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TEMPORAL OVERLAP, COMPETITION, AND PRIORITY EFFECTS IN LARVAL ANURANS[1]

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Abstract. Interspecific competitors often colonize communities at different times, but few studies have experimentally tested whether the strength of interspecific competition hinges on the order or temporal separation of species' arrivals. We added hatchlings of two sympatric anuran species (*Hyla* [= *Pseudacris*] *crucifer* and *Bufo woodhousii*) to artificial ponds on three different dates to manipulate the order and temporal separation of their arrival. Measurement of the growth and survival of each species in ponds where the second species arrived simultaneously (day 0), or after a delay of 7 or 14 d, indicated whether differences in the history of introductions affected interspecific competition. Other ponds contained *H. crucifer* alone, introduced on the same three dates, or *B. woodhousii* alone, introduced on the first or second date. These provided controls for seasonal differences in performance in the absence of competition from the other anuran species.

Introductions of tadpoles at different times produced small differences in growth rates and larval periods when each anuran species occurred alone. In ponds containing both species, differences in the order and temporal separation of introductions had complex effects on the intensity of interspecific competition. When *Bufo* preceded *Hyla*, *Hyla* had prolonged larval periods and reduced mass and growth. When *Hyla* preceded *Bufo*, it was unaffected by *Bufo*. *Hyla* had no effects on *Bufo*, whether its introduction preceded or followed the introduction of *Bufo*.

Asymmetric priority effects were not easily explained as a simple size-dependent competitive advantage of earlier arrivals. Early arrival increased the competitive impact of *Bufo* on *Hyla*, but failed to generate a competitive effect of *Hyla* on *Bufo*. *Bufo* tadpoles are more active than *Hyla*, and so may consume resources at higher rates that cannot be offset by a temporal advantage. Competition from *Bufo* was strongest when *Hyla* arrived 7 d later, suggesting that *Hyla* arriving 14 d after *Bufo* benefited from a longer period of reduced competition after *Bufo* metamorphosed from the ponds. The natural pattern, where *Hyla* breeds before or simultaneously with *Bufo*, permits *Hyla* to minimize competition from *Bufo*, while *Bufo* suffers no measurable cost from the size advantage obtained by competitively weaker *Hyla* tadpoles. *Bufo* may be prevented from breeding any earlier in the season by physiological constraints acting on eggs or breeding adults.

Key words: asymmetric competition; breeding phenology; Bufo woodhousii; *competition among larval anurans;* Hyla crucifer; *interspecific competition; priority effects; temporal overlap; temporal partitioning.*

INTRODUCTION

Some communities, such as temporary ponds, undergo repeated periods of development as sets of species vie for the use of ephemeral resources or seasonally regenerated habitats. Interspecific interactions within these communities, and the patterns of species composition that result, can depend on the historical details of community development (e.g., Sutherland 1974, Sousa 1979, Dean and Hurd 1980, Robinson and Dickerson 1987). Species arrive at communities in a sequence reflecting interspecific differences in breeding phenology. In turn, interspecific differences in breeding

phenology can vary somewhat among years (Semlitsch 1985, Caldwell 1987). Within years, intraspecific variation in the timing of breeding (e.g., Harris 1980) can also affect the amount of temporal separation among species. Such variation can alter both the order of arrival of species and the temporal separation between the arrivals of different species.

Manipulations of experimental communities can test whether interspecific interactions depend on the order and temporal separation of the arrivals of species. Although differences in breeding phenology are often interpreted as a strategy for reducing the intensity of interspecific interactions (e.g., Crowley and Johnson 1982, Wolda 1987), few experiments have directly tested whether temporal separation affects the strength of interspecies interactions. Similarly, the order of arrival of species during community development is often assumed to be adaptive (MacArthur and Wilson 1967),

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TABLE 1. Breeding phenologies of *Hyla crucifer* and *Bufo woodhousii* in New Jersey Pine Barrens ponds in 1986–1988.*

Year	Species	1st chorus	1st pair	Last pair
1986	*Hyla*	19 March	19 March	30 April
	Bufo	19 April	29 April	2 July
1987	*Hyla*	24 March	26 March	21 April
	Bufo	20 April	20 April	10 May†
1988	*Hyla*	12 March	31 March	6 May
	Bufo	4 April	6 May	23 June

* We visited 5–10 ponds (in which both species breed) every 4–10 d during the breeding season (March–July), and recorded breeding activity. 1st chorus = the first night on which we heard males call, which signals the beginning of the breeding season. Males call on some nights when females do not breed, so we present the dates on which the first and last breeding pairs were found, to better delineate actual breeding periods. Note that the first *H. crucifer* pairs were found at least 2–3 wk before the first *B. woodhousii* pairs within each year.

† In 1987 we did not sample between 10 May and 1 August, and so probably missed any June or July breeding activity.

but manipulations of colonization order are rare (see Drake 1990).

Interspecific differences in breeding phenology may simply reflect individualistic responses by species to a seasonally changing environment. Of course, phenological differences may also be responses to seasonal interactions with other species of competitors or predators. We use the terms "seasonal effects" and "priority effects" to emphasize the distinction between individualistic and interactive causes of phenological differences. "Seasonal effects" refers to direct impacts of seasonally varying abiotic factors on a species or on the resources that the species requires. For example, seasonal variation in the primary production of the algae consumed by herbivorous tadpoles could generate a seasonal effect on tadpole growth or performance. In contrast, "priority effects" refers to interspecific interactions whose outcome depends on the relative or absolute timing of the arrival, breeding, or activity of the interacting species.

Intraspecific differences in the seasonality of breeding can affect reproductive success and ultimately influence the evolution of breeding phenologies (Harris 1980, Morin et al. 1990). Few experiments have attempted to separate the potential contributions of seasonal effects and priority effects to seasonal variation in reproductive success. Seasonal effects are best measured by introducing target species to competitor- and predator-free communities over a range of times corresponding to the natural within-year variation in the breeding season. Priority effects can be measured by varying the order and temporal separation of the arrivals of two or more species.

Experimental studies of seasonal community development clearly support the existence of priority effects among interspecific competitors (e.g., Dean and Hurd 1980, Alford and Wilbur 1985). The exact mechanisms responsible for the priority effects are less clear. Resource preemption before head-to-head competition begins, or the duration of temporal overlap after the arrival of the second species, may both be important. The first species entering the community often retains a size advantage over later arrivals during subsequent periods of temporal overlap. Even when species are of similar size, differences in arrival time can affect the duration of direct head-to-head competition.

If initial size differences or the time available for resource preemption determines the strength of priority effects, the performance of a given species should decline as it is introduced increasingly later than its competitor (Morin 1987, Alford 1989). If competition occurs primarily during temporal overlap, and if there is no size difference or size advantage, a species should perform progressively better as its temporal overlap with competitors decreases (Alford 1989). These mechanisms may also combine to produce intermediate patterns. For example, an organism competing directly against a small competitor during a long period of temporal overlap might not grow as well as the same organism competing against a large competitor during a shorter period of temporal overlap.

We explored the extent to which seasonal effects and/or priority effects acting during larval development could account for the breeding phenology of the anurans *Hyla crucifer* (= *Pseudacris crucifer*, Hedges 1986) and *Bufo woodhousii*. Larvae of both species feed on periphyton, phytoplankton, and detritus. Both species have larval periods of similar duration, and frequently breed in the same ponds in the New Jersey Pine Barrens in early spring (late March through May or June). *H. crucifer* typically begins to breed earlier than *B. woodhousii* (Table 1), perhaps because the adults can be active on colder nights (John-Alder et al. 1988). *H. crucifer* eggs can also develop at lower temperatures than *B. woodhousii* eggs. The result is that *H. crucifer* tadpoles usually hatch and begin feeding well before *B. woodhousii*. Because *Bufo* often begins breeding considerably after the *Hyla* in the same pond, it would be particularly intriguing to reverse the normal order of arrival to test whether the normal order is optimal for both species. Predaceous vertebrates can eliminate priority effects in some communities (Morin 1984, 1987), but we ignore the effects of predators here because *H. crucifer* and *B. woodhousii* often breed in temporary ponds without predatory salamanders or fish.

METHODS

Artificial ponds

We manipulated the order and temporal separation of introductions of hatchling larvae of *Bufo woodhousii* (spelling following Frost 1985; = *B. woodhousei*) and *Hyla crucifer* (hereafter "*Bufo*" and "*Hyla*") into replicated artificial ponds. Artificial ponds (similar to ones described by Morin [1983]) were located in a field at

TABLE 2. Summary of the design of an outdoor tank experiment, showing the time of anuran species introductions (200 hatchlings per species) in different numbered treatments. Early = 5 May, middle = 12 May, late = 19 May, ··· = absent.

	Treatments					
	Single species			Both species		
	No.	*Hyla cructfer*	*Bufo woodhousii*	No.	*Hyla cructfer*	*Bufo woodhousii*
Timing of introductions	1.	Early	···	6.	Early	Early
	2.	Middle	···	7.	Early	Middle
	3.	Late	···	8.	Early	Late
	4.	···	Early	9.	Middle	Early
	5.	···	Middle	10.	Late	Early

Hutcheson Memorial Forest (East Millstone, Somerset County, New Jersey). We created pond communities in 30 galvanized steel cattle-watering tanks, coated inside with epoxy paint. Ponds contained ≈1 m³ of stream water (pumped from nearby Spooky Brook through an 88-μm mesh plankton net), 600 g of dry grassy litter, 50 g of Purina Trout Chow, six rooted stems of *Elodea*, and 400 mL of a mixed-plankton inoculum (plankton were collected from a pond in Greenwood Forest Wildlife Management Area, Ocean County, New Jersey, and from other artificial ponds). The grassy litter provided an ≈3-cm layer of cover on the tank bottoms, which is similar to litter levels that we observe in natural ponds in the New Jersey Pine Barrens. Trout Chow supplied nutrients that would normally be supplied by decaying plant and animal material and from ground runoff during rainstorms. This method provided conditions for tadpole growth that were at least as good as conditions in natural ponds. In our collections from natural ponds, recently metamorphosed *Bufo woodhousii* ranged in mass from 42 through 260 mg, and *H. crucifer* metamorphs ranged from 39 through 272 mg. Mean masses of metamorphs in our experiment were at the high end of this range (see Table 3). We therefore expect that any competitive effects found in our experiment will be a conservative estimate of competition in natural communities, where nutrients are apparently more limiting.

We added water and litter on 2 May 1989, plankton and 25 g of the Trout Chow on 3 May, *Elodea* on 6 May, and the remaining 25 g of Trout Chow on 2 June.

Artificial ponds were uncovered for much of the experiment to allow natural colonization by insects (such as mosquitoes and chironomids). A variety of insects occur in natural temporary ponds and can have substantial competitive effects on larval anurans (Morin et al. 1988). From 20 to 25 May we covered all tanks with screen lids to prevent the local population of gray treefrogs (*Hyla versicolor*) from ovipositing in the tanks. Gray treefrogs breed in very few Pine Barrens ponds (only those on the edges of the Pine Barrens), so we excluded them from this study. From 26 May to 6 June we removed tank lids during the day and replaced them at night to allow some colonization by diurnal insects while excluding nocturnally breeding frogs. All tanks

remained continuously covered after 6 June to retain metamorphosing anurans.

Tadpole additions

We added hatchling tadpoles to subsets of artificial ponds on three dates: 5 May ("early"), 12 May ("middle"), and 19 May ("late"). Densities used (200 hatchlings per species per tank) were within the observed natural range for these species. The full experimental design consisted of five single-species treatments and five two-species treatments, each replicated three times (Table 2). The single-species treatments (hereafter "controls") were early, middle, or late introductions of *Hyla*, and early or middle introductions of *Bufo*. We did not include a late introduction of *Bufo* because of a shortage of tanks. The two-species treatments were both species arriving early, each species arriving early while the other arrived 7 d (middle) or 14 d (late) later (Table 2).

The introductions listed above allowed us to measure the effects of early arriving tadpoles of each species on tadpoles of the other species that arrived either simultaneously (early–early treatment), or 7–14 d later in community development. Two-species treatments where *Hyla* arrived early represent different amounts of temporal separation seen in the natural breeding phenology. Two-species treatments where *Bufo* arrived before *Hyla* gave us an opportunity to examine whether the order of arrival of species not usually seen in nature affected either species. Pronounced negative effects of this contrived phenology on either species might indicate why it is not usually observed in nature.

Introductions of single anuran species into tanks at different times allowed measurement of short-term seasonal differences in tadpole performance that were not caused by priority effects exerted by other anuran species. Such seasonal effects on growth or survival could imply that breeding phenologies differ because each species performs best at different times of the year. The maintenance of different breeding times to minimize interspecific competition only becomes plausible if the two species compete less when their introductions are temporally separated, and if differences in performance that occur in the absence of the interspecific competitor cannot account for the observed phenology.

All introductions occurred within the natural range of breeding dates for both species. We used a mixture of approximately equal numbers of hatchlings from at least four different clutches per species for all introductions so that animals introduced on different dates had a mixture of genetic backgrounds. Clutch numbers per introduction were 17 (early and middle *Hyla*), 13 (late *Hyla*), 15 (early *Bufo*), 6 (middle *Bufo*), and 4 (late *Bufo*). Hatchlings of both species are of similar size.

We were able to manipulate the introduction times of hatchlings both by collecting breeding adults at different times and by refrigerating eggs to slow development and delay hatching. We collected amplectant pairs of frogs from several temporary ponds in the New Jersey Pine Barrens (Ocean County, New Jersey). Pairs oviposited in water-filled, covered dishpans, and the resulting eggs were aerated until they hatched. Cooling one-half of the eggs from several clutches delayed their development to yield new hatchlings for later introductions. We used eggs laid on 1 May for the early and middle *Hyla* additions, and for the early *Bufo* addition. Eggs for the late *Hyla* addition were laid on 6 May, and the eggs for the middle and late *Bufo* additions were laid on 7 May.

Hatchlings used for the early introductions of both species and for the middle *Bufo* introduction came from unrefrigerated eggs. Hatchlings used for the middle addition of *Hyla* and for the late additions of both species came from refrigerated eggs. *Bufo* eggs developed slowed at 15°C until they were needed, when they were returned to room temperature to hatch. *Hyla* eggs were held in a 5°C cold room until needed (*Hyla* eggs developed too rapidly at 15°C to use in our experimental design). Hatchlings from refrigerated eggs looked normal and behaved similarly to their unrefrigerated siblings. Volpe (1953) reported normal development in *Bufo fowleri* (= *woodhousii*) at 15°C.

The experiment ran until the last tadpoles metamorphosed on 18 July. We collected metamorphosing frogs daily. Metamorphs remained unfed for 1–2 d in the laboratory until tail resorption was complete. We then weighed each frog to the nearest milligram, and recorded its date of collection. From these data we determined survival to metamorphosis, mean mass at metamorphosis, mean larval period, and mean growth rate of each species in each tank. Growth rate was estimated by dividing mean mass by mean larval period. We released the frogs after their measurement.

Statistical Analysis

Multivariate analyses of variance (MANOVA) tested whether the survival, mass at metamorphosis, larval period, and growth rate of each species exhibited seasonal variation in single-species settings or priority effects in mixed-species treatments. The MANOVA, which corrects significance levels for tests on multiple, potentially correlated, variables, is an appropriate statistical test given our a priori interest in several variables (see Morin [1983] for a detailed justification of the approach). For example, mean mass is often negatively correlated with survival in larval anurans (e.g., Morin 1986). We analyzed means for each tank because individuals within each population were not statistically independent. We angularly transformed survival and log-transformed mass before analysis. Treatment means and standard deviations for all variables are listed in Table 3.

Where MANOVAs were significant ($P < .05$), we used Bonferroni tests to determine which variables differed among pairs of treatments. Any differences discussed below were significant at $P < .05$ in both the MANOVA and the Bonferroni test, unless stated otherwise. We sometimes discuss trends when the overall MANOVA was nonsignificant ($P > .05$) but the analyses of variance (ANOVAs) for single response variables indicated differences between treatments. Below, we outline each null hypothesis and corresponding analysis.

1. *Seasonal effects.* —Date of introduction does not affect larval performance in the absence of anuran interspecific competitors. *Analysis:* Separate MANOVAs for each species on the single-species controls tested for seasonal effects (Table 4).

2. *Priority effects of early-arriving* Bufo *on* Hyla.—
(a) Early-arriving *Bufo* do not affect *Hyla*.

(b) Effects of early-arriving *Bufo* on *Hyla* do not depend on temporal separation. *Analysis:* To test for effects of early *Bufo* on *Hyla*, we used a two-factor MANOVA with the presence or absence of early *Bufo* and the date of *Hyla* introduction as factors (Table 5a).

(c) The strength of the effect of early *Bufo* on *Hyla* does not change with *Hyla* time of arrival. An interaction between *Bufo* presence and *Hyla* timing in the two-factor analysis indicated that the strength of the effect of *Bufo* on *Hyla* depended on *Hyla* arrival time. *Analysis:* To discover whether early *Bufo* had a stronger effect on early, middle, or late *Hyla*, we performed an additional MANOVA on the differences between *Hyla* controls and *Bufo* early treatments for each *Hyla* arrival time (Table 5b). We corrected each variable for possible seasonal effects by subtracting the mean of the appropriate controls from each two-species competition treatment, and then we performed a MANOVA on these differences. For example, we estimated the strength of the effect of *Bufo* on the mass of early *Hyla* by first subtracting the mean of the three *Hyla* early controls from each of the three *Hyla* early–*Bufo* early replicates, and then analyzing the differences in a MANOVA.

3. *Priority effects of early-arriving* Hyla *on* Bufo.—
(a) Early-arriving *Hyla* do not affect *Bufo*. *Analysis:* Lack of a late *Bufo* control precluded use of a two-factor MANOVA of the effects of *Hyla* presence/absence and the date of *Bufo* introduction. Instead, we tested whether early-arriving *Hyla* affected *Bufo* with a MANOVA of treatments 4–8 (both *Bufo* controls,

TABLE 3. Results of an outdoor tank experiment in New Jersey, USA, in which the arrival dates of hatchlings of two anuran species were artificially manipulated. Treatment numbers match those shown in Table 2. A = absent, E = added 5 May, M = added 12 May, L = added 19 May. Survival was angularly transformed.

Treatment			Mass (mg)	Larval period (d)	Growth (mg/d)	Survival (%)
No.	Hyla	Bufo	Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD
			a. Bufo woodhousii			
4.	A	E	263.76 ± 58.96	40.68 ± 2.07	6.53 ± 1.69	43.34 ± 23.88
5.	A	M	280.03 ± 31.71	36.96 ± 1.48	7.58 ± 0.91	54.79 ± 10.82
6.	E	E	217.71 ± 27.44	41.77 ± 0.72	5.20 ± 0.56	49.76 ± 14.50
7.	E	M	220.94 ± 38.39	41.00 ± 2.75	5.43 ± 1.23	50.42 ± 9.29
8.	E	L	295.59 ± 23.23	34.02 ± 0.75	8.68 ± 0.51	33.26 ± 9.99
9.	M	E	192.81 ± 16.72	42.44 ± 0.92	4.54 ± 0.35	35.21 ± 14.99
10.	L	E	259.94 ± 16.27	41.51 ± 1.20	6.25 ± 0.21	40.54 ± 4.31
			b. Hyla crucifer			
1.	E	A	246.84 ± 17.30	45.91 ± 3.51	5.41 ± 0.75	51.07 ± 8.97
2.	M	A	269.16 ± 12.94	39.64 ± 0.62	6.79 ± 0.42	52.12 ± 7.51
3.	L	A	261.46 ± 10.34	36.92 ± 1.50	7.08 ± 0.32	50.89 ± 7.54
6.	E	E	190.02 ± 16.93	45.30 ± 0.89	4.19 ± 0.42	57.01 ± 8.56
7.	E	M	209.63 ± 11.31	45.66 ± 2.13	4.59 ± 0.33	42.98 ± 8.23
8.	E	L	228.21 ± 24.60	44.18 ± 1.31	5.15 ± 0.42	52.62 ± 8.76
9.	M	E	157.71 ± 9.15	45.10 ± 2.17	3.50 ± 0.37	50.25 ± 8.32
10.	L	E	226.73 ± 35.49	43.50 ± 0.73	5.20 ± 0.75	42.67 ± 12.78

plus Hyla arriving early with Bufo early, middle, or late), with the five treatments considered as different levels of a single factor (Table 6a).

(b) Effects of early-arriving Hyla on Bufo do not depend on temporal separation. Analysis: A separate MANOVA tested whether early-arriving Hyla had an overall effect on Bufo using early and middle Bufo controls and early and middle Bufo treatments with early Hyla (Table 6b).

4. Later-arriving competitors have no effect on early-arriving species. —Analysis: We also tested whether early-, middle-, and late-arriving tadpoles of each species had any effects on early arrivals of the other species, using single-factor MANOVAs with presence of the later-arriving competitor as the single factor (Tables 5c and 6c).

RESULTS

Seasonal effects

The date of introduction did not affect the overall responses of Hyla crucifer in ponds without Bufo woodhousii, although larval periods decreased and growth rates increased for animals introduced progressively later in the season. While the overall analysis showed no significant effects of the date of introduction on Hyla

in treatments without Bufo (Tables 2 and 4a), the ANOVA for larval period within the MANOVA showed a seasonal effect ($F = 12.73$, df = 2,6, $P < .007$), and a Bonferroni-adjusted t test showed that larval periods of animals from the earliest introduction were 7–8 d longer than for later introductions. This was also reflected in a trend toward lower growth rate in the early group (ANOVA $F = 8.38$, df = 2,6, $P < .02$).

Seasonal effects on Bufo were also weak or absent. Bufo showed no overall differences in performance between early and middle arrival times (Tables 2 and 4b), although there was a trend toward a longer larval period in the early group (ANOVA $F = 6.41$, df = 1,4, $P < .07$). Even without the late Bufo control, the short larval periods of late Bufo in treatments with early Hyla indicate a continuing trend toward reduced larval periods for animals introduced later in the season.

Effects of Bufo on Hyla

Effects of early Bufo on Hyla. —Early Bufo depressed the mean mass and growth rate of Hyla, and the magnitude of this competitive effect depended on when Hyla was introduced (Tables 2 and 5a). Overall, Hyla interacting with early Bufo weighed less and had longer larval periods than Hyla in controls. These effects combined to yield the lower growth rates of Hyla in treat-

TABLE 4. Summary of MANOVAs for seasonal effects (effects of date of introduction of anuran larvae to outdoor tanks) occurring in the absence of interspecific competitors. Variables = survival, mass, larval period, and growth rate. Treatment numbers are from Table 2.

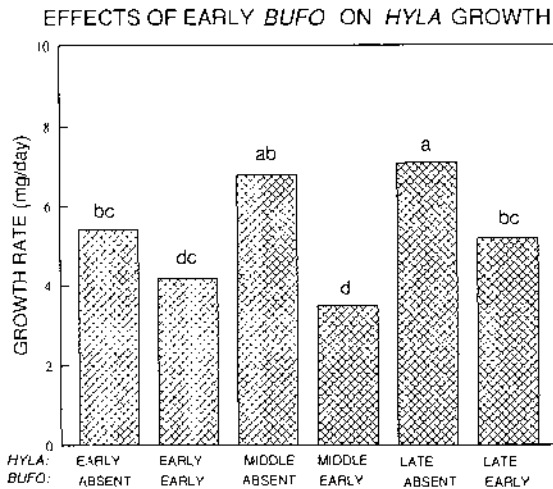| Test	Treatment no.	Source of variation	Numerator df	Denominator df	Wilks' Lambda	F	P
a. Hyla timing	1, 2, 3	Timing	8	6	0.068354	2.118	.1879
b. Bufo timing	4, 5	Timing	4	1	0.173985	1.186	.5894

EFFECTS OF EARLY *BUFO* ON *HYLA* GROWTH

FIG. 1. Effects of early-arriving *Bufo woodhousii* on *Hyla crucifer* growth in an outdoor tank experiment in New Jersey, USA, in which the arrival dates of hatchlings of these two anuran species were artificially manipulated. Letters above bars indicate whether treatments showed growth-rate differences in Bonferroni-adjusted *t* tests. Bars with the same letters above them are not significantly different.

ments with *Bufo* (Fig. 1, Table 3). Survival was variable, and did not differ significantly among treatments.

The strength of competition (e.g., reduced growth) caused by *Bufo* depended on when *Hyla* was introduced (Tables 2 and 4a and b). When both species arrived early, effects of *Bufo* on *Hyla* mass and growth rate were negative, but nonsignificant. Early *Bufo* had little effect on the larval period of early *Hyla*, but increased *Hyla* larval periods by 5–6 d in both the middle and late *Hyla* groups. *Hyla* that arrived 7 or 14 d after *Bufo* displayed reduced mass and/or growth rates relative to controls. When *Hyla* arrived 7 and 14 d after *Bufo*, *Bufo* correspondingly reduced *Hyla* mass by 111 mg and 34 mg, respectively.

Effects of early, middle, and late Bufo *on early* Hyla.— *Bufo* introduced 0, 7, and 14 d after *Hyla* had negative effects of decreasing strength on *Hyla* mass (ANOVA $F = 5.30$, df = 3,8, $P = .0264$). *Bufo* introduced 7 and 14 d after *Hyla* had no overall effect on *Hyla* mass

(Table 5c). In general, the negative effects of *Bufo* on *Hyla* were reduced when *Hyla* entered the ponds before or simultaneously with *Bufo*.

Priority effects of Hyla on Bufo

Effects of early Hyla *on* Bufo.—*Bufo* performance differed among treatments (Table 6a), but Bonferroni tests showed that all significant differences were between the early *Hyla*–late *Bufo* treatment (for which we lacked a late *Bufo* without *Hyla* seasonal control) and others. In tanks with early *Hyla*, late *Bufo* showed a higher mean mass and growth rate than early- or middle-arriving *Bufo* (Fig. 2). This result is consistent with both temporal resource partitioning and seasonal habitat improvement unrelated to competition, and we cannot judge the relative importance of these mechanisms without the late *Bufo* control. There were no significant differences in survival, which varied greatly among replicates.

Early-arriving *Hyla* showed only a trend toward an overall competitive effect on *Bufo* when the *Bufo* late treatment was excluded from the analysis (Table 6b). *Bufo* mass and growth rates tended to be lower in treatments with *Hyla* than in controls.

Effects of early, middle, and late Hyla *on early* Bufo.— *Hyla* did not significantly affect *Bufo* when *Hyla* entered the communities simultaneously, or 7 or 14 d after *Bufo* (Table 6c).

DISCUSSION

Interspecific competition and the breeding phenology

Hyla crucifer usually breeds before *Bufo woodhousii*, but we did not observe interspecific differences in seasonal optima for larval performance in the absence of interspecific competition (strictly seasonal effects) that could readily account for this natural phenology. Several measures of the performance of *Hyla* and *Bufo* barely responded to a 14-d range of introduction times when each species developed in the absence of the other. If anything, the tendency for both species to develop more slowly when added to the ponds on the earliest date suggests that both species could benefit

TABLE 5. Summary of MANOVAs for effects of *Bufo woodhousii* on *Hyla crucifer* in an outdoor tank experiment in which the arrival dates of anuran hatchlings were artificially manipulated. Variables = survival, mass, larval period, and growth rate. Treatment numbers are from Table 2.

Test	Treatment no.	Source of variation	Numerator df	Denominator df	Wilks' Lambda	F	P
a. Effects of *Hyla* timing and early *Bufo* on *Hyla*	1, 2, 3, 6, 9, 10	Timing	8	18	0.068346	6.357	.0006
		Bufo	4	9	0.131006	14.925	.0005
		Timing × *Bufo*	8	18	0.097239	4.965	.0023
b. Seasonal differences between *Bufo* early and *Hyla* controls	6 − 1, 9 − 2, 10 − 3	Timing	8	6	0.000342	39.817	.0001
c. Effects of early, middle, and late *Bufo* on early *Hyla*	1, 6, 7, 8	*Bufo*	12	13.5	0.119717	1.387	.2799

TABLE 6. Summary of MANOVAs for effects of *Hyla crucifer* on *Bufo woodhousii* in an outdoor tank experiment in which the arrival dates of anuran hatchlings were artificially manipulated. Variables = survival, mass, larval period, and growth rate. Treatment numbers are from Table 2.

Test	Treatment no.	Source of variation	Numerator df	Denominator df	Wilks' Lambda	F	P
a. Effects of *Bufo* timing and early *Hyla* on *Bufo*	4, 5, 6, 7, 8	Treatment	16	22	0.043184	2.474	.0249
b. Overall effect of early *Hyla* on *Bufo*	4, 5, 6, 7	*Hyla*	4	5	0.355788	2.263	.1971
		Bufo timing	4	5	0.476615	1.373	.3620
		Interaction	4	5	0.699866	0.536	.7172
c. Effects of early, middle, and late *Hyla* on early *Bufo*	4, 6, 9, 10	*Hyla*	12	13.5	0.123214	1.359	.2917

from breeding later, since both should then develop faster. The prolonged development of larvae early in the breeding season could result from direct negative effects of low temperature on growth (Berven et al. 1979), or could reflect potential effects of low temperatures on algal productivity. It is difficult to attribute the observed phenological differences between *H. crucifer* and *B. woodhousii* to the use of seasonal resources that appear at different times, since both species responded similarly to our manipulations of breeding phenology.

The consequences of altering the order of species introductions offer more insight into possible reasons for the natural breeding phenology. *Hyla* and *Bufo* did not compete when *Hyla* preceded *Bufo*. However, *Bufo* had a clear competitive effect on *Hyla* when it preceded *Hyla*. This pattern suggests that *Hyla* can minimize competition with *Bufo* by breeding earlier, although it may suffer some cost in prolonged development by doing so. In contrast *Bufo* gains nothing by breeding any earlier in the season, since it is largely unaffected by *Hyla*. Other factors, including thermal constraints, may oppose earlier breeding by *Bufo*. We observed that *B. woodhousii* eggs incubated in a 5°C cold room died, while *H. crucifer* eggs raised under the same conditions developed slowly by normally. Others have shown that *Bufo woodhousii* eggs developed abnormally or die at temperatures below 10°C (Volpe 1953).

Although we have emphasized the potential role of larval ecology in shaping the observed breeding phenology, other factors, including thermal constraints on adult locomotion, may be important. Adult *Hyla crucifer* have exceptionally broad temperature tolerances (John-Alder et al. 1988), and their unusual tolerance for low temperatures may offset the poor competitive ability of larvae (see Morin 1983, Morin and Johnson 1988) by permitting breeding to occur well before the arrival of less eurythermal species that are otherwise competitively superior.

The optimal breeding phenology for most species probably reflects an interplay among several abiotic and biotic factors (e.g., Miller 1987, Evans et al. 1989). Species using temperate, ephemeral ponds should breed as early as possible, so that larvae have the longest

possible period in which to complete development. For many amphibian species this time will occur shortly after rain or snowmelt fills ponds, as long as temperature and other abiotic factors are within the physiological limits of the adults, eggs, and larvae. Amphibians that breed too early may risk loss of their entire clutch through cold damage, or may themselves be killed by low temperatures (Harris 1980). Breeding soon after ponds fill ensures that the competitors and predators encountered by hatchling amphibians are small in size and low in abundance.

Priority effects, temporal separation, and the intensity of competition

Our results suggest that asymmetric competition between *Hyla* and *Bufo*, and the priority effects resulting from their different orders of introduction, are probably not a simple result of size-dependent advantages (e.g., Wilbur 1984, Morin and Johnson 1988) or pre-emption of resources by early arrivals (Wilbur and Alford 1985, Morin 1987). A 14-d growth advantage,
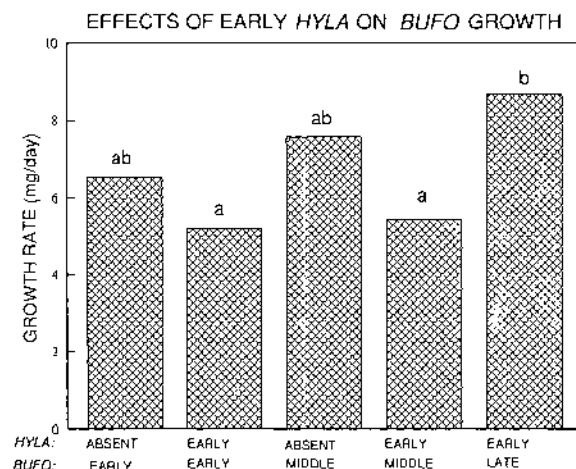

FIG. 2. Effects of early-arriving *Hyla crucifer* on *Bufo woodhousii* growth in outdoor tanks when the arrival dates of anuran hatchlings had been experimentally manipulated. Letters above bars indicate whether treatments showed growth rate differences in Bonferroni-adjusted *t* tests. Bars with the same letters above them are not significantly different.

amounting to nearly 25% of its typical larval period, did not make *Hyla* a significant competitor of *Bufo*. In contrast, a similar initial growth advantage rendered *Bufo* tadpoles even stronger competitors of *Hyla*. Interspecific differences in the ability to parlay an initial period of competitor-free growth into enhanced competitive effects on other species may depend on interspecific differences in behavior. High activity levels have been linked to competitive ability in larval anurans (Morin 1983, Woodward 1983), and *Bufo woodhousii* tadpoles are much more active than *Hyla crucifer* tadpoles (Lawler 1989). We assume that *Bufo* introduced into ponds after *Hyla* interacted with larger but relatively inactive *Hyla* tadpoles, while *Hyla* introduced into ponds after *Bufo* interacted with larger and actively foraging *Bufo* tadpoles. Large, active *Bufo* tadpoles might have a proportionally greater impact on shared resources than equally large, sedentary *Hyla*, if high rates of resource use are correlated with high activity levels. We cannot exclude the possibility that these interactions arise from differences in interference unrelated to resource use, although there is little evidence for interference among tadpoles under semi-natural conditions (Morin and Johnson 1988, Petranka 1989).

The amount of temporal separation between the introductions of *Hyla* and *Bufo* influenced the intensity of the interactions. The competitive impact of *Bufo* on *Hyla* (measured by mass at metamorphosis) decreased as the temporal separation of their respective introductions increased, in ponds where *Hyla* tadpoles introduced early in community development interacted with *Bufo* introduced at the same time or later. Interactions between *Bufo* tadpoles introduced early in community development and *Hyla* introduced at the same time or later were more complex. The competitive impact of *Bufo* on *Hyla* was stronger for *Hyla* added 7 d after *Bufo* than for *Hyla* added either simultaneously with *Bufo* or 14 d after *Bufo*. The apparent nonlinear relation between the intensity of competition experienced by *Hyla* and the amount of temporal separation between competitor introductions could reflect the combined impact of different size advantages of early *Bufo* acting over larval periods that overlapped for different amounts of time. When *Hyla* were introduced 1 wk after *Bufo*, larval periods overlapped an average of 35.4 d, while *Hyla* introduced 2 wk later overlapped with early *Bufo* by only 27.5 d.

Bufo tadpoles may depress phytoplankton and periphyton abundances (Morin et al. 1990), and these resources probably recover to some extent after tadpoles metamorphose. Periphyton abundance begins to recover soon after tadpoles metamorphose from similar artificial pond systems, but complete recovery of this resource takes several days (Morin and Johnson 1988, Morin et al. 1990). Priority effects might linger until algae recover from grazing. This delay in resource recovery may explain why *Hyla* tadpoles that arrive 2

wk after *Bufo* metamorphosis grow larger than *Hyla* that arrive only 1 wk after it, since the later arrivals enjoyed an average of 6.3 more days in the ponds without larger *Bufo*. During this final period of growth after *Bufo* have left, resource levels could increase further from inputs of nutrients from rainfall (Cole and Fisher 1979, Seale 1980).

Although the order and timing of species introductions affected competition between *Bufo* and *Hyla*, the resulting priority effects were not strong enough to alter community composition (as measured by the survival of either species). Our results should not be construed as evidence for assembly rules or alternate community states. The relatively subtle differences in growth, larval period, and mass at metamorphosis that we observed could eventually translate into differences in community composition, but much more research is needed to demonstrate that this actually occurs. Instead, these differences could influence the evolution of competitive ability or breeding phenology so that neither competitor is excluded from the community.

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