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ECOLOGY AND BREEDING PHENOLOGY OF LARVAL *HYLA ANDERSONII*: THE DISADVANTAGES OF BREEDING LATE[1]

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Abstract. We exploited natural variation in the breeding phenology of *Hyla andersonii*, the Pine Barrens Treefrog, to test whether offspring hatching at different times during the breeding season differed in growth and survival. We studied the growth and survival of two successive cohorts of *Hyla* tadpoles in 12 artificial ponds, where we also manipulated abundances of two kinds of organisms that might interact seasonally with *Hyla*: aquatic insects and *Bufo* tadpoles. We also measured whether the abundance of periphyton changed seasonally in response to manipulations of aquatic insects and tadpoles, to describe temporal patterns of resource availability that might affect tadpole growth and survival. Additions of hatchlings occurred 34 d apart, and the first cohort completed development before the addition of the second cohort.

Additions of aquatic insects and *Bufo woodhousii* tadpoles, separately or together, did not significantly affect survival in either cohort. Although the initial larval density of the first cohort was 1.5 times that of the second, the first cohort survived better, grew and developed more rapidly, and metamorphosed at larger size than the second cohort. Competition from *Bufo* tadpoles and insects, as inferred from reduced growth rates relative to controls without these interspecific competitors, was more pronounced in the first cohort than in the second, and coincided with reduced standing crops of periphyton, an important food for tadpoles.

Although breeding late in the season reduced the growth and survival of offspring, potential reductions in the fitness of late-breeding adults are problematic because of uncertainties about the number of breeding efforts made by each female each year. Breeding late would be disadvantageous if different subpopulations breed only early or only late in the season, and if the patterns seen in our study hold for natural ponds. However, if late breeding efforts represent additional clutches deposited by adults that have already reproduced earlier that year, production of additional offspring later in the season could increase fitness.

Key words: anurans; Bufo woodhousii; *competition;* Hyla andersonii; *insects; interphyletic competition; interspecific competition; mesocosms; New Jersey; phenology; ponds; predation; priority effects.*

INTRODUCTION

Adaptive links between breeding phenology and reproductive success are often inferred, but seldom experimentally tested. Organisms in seasonal environments should time their breeding to coincide with predictable changes in habitat quality that maximize offspring survival and growth (Lack 1954). However, populations often have > 1 peak of reproduction during each annual breeding season. These multiple bouts of breeding in seasonal environments have multiple interpretations, including the repeated occurrence of favorable conditions for reproduction, temporal habitat partitioning, or opportunistic reproduction in response to an inability to predict when the most favorable conditions will occur. We exploited natural variation in the breeding phenology of *Hyla andersonii*, the Pine Barrens Treefrog, to test whether offspring hatching at different times during the breeding season completed larval development with equal success. We measured differences in larval growth and survival to identify potential constraints that might influence when frogs reproduce in temporary ponds during an extended breeding season.

The anuran tadpoles that dwell in temporary ponds are well-suited for experimental studies of a broad range of processes in seasonal nonequilibrium communities (Morin 1989). Temporary ponds undergo dramatic seasonal variation in habitat quality, since the abundances of resources, competitors, and predators can all fluctuate during annual episodes of community development. If habitat quality changes in a predictable

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manner, frogs could maximize their fitness by breeding when conditions are most favorable for the development of their herbivorous aquatic offspring.

Unlike some anurans that breed synchronously on only 1-2 d/yr (see Wells 1977), *Hyla andersonii* breeds asynchronously over periods of many weeks. In New Jersey, *Hyla andersonii* oviposits from late April to mid-July. A priori, the prolonged breeding season of *Hyla andersonii* seems paradoxical, because tadpoles hatching late in the breeding season might experience several disadvantages.

One possible disadvantage of delayed breeding is that late arrivals potentially compete with older, larger, competitively superior, tadpoles for periphyton and phytoplankton (Morin 1987). Even if preceding cohorts of tadpoles have already metamorphosed when later cohorts hatch, late arrivals may still suffer from the depletion of nutrients exported by metamorphosed froglets. Ponds can also become less productive over time (Seale 1980), perhaps as the initial flush of nutrients in a newly formed pond becomes sequestered in organisms that tadpoles cannot consume. Ponds may also become more dangerous as predatory aquatic insects accumulate during the breeding season (Smith 1983, Roth and Jackson 1987). Herbivorous aquatic insects can also compete with tadpoles (Morin et al. 1988), but it is unclear whether the intensity of competition between tadpoles and insects changes seasonally.

Potential advantages of delayed breeding are less obvious. Seasonal changes in physical factors, such as water temperature, could alter productivity or tadpole growth rates (Berven et al. 1979) to offset the other deteriorations in habitat quality suggested above. Interspecific differences in breeding phenology are often explained as manifestations of temporal habitat partitioning to minimize competition (e.g., see Toft 1985), and it may sometimes be better to risk the rigors of a deteriorating pond later in the season than to compete head-to-head with other tadpoles earlier in the season. Despite these intriguing possibilities, little is known about intraspecific variation in larval performance arising when hatchling tadpoles arrive in ponds at different times in the breeding season.

We compared the performance of two cohorts of hatchling *Hyla andersonii* tadpoles added to experimental ponds in 1986. The two introductions were separated by 34 d, and animals from the first introduction had metamorphosed from the ponds before the second addition of hatchlings. We specifically tested whether the timing of hatchling addition affected larval performance. We also tested whether tadpoles added to ponds at different times responded differently to manipulations of potential competitors and predators that potentially changed in importance as the breeding season progressed. One manipulation, the addition of *Bufo woodhousii fowleri* tadpoles to some ponds, generated a transient perturbation in the abundance of an interspecific competitor that only persisted for about the first month of community development. *Bufo* developed rapidly and metamorphosed before the addition of the second *Hyla* cohort (Morin et al. 1988). A second manipulation, involving the exclusion or natural colonization of ponds by aquatic insects, generated a persistent perturbation in the presence or absence of insects among ponds, although insect abundance and species composition could change seasonally in the ponds open to insect colonization. We have shown elsewhere that the first cohort of *Hyla andersonii* responded to aquatic insects and tadpoles of *Bufo woodhousii fowleri* as competitors (Morin et al. 1988). In this paper we reanalyze the published responses of the first *Hyla* cohort together with unpublished data from the second later *Hyla* cohort to explore whether tadpoles entering the community at different times responded differently to the transient and persistent perturbations outlined above.

METHODS AND MATERIALS

Artificial ponds

We studied the growth and survival of *Hyla andersonii* tadpoles in 12 artificial ponds located at the Hutcheson Memorial Forest (East Millstone, New Jersey) of Rutgers University. The artificial ponds were cylindrical, galvanized steel tanks (1.52 m in diameter and 0.61 m deep), painted with epoxy enamel, and filled with 1000 L of water pumped from a nearby stream through an 88-μm mesh plankton net. Each tank contained similar amounts of dry grassy litter (14 L, tightly packed), macrophytes (50 stems of *Elodea canadensis*), 50 g of commercial trout food for nutrients, and a standard 0.64-L inoculum of plankton from natural ponds, following the general protocol used in previous experiments (Morin 1981).

Experimental manipulations

We manipulated abundances of aquatic insects and *Bufo* tadpoles in artificial ponds, and then observed responses of two temporally nonoverlapping cohorts of *Hyla andersonii* tadpoles (representing early and late bouts of breeding) to those manipulations. Screen lids (7 meshes per centimetre) excluded insects from six randomly selected tanks, while insects could freely colonize the remaining six uncovered tanks. Tanks selected to receive insects remained uncovered from 19 May until 4 June 1986, and from 27 June until 26 July. All 12 tanks remained covered at other times to retain metamorphosing froglets. We added 150 *Bufo* hatchlings per tank to three covered and three uncovered tanks (selected at random) on 19 May 1986. These manipulations of insects and *Bufo* established a completely crossed set of factors applied to the tanks. These treatment combinations are hereafter termed "control" (=no *Bufo* and tank covered), "*Bufo*" (=150 *Bufo* and tank covered), "insects" (=no *Bufo* and tank uncovered), and "insects and *Bufo*" (=150 *Bufo* and tank covered). We added cohorts of *Hyla* tadpoles to each tank on two different dates, early and late in community development, to bioassay seasonal shifts in the effects of these treatments on *Hyla* tadpoles.

To each tank we added 150 hatchlings of *Hyla andersonii* on 19 May 1986 (hereafter, the "May cohort" or "cohort 1") and another 100 hatchling *Hyla* on 22 June 1986 (hereafter, the "June cohort" or "cohort 2"). Hatchlings in both cohorts were at similar developmental stages (not yet feeding, and with some unresorbed yolk still visible) when added to the tanks. All initial densities were within the range observed in natural ponds. *Hyla* added in May metamorphosed shortly before the second addition of *Hyla* in June. Both introductions coincided with natural pulses of breeding in the New Jersey Pine Barrens. We collected breeding pairs of frogs from natural ponds, allowed the frogs to oviposit in the lab, and aerated the eggs until hatching. We mixed hatchlings from several pairs before their addition to the experimental ponds, to homogenize any genetic differences in tadpole performance over all replicates.

Different initial densities of the two *Hyla* cohorts complicate comparisons of their performance. Different densities arose from unavoidable differences in hatchling availability between dates. Fortunately the bias introduced by different initial densities is predictable, permitting conservative tests for differences between cohorts. Under similar conditions, the lower density of the June cohort would bias responses toward greater body size and growth rates relative to the May cohort. Consequently, if individuals in the June cohort exhibit reduced growth or prolonged development relative to the May cohort, despite an initial low density advantage, we interpret such effects as a deterioration in pond conditions later in the season. Many factors might change seasonally to generate such an effect, including nutrient levels, the species composition of algae consumed by tadpoles, and many physical/chemical aspects of the pond. Negative effects of competition on growth and development of larval amphibians are well known (Wilbur and Collins 1973), and Allee effects are improbable at these moderate tadpole densities (Wilbur 1980).

Insect samples taken on 27 June 1986, shortly after the last tadpoles in the May cohort metamorphosed, showed that screen lids effectively manipulated insect abundance ($\bar{X} \pm \text{SE} = 1.17 \pm 0.54$ insects per sample in covered tanks vs. 39.50 ± 16.40 in uncovered tanks; see Morin et al. 1988). Insects collected from the tanks early in the experiment included mosquitoes (Diptera: Culicinae), midges (Diptera: Chironomidae and Chaoborinae), water boatmen (Hemiptera: Corixidae), and mayflies (Ephemeroptera: Baetidae), none of which prey on tadpoles. Predatory insects, such as odonates and notonectids, only appeared later in community development. We collected odonate exuviae throughout the experiment to monitor their abundance. Odonates began to oviposit in the tanks shortly before the first cohort of *Hyla* metamorphosed in June. In July and August various combinations of three odonates, *Pantala flavescens, Pantala hymenea,* and *Anax junius,* metamorphosed from three of six open tanks. The three tanks respectively yielded 9 *Pantala* plus 6 *Anax*, 38 *Pantala*, and 3 *Pantala*. These rather variable patterns of odonate colonization suggest that tadpoles added to tanks in late June could encounter more predatory insects than tadpoles added in May, but the presence of odonates was not a consistent feature of all of the ponds open to insect colonization.

Response variables

Relative intensities of competition experienced by tadpoles can be inferred from interpopulation differences in mean mass at metamorphosis, larval period, or growth rate. Increased competition reduces mean mass at metamorphosis and/or prolongs larval development (Wilbur and Collins 1973, Wilbur 1976). We collected, identified, and counted all newly metamorphosed froglets daily, and weighed each froglet to 1 mg precision. From this complete census of surviving anurans we calculated survival to metamorphosis, mean mass, mean larval period, and a linear approximation of mean growth rate (mean mass/mean larval period) of froglets from each cohort in each tank.

Many tadpoles feed on periphyton (Dickman 1968). Seasonal changes in periphyton abundance can suggest temporal patterns of resource availability that may affect tadpole growth. We used the trichromatic method of Strickland and Parsons (1968) to estimate the standing crop of periphyton (in micrograms of chlorophyll *a*) on 75 × 25 mm glass microscope slides harvested from the tanks at approximately weekly intervals. The slides were suspended at mid-depth along the walls of each tank, and were attached by silicone adhesive to strips of fiberglass screen. As much periphyton as possible was scraped with a sharp razor blade from the grazed surface of harvested slides onto a glass fiber filter, then chlorophyll was extracted following the standard protocol in Strickland and Parsons (1968). The use of glass slides to sample periphyton communities is analogous to procedures used by others in lotic systems (Patrick 1967).

Statistical analyses

A three-factor multivariate variance analysis (MANOVA) tested whether manipulations of aquatic insects (covered vs. uncovered tanks), *Bufo* tadpoles, and the timing of *Hyla* addition (cohort) affected the survival, mean mass at metamorphosis, mean larval period, and mean growth rates of *Hyla andersonii*. We analyzed population (i.e., tank) means for each *Hyla* cohort, rather than individual metamorph values, because the latter were not independent measures of the treatment effects. We treated the timing of *Hyla* introduction as a third factor, called "cohort," which was crossed with the two independently manipulated factors, "aquatic insects" and "*Bufo.*" The choice of a three-factor analysis explicitly focused on *Hyla* cohorts, rather than artificial ponds, as the unit of study. The three-factor analysis also permitted direct comparisons of the responses of two different cohorts to the same initial manipulations of the artificial ponds.

We tested three main null hypotheses: (1) no effect of insects, (2) no effect of *Bufo,* (3) no effect of cohort (early vs. late introduction, confounded with differences among cohorts in initial intraspecific density). Within cohorts, we inferred that competition differed in intensity among treatments if either insects, or *Bufo,* or both reduced *Hyla* mass relative to the controls. Between cohorts we used a conservative criterion to allow for possible effects of reduced intraspecific density on responses measured for the second cohort. For *Hyla* cohort 1 (the May cohort), relative intensities of competition exerted by insects and *Bufo* could be inferred by comparing the reductions in mean mass caused by the respective treatments. For *Hyla* cohort 2, the same comparisons could be used to test for priority effects exerted by (1) insects plus cohort-1 *Hyla,* (2) *Bufo* plus cohort-1 *Hyla,* and (3) insects and *Bufo* plus cohort-1 *Hyla.* Higher order interactions, such as a "cohort × *Bufo*" or "cohort × insect" interaction, would indicate that the effects of *Bufo* tadpoles or insect colonization depended on the responding *Hyla* cohort. This would happen if *Bufo* affected cohort 1 but not cohort 2, or if insects reduced the survival of cohort 2 but not cohort 1. Presentation of univariate ANOVAs of each variable aids the identification of variables contributing to significant multivariate responses, but overall statements about statistical significance rely on the MANOVA.

A two-factor repeated-measures MANOVA tested three hypotheses regarding effects of aquatic insects and *Bufo* on the abundance of chlorophyll *a* in periphyton over time: (1) no effects of insects, (2) no effect of *Bufo,* and (3) no interaction between the effects of insects and *Bufo.* Differences in chlorophyll among treatments initially measured the relative impact of insects and *Bufo* tadpoles on periphyton, and described whether initial effects changed over time. A logarithmic transformation of chlorophyll values before analysis eliminated a correlation between the mean and variance in the untransformed data.

RESULTS

Hyla andersonii: *multivariate results*

A MANOVA indicated that the May and June cohorts differed in their combined responses of survival, larval period, mean mass, and growth rate (see the significant cohort effect in Table 1). The MANOVA also showed that effects of insects and *Bufo* depended on the identity of the responding cohort (see the sig-

TABLE 1. MANOVA of the effects of *Bufo,* insects, and cohort on four growth measures of *Hyla andersonii* tadpoles. The multivariate test criterion, Wilks' λ, also has an exact relation with the *F* statistic that follows it.

	MANOVA			
Source	Wilks' λ	*F*	df	*P*
Cohort	0.02771	105.26	4, 12	.0001
Insects	0.14948	17.07	4, 12	.0001
Cohort × Insects	0.17105	14.54	4, 12	.0001
Bufo	0.31774	6.44	4, 12	.0052
Cohort × *Bufo*	0.34902	5.60	4, 12	.0089
Insects × *Bufo*	0.63423	1.73	4, 12	.2079
Cohort × Insects × *Bufo*	0.56326	2.33	4, 12	.1156

ANOVA: Survival to metamorphosis

Source	df	SS	*F*	*P*†
Cohort	1	3112.93	33.08	.0001
Insects	1	234.30	2.49	.1354
Cohort × Insects	1	243.25	2.58	.1287
Bufo	1	19.66	0.21	.6541
Cohort × *Bufo*	1	47.04	0.50	.4904
Insects × *Bufo*	1	167.68	1.78	.2018
Cohort × Insects × *Bufo*	1	83.23	0.88	.3619
Error	15	1411.56		

ANOVA: Larval period

Source	df	SS	*F*	*P*
Cohort	1	4378.6	76.10	.0001
Insects	1	218.5	3.80	.0703
Cohort × Insects	1	156.8	2.73	.1195
Bufo	1	0.3	0.01	.9376
Cohort × *Bufo*	1	12.2	0.21	.6516
Insects × *Bufo*	1	21.7	0.38	.5479
Cohort × Insects × *Bufo*	1	27.6	0.48	.4988
Error	15	863.0		

ANOVA: Mass at metamorphosis

Source	df	SS	*F*	*P*
Cohort	1	67879.8	34.75	.0001
Insects	1	55902.6	28.62	.0001
Cohort × Insects	1	13203.5	6.76	.0201
Bufo	1	25138.8	12.87	.0027
Cohort × *Bufo*	1	6942.3	3.55	.0789
Insects × *Bufo*	1	2214.8	1.13	.3038
Cohort × Insects × *Bufo*	1	7148.4	3.66	.0750
Error	15	29299.2		

ANOVA: Growth rate

Source	df	SS	*F*	*P*
Cohort	1	382.3	373.05	.0001
Insects	1	75.0	73.26	.0001
Cohort × Insects	1	16.4	16.03	.0012
Bufo	1	25.9	25.35	.0001
Cohort × *Bufo*	1	17.7	17.33	.0008
Insects × *Bufo*	1	5.3	5.27	.0366
Cohort × Insects × *Bufo*	1	4.8	4.78	.0451
Error	15	15.3		

† Probabilities for the univariate tests should be compared against the Bonferroni-adjusted significance level for four variables, which is 0.0127.

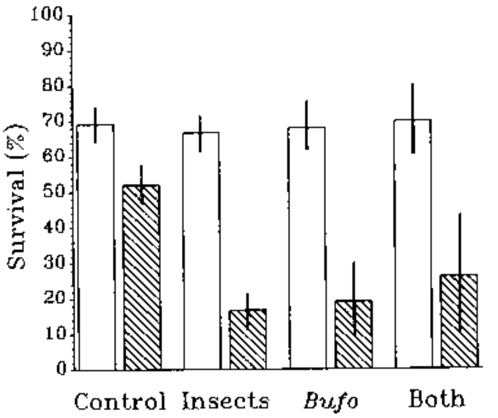


FIG. 1. Survival to metamorphosis for cohorts 1 (open bars) and 2 (hatched bars) of *Hyla* in the four treatments. The treatments were: Control (no *Bufo* tadpoles, no insects), Insects (no *Bufo*, uncovered tank), *Bufo* (*Bufo* tadpoles, no insects), and Both (*Bufo* tadpoles, uncovered tank). Each bar shows the mean of three replicates; vertical lines denote ±1 SE. Data for cohort 1 (May, open bars) are from Morin et al. (1988).

nificant cohort × insects and cohort × *Bufo* interactions in Table 1). The following univariate results identify the variables responsible for these overall treatment effects.

Hyla andersonii: univariate results

Tadpoles introduced in May survived better than those introduced in June (Fig. 1, Table 1). Manipulations of *Bufo* and aquatic insects did not significantly affect the survival of either *Hyla* cohort, even though the June cohort appeared to survive best in ponds without *Bufo* and/or without insects.

TABLE 2. ANOVA and means of estimated daily mortality rates for both cohorts of *Hyla andersonii* in all treatments. N = the sample size (number of experimental populations) for each mean.

Source	df	SS	*F*	*P*
Cohort	1	0.00081677	7.08	.0178
Insects	1	0.00019091	1.65	.2179
Cohort × Insects	1	0.00018638	1.61	.2232
Bufo	1	0.00006483	0.56	.4652
Cohort × *Bufo*	1	0.00009208	0.80	.3859
Insects × *Bufo*	1	0.00004500	0.39	.5418
Cohort × Insects × *Bufo*	1	0.00001793	0.16	.6990
Error	15	0.00173155		

Hyla added to the ponds in June required about twice as much time as the May cohort to complete development (despite the initial low-density advantage of cohort 2; Fig. 2; Table 1). Reduced survival-to-metamorphosis in the June cohort could reflect greater attrition caused by a common daily mortality rate acting over the longer larval period of the June cohort. Estimation of daily mortality rates for each cohort in each tank used the relation

$$N_t = N_0 e^{-mt}$$

to solve for the daily mortality rate, m, where N_t is the number of metamorphosing tadpoles, N_0 is the original number of hatchling tadpoles added to the tank, t is the mean length of the larval period in days, and e is the base of the natural logarithms.

Daily mortality rates differed significantly between cohorts, but remained unaffected by manipulations of *Bufo* tadpoles or aquatic insects (Table 2). The mortality rate for the June cohort ($\bar{X} \pm$ SE = 0.0248 ± 0.0044) averaged about twice that of the May cohort (0.0128 ± 0.0014). Consequently, the reduced survival to metamorphosis of the June cohort was consistent with the combined effects of prolonged larval development and an increased daily risk of mortality.

Within each combination of the original manipulations of *Bufo* tadpoles and aquatic insects, froglets from the June cohort metamorphosed at smaller sizes than froglets from the May cohort (Fig. 3, Table 1).

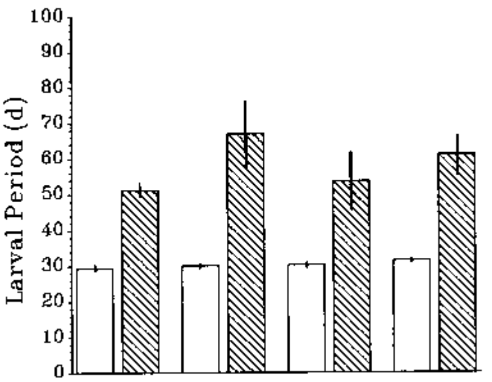


FIG. 2. Larval period of *Hyla* tadpoles from both cohorts. Format as in Fig. 1. Means ± 1 SE are shown. Data for cohort 1 (May, open bars) are from Morin et al. (1988).

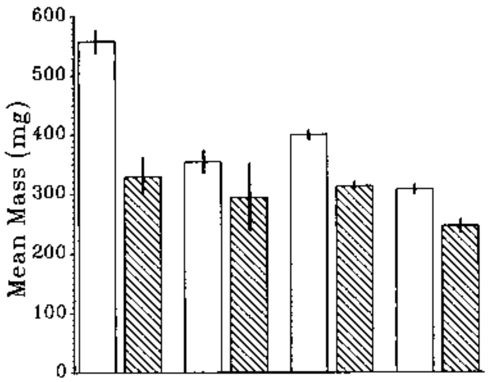


FIG. 3. Mass of froglets emerging from the four experimental treatments. Format as in Fig. 1. Means ± 1 SE are shown. Data for cohort 1 (May, open bars) are from Morin et al. (1988).

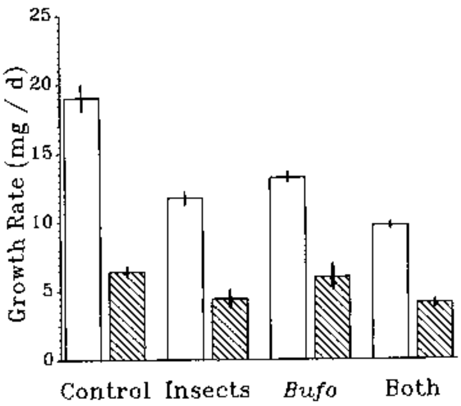


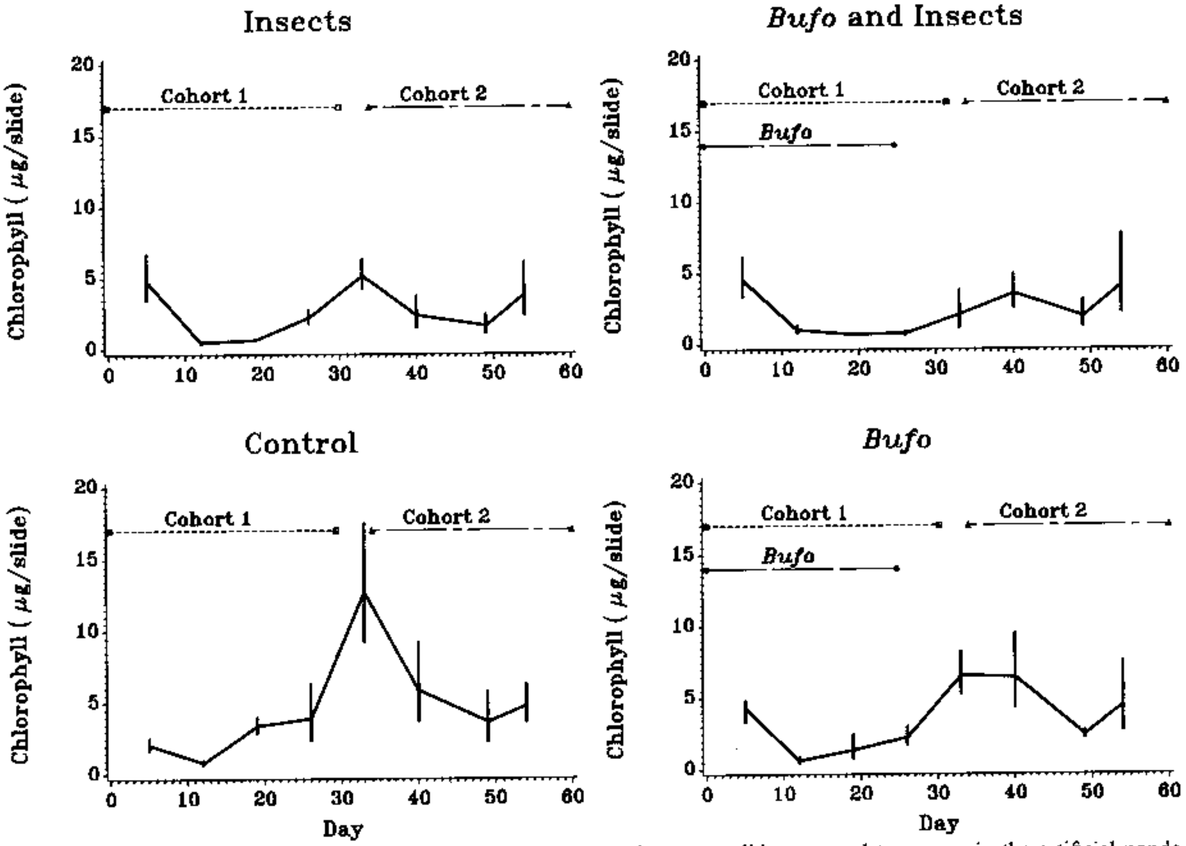
FIG. 4. Growth rates of *Hyla* tadpoles from both cohorts. Format as in Fig. 1. Means ± 1 SE are shown. Data for cohort 1 (May, open bars) are from Morin et al. (1988).

The impact of manipulations of *Bufo* tadpoles and aquatic insects on *Hyla* size at metamorphosis was greater early in community development, as these treatments caused greater reductions in mean mass for the May cohort than for the June cohort.

Tadpoles in the June cohort grew more slowly than those in the May cohort, since the June cohort metamorphosed at smaller sizes after taking twice as long to complete larval development. The impacts of manipulations of *Bufo* tadpoles and insects on *Hyla* growth rates depended on the responding cohort (Fig. 4, Table 1). Responses to *Bufo* and insects were stronger in cohort 1, while *Hyla* tadpoles grew uniformly slowly in cohort 2 and responded little to previous manipulations of *Bufo* and insects.

Periphyton

Periphyton remained less abundant and less variable in abundance over time in tanks containing aquatic insects (Fig. 5, Table 3). Periphyton declined in most tanks soon after the first introduction of *Hyla* tadpoles in May, and remained depressed until the first cohort of tadpoles metamorphosed. Periphyton then increased briefly in all treatments, rebounding from grazing most in controls and least in tanks with insects. Following the second addition of *Hyla* tadpoles in late June, periphyton declined again to levels similar to those seen during the development of the first *Hyla*


Insects

***Bufo* and Insects**

Control

Bufo

FIG. 5. Mass of chlorophyll *a* extracted from periphyton on microscope slides exposed to grazers in the artificial ponds. Means ± 1 SE are shown. Each panel corresponds to one of the original treatment combinations. Dashed lines indicate when *Hyla* tadpoles of cohorts 1 (May) and 2 (June) and *Bufo* tadpoles were present in the tanks. Tadpoles in *Hyla* cohort 1 were added to the tanks on day 0. Means and standard errors are back transformed from $\log_{10}$-transformed data. See Table 3 for statistical analyses. Data for day 19 are from Morin et al. (1988).

TABLE 3. Repeated-measures MANOVA for the $\log_{10}$-transformed amount of chlorophyll *a* per sampled glass slide. The multivariate test criterion, Wilks' λ, also has an exact relation with the *F* statistic that follows it. Data are summarized in Fig. 4.

Source	Wilks' λ	*F*	df	*P*
Time	0.01649	17.03	(7,2)	.0566
Time × *Bufo*	0.02333	11.96	(7,2)	.0793
Time × Insects	0.00955	29.64	(7,2)	.0330
Time × *Bufo* × Insects	0.15630	1.54	(7,2)	.4484

cohort. The significant time × insect interaction in the repeated-measures analysis (Table 3) indicates that abundance of periphyton over time depended on the presence or absence of insects, and reflects the less striking recovery of periphyton abundance in tanks with insects following the metamorphosis of the first *Hyla* cohort.

The screen lids used to exclude insects also shaded the tanks slightly, potentially reducing the abundance of photosynthetic periphyton. However, periphyton was more abundant in covered tanks without insects than in uncovered tanks with insects. This observation suggests that if it had been possible to exclude insects without shading the tanks, even greater abundances of periphyton might appear in unshaded tanks without insects. Consequently, we contend that our approach probably yielded a conservative underestimate of the impact of insects on tadpoles and tadpole resources.

DISCUSSION

Seasonal differences in the performance of Hyla *tadpoles*

The reduced growth rates and prolonged development of tadpoles added to artificial ponds later in the breeding season are consistent with increased per-capita intensities of competition for dwindling resources. We cannot separate the proposed effect of declining resource availability late in community development from other kinds of seasonal deteriorations in resource quality, such as shifts in periphyton species composition to more grazer-resistant forms, or the appearance of grazer-induced defenses. Regardless of the proximal mechanism for the declining performance as the season progressed, it was clearly advantageous for hatchling tadpoles to enter the ponds early in community development.

Our study provides somewhat equivocal evidence for priority effects caused by species arriving early in community development. Because both *Hyla* cohorts exploited all of the artificial ponds, we cannot estimate the contribution of the first *Hyla* cohort to the declining performance of the second. *Bufo* tadpoles were added to only half of the tanks, however, and their impact on both *Hyla* cohorts can be estimated. *Bufo* tadpoles metamorphosed after a larval period of ≈25 d (see Morin et al. 1988), well before the introduction of the second *Hyla* cohort. *Bufo* had a competitive effect on the first *Hyla* cohort, but the second *Hyla* cohort remained unaffected. This result is only superficially consistent with the hypothesis that increasing temporal separation might reduce interspecific competition among tadpoles. The problem is that although June-cohort *Hyla* showed little response to previous use of the ponds by *Bufo*, the second cohort of *Hyla* still performed far worse than members of the May cohort that responded negatively to *Bufo*. We cannot rule out a competitive effect of the first *Hyla* cohort on the second, but other factors may have contributed to the late-season decline in performance. Some of these complicating factors are outlined below.

We did not measure and cannot exclude the importance of seasonal changes in food quality or periphyton species composition that might reduce tadpole growth without appearing as changes in standing crop. The periphyton standing crop later in the season was comparable to or higher than that exploited by early cohorts. Studies of seasonal changes in nutrient availability in natural ponds are needed to determine whether the priority effects observed in our artificial ponds generalize to natural systems. Seale (1980) has suggested that tadpoles depress nutrient availability in natural ponds, and thereby contribute to the failure of later arriving cohorts of tadpoles.

Increased water temperatures later in the summer could reduce the size at metamorphosis of *Hyla andersonii* added to the ponds later in the season. Some anurans metamorphose at smaller sizes in response to increased water temperature during development (Berven et al. 1979, Marian and Pandian 1985, Pandian and Marian 1985). Reductions in size at metamorphosis caused by elevated temperature are usually accompanied by decreases in the time required to complete development (Marian and Pandian 1985), because temperature causes a greater increase in development rate than in growth rate. Instead, our results showed that the decreased size at metamorphosis of *Hyla* later in the summer was accompanied by a doubling of the time required to complete development, a pattern inconsistent with a simple thermal acceleration of differentiation rates.

Other studies of interspecific priority effects have shown that early breeders can reduce the growth of tadpoles of later-breeding species in artificial ponds (Wilbur and Alford 1985, Morin 1987). These studies differed from ours in that they involved at least some temporal overlap between early- and late-breeding species. Priority effects can also become less important if predators reduce tadpole densities and thereby lower demand on dwindling resources later in community development (Morin 1987). The strength of priority effects among rather different kinds of organisms, such as larval dragonflies, also depends on whether predation reduces prey densities to the point where historical effects become trivial (Morin 1984).

The disadvantages of breeding late

Our results suggest that *Hyla andersonii* that hatch late in the breeding season will suffer reduced growth rates, prolonged development, and stunted size at metamorphosis. These disadvantages occurred despite the potential advantage conferred by lower density at introduction compared to the cohort of tadpoles introduced earlier in the same season. Survival was also much more variable and lower in late cohorts than in early cohorts. These results are consistent with the operation of increased per-capita intensities of competition among tadpoles later in the season, despite lower tadpole densities.

The late-June cohort, which did not overlap in time with *Bufo* tadpoles, did not respond to previous differences in the use of ponds by *Bufo,* while the May cohort, which was added to ponds contemporaneously with *Bufo,* responded measurably to competition from *Bufo* (see also Morin et al. 1988). There are several reasons why the June cohort may not have responded to transient *Bufo* treatments early in community development. Nutrient depletion by the entire complement of preceding species (*Hyla, Bufo,* and insects), regardless of species composition, may have severely limited the growth of tadpoles subsequently added to the tanks, leaving little latitude for a measurable competitive effect to appear. Alternatively, increased competition potentially caused by nutrient depletion in *Bufo* and insect treatments may have been offset by lowered survival, lowered *Hyla* densities, and lower demand for resources. Also, the original differences among ponds generated by *Bufo* early in the experiment may have been transient, and may have disappeared by the time that the June cohort arrived. Although these hypotheses cannot be separated with the data presented here, it appears that the transient perturbation of *Bufo* abundance had only transient effects on the community.

Early and late cohorts of *Hyla* tadpoles also responded differently to persistent perturbations involving aquatic insects. Insects reduced *Hyla* growth and mass early in community development, but insects had little apparent additional effect on the stunted tadpoles later in the season. Insects also reduced *Bufo* mean mass (Morin et al. 1988), another effect that occurred early in community development. Because insects reduced tadpole growth rates and resource levels (periphyton) without depressing tadpole survival, we have argued elsewhere that the primary impact of insects on tadpoles involved competition for periphyton (Morin et al. 1988). Many of the insects that colonized the ponds early in community development were either herbivores or were very small predators that could not prey effectively on tadpoles. The abundance of larger predatory insects, specifically the larval odonates that appeared later in community development, varied greatly among artificial ponds. This variation may have obscured any negative effects of insects on the survival of tadpoles added to the ponds later in the summer. It is unclear why persistent differences in the presence or absence of insects only had marked effects on tadpoles early in community development.

Later in community development the daily mortality rates estimated for *Hyla* tadpoles increased significantly. One proposed advantage of early breeding, the avoidance of predatory insects later in seasonal succession (Morin 1987), offers only a partial and problematic explanation for reduced survival. The absence of a strong relation between tadpole mortality and our manipulations of aquatic insects is troubling, given that tadpoles hatched concurrently with or after larval odonates, grew more slowly than earlier in the season, and experienced prolonged exposure to increased numbers of predators. Other studies have documented negative effects of larval odonates on tadpole survival in some settings (Caldwell et al. 1980, Smith 1983, Travis et al. 1985, Banks and Beebee 1988). The additional insect prey that accumulated along with predatory insects in uncovered tanks may have offset the impact of predatory insects on tadpoles in our study.

Why breed late?

The impact on parental fitness of disadvantages experienced by late-season offspring depends on how female frogs distribute their reproductive effort within years. If individual females have different breeding strategies, so that a frog either reproduces early or late in the season, and females can only oviposit once per year, our study suggests that frogs breeding later in the year will produce fewer surviving offspring of lower quality. If frogs can produce multiple egg clutches each year, production of a second later clutch may even be advantageous, as long as it does not detract from the female's future survival and reproduction. Even if relatively few low-quality offspring survive from second breeding efforts late in the season, they would represent additional progeny above and beyond those produced under better conditions early in the breeding season.

Many north temperate frogs regularly produce >1 clutch of eggs per year (Wells 1976, Howard 1978, Perrill and Daniel 1983). We do not know whether *Hyla andersonii* produces multiple clutches. Repeated breeding by females could resolve the apparent paradox posed by the diminished performance of offspring hatched late in the season. We suspect that the production of multiple clutches per female, rather than the existence of distinct early- vs. late-breeding strategies, may explain the continued existence of a prolonged multimodal breeding phenology in some populations of temporary pond amphibians.

Breeding late may not always be disadvantageous. We have only considered the case where ponds fill early in the season and remain full throughout the summer. Ephemeral ponds may dry and refill several times within a year. Early pond drying could eliminate tadpoles produced in early bouts of breeding, while reducing the dual peril of competition and predation from insects, and regenerating nutrients locked up in aquatic organisms that die when ponds dry. If refilled ponds retain water long enough for a second cohort to complete development, late-breeding frogs might even produce more offspring than early breeders. Such second cohorts might do relatively well in newly refilled ponds compared to the declining performance that we saw in our persistent artificial ponds.

Finally, frogs might simply pursue a "better late than never" breeding strategy. If female frogs that mature late in the breeding season also have a low probability of surviving to the next season, it may be better to breed late than to postpone breeding and risk not surviving to breed at all. Given the apparent disadvantages of delayed breeding for offspring, more information about breeding frequency within years, age at first reproduction, and adult survival will be needed to explain the existence of multimodal breeding phenologies in temporary pond amphibians, and in other organisms exploiting seasonal environments.

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