variance in community parameters among these three interacting factors. The final caveat is that factorial experiments, such as this one, can explore possibilities and separate complex causal relationships. Their relevance to explaining the distribution and abundance of species in natural communities hinges on how well experimental mesocosms duplicate real environments (Diamond 1986). The continuum between laboratory experiments, contained communities in the field, true field experiments, and comparative natural history needs rigorous appraisal as ecology moves from developing a theory of what can happen to evaluation of what does happen.

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