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COMPETITION, pH, AND THE ECOLOGY OF LARVAL *HYLA ANDERSONII*[1]

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Abstract. I investigated the effects of an abiotic factor, pH, and a biotic factor, interspecific competition, on breeding success in a low-pH tolerant anuran, *Hyla andersonii.* I tested whether low pH would indirectly facilitate *H. andersonii* by lessening the impact of competition from two less acid-tolerant species. I also tested whether the competitive effect of an allotopic, closely related species (*Hyla versicolor*) would be greater than that of a syntopic, more distantly related species (*Rana sphenocephala*). I exposed *H. andersonii* tadpoles to two levels of pH (3.9, ambient) and three levels of competition (*H. versicolor, R. sphenocephala,* and none). Reduced pH had no direct effect on any of the species and did not influence the outcome of interspecific competition. Competition from *R. sphenocephala* decreased survival and mass of *H. andersonii,* whereas competition from *H. versicolor* only decreased mass, without affecting survival of *H. andersonii.* These results suggest that some other correlate of low pH in natural ponds limits *H. andersonii* to acidic ponds. Further, the assumptions that co-occurrence or level of relatedness can be used as a gauge of competitive strength are shown to be unreliable.

Key words: acidity; amphibians; competition; distribution; pH.

INTRODUCTION

Each species has a set of tolerances to physical conditions that determines its potential range in the absence of other organisms or barriers to dispersal. Acidity is one important factor limiting species' distributions (Gosner and Black 1957, Johnson 1967, Bell 1971, Dunson and Martin 1973, Sutcliffe and Carrick 1973, Dunson et al. 1977, Havas and Hutchinson 1982, Townsend et al. 1983, Leuven et al. 1986, Rosemond et al. 1992, Sadinski and Dunson 1992). Biotic factors, such as competition, impose further limits on distributions (Connell 1983, Schoener 1983, Gurevitch et al. 1992). Many authors have attempted to predict the strength of competition from characteristics of the species involved. Specifically, competition has been proposed to be strongest between related species and between species that co-occur (Darwin 1958, Hairston 1949, 1951, 1980, Terborgh 1971, Schoener 1983). Abiotic factors, such as pH, and biotic factors, such as competition, may also interact to yield patterns not predicted from responses to either set of factors alone (Tansley 1917, Park 1954, Jaeger 1971, Gonzalez and Dunson 1989, 1991, Dunson and Travis 1991, Warner et al. 1991, 1993).

I examined the effect of pH and competition with two anurans, one an allotopic congener and one a less closely related syntopic species, on *Hyla andersonii,* the Pine Barrens treefrog. *H. andersonii* is limited to areas with acidic waters such as the Pine Barrens of New Jersey and the Sandhills of North Carolina and is listed as an endangered species in New Jersey (Gosner and Black 1957, Freda and Dunson 1986, Conant and Collins 1992). *H. andersonii* reproduces most successfully in acidic waters, a conclusion supported by field surveys of breeding choruses, tadpoles, and metamorphs, as well as laboratory toxicity studies (Gosner and Black 1957, Freda and Morin 1984, Freda and Dunson 1986, Pehek 1994). The distribution of *H. andersonii* could be a direct result of a requirement for an acidic larval habitat, or acidity could indirectly create a refuge from competition with other, less acid-tolerant, anuran tadpoles.

I proposed that the distribution of *H. andersonii* is caused by an interaction between pH and competition. Nearly all anurans found within or adjacent to the New Jersey Pine Barrens are less acid tolerant than *H. andersonii* in laboratory assays. I predicted that tadpoles of *H. versicolor* and *R. sphenocephala* would outcompete tadpoles of *H. andersonii* unless the pond environment was acidic enough to slow growth or otherwise interfere with the competitive ability of competitor tadpoles. Both competitor species used in this experiment are reported to be less acid-tolerant than *H. andersonii,* which could allow *H. andersonii* to find a potential refuge from competition in very acidic ponds (Gosner and Black 1957, Freda 1986). I further predicted that *H. versicolor* would have a stronger competitive effect on *H. andersonii* than would *R. sphenocephala,* based on the assumptions that competition is strongest between related species, and that the local distributions of strongly competing species will not overlap. *R. sphenocephala,* the southern leopard frog, is only distantly related to *H. andersonii,* but co-occurs with *H. andersonii* on a local scale. Ongoing competition with

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R. sphenocephala could contribute to the patchy distribution of *H. andersonii* within the New Jersey Pine Barrens. *Hyla versicolor*, the gray treefrog, is the closest living relative of *H. andersonii* (Hedges 1986), but does not co-occur with *H. andersonii* on a local scale. Past competition with *H. versicolor* could have prevented the spread of *H. andersonii* outside its limited range. Finally, I predicted that low pH would decrease the competitive effect of *H. versicolor* on *H. andersonii* more than it would decrease the competitive effect of *R. sphenocephala* on *H. andersonii*. I based this prediction on results of laboratory assays, which have found that *H. versicolor* is less acid-tolerant than is *R. sphenocephala* (Freda 1986).

To test the effects of pH on larval *H. andersonii, H. versicolor*, and *R. sphenocephala*, I exposed tadpoles to two levels of pH within the range found in natural ponds (Pehek 1994). To test whether co-occurrence and relatedness may be used to predict the strength of competition, I exposed *H. andersonii* tadpoles to competition with the distantly related, syntopic competitor, *Rana sphenocephala*, or the closely related, allotopic competitor, *Hyla versicolor*. I did not test the competitive effect of *H. andersonii* on itself or the other two species due to the limited number of experimental ponds available.

I tested five hypotheses related to the predictions stated above: (1) Low pH decreases the survival or larval performance (mass at metamorphosis, growth index and/or length of larval period) of *H. andersonii, Hyla versicolor* and/or *Rana sphenocephala*. (2) Competition by *H. versicolor* or *R. sphenocephala* decreases the survival or larval performance of *H. andersonii*. (3) Low pH decreases the competitive effect of *H. versicolor* or *R. sphenocephala* on *H. andersonii*. (4) *H. versicolor* (a closely related, allotopic species) has a stronger effect on the survival or larval performance of *H. andersonii* than does *R. sphenocephala* (a more distantly related, syntopic species). And finally, (5) Low pH would decrease the effect of competition from the allotopic competitor, *H. versicolor*, on *H. andersonii*, but would not alter the effect of competition from the syntopic competitor, *R. sphenocephala*, on *H. andersonii*.

METHODS

Experimental design

I used a 2 × 3 factorial design, crossing two levels of pH (3.9 and ambient [mean = 6.25]) with three levels of interspecific competition (none, *Hyla versicolor* only, *Rana sphenocephala* only). I used the experimental ponds at ambient (unadjusted) pH with no interspecific competition as controls. Densities of tadpoles (200 tadpoles/1000 L for *H. andersonii* alone and 400 tadpoles/1000 L when competitors were present) are within the range of densities found in natural ponds in the New Jersey Pine Barrens (Pehek 1994). The pH of ambient tanks ranged from 5.90 to 8.40 with a mean of 6.25. This is comparable to the range and mean of pH found in ambient tanks from a previous year's experiment (5.25–8.75, mean 5.66). I chose a pH of 3.9 for the low pH treatment to approximate the average pH of ponds where *H. andersonii* successfully breeds. In a previous field study I found a mean pH of 3.76 in ponds where *H. andersonii* metamorphs were found (Pehek 1994). Each combination of pH and competition treatments was replicated four times.

Experimental protocol

Most studies of the effects of pH on amphibian distributions have been observational or, if experimental, conducted in the laboratory (but see Warner et al. 1991, 1993). The present experiment was conducted in semi-natural ponds where I could isolate the factors of interest while at the same time achieving a higher level of realism than is possible in the laboratory (Morin 1989). I established semi-natural ponds in 1000-L cattle tanks located in Hutcheson Memorial Forest of Rutgers University, East Millstone, New Jersey. Tanks were filled with water from nearby Spooky Brook. Fresh hay (0.5 kg/tank) was added to provide nutrients and to simulate the litter layer in natural ponds. I provided further spatial heterogeneity by adding 18 washed stems of *Elodea canadensis* to each tank. I initiated the plankton community in each tank by adding 250 mL of a zooplankton inoculum collected from ponds in the New Jersey Pine Barrens (Burlington and Ocean Counties). Plankton was thoroughly stirred before each 250 mL aliquot was extracted. Hexagonal lids constructed of fiberglass screening and wood retained metamorphs until collection and prevented colonization by insects other than early instars introduced with the zooplankton.

After randomly assigning treatments to tanks, I added H_2SO_4 to adjust the pH where necessary in low pH tanks. After initially setting the pH, I checked pH levels every 48 h, or within 24 h following rain, and adjusted if necessary. If a pH treatment tank had a higher pH than the required level, H_2SO_4 was added to lower the pH. If a pH treatment tank had a lower pH than the required level, a situation that sometimes occurred after rainstorms, NaOH was added to raise the pH. Tanks varied slightly or not at all from target pH in 48 h.

I collected amplexing pairs of adult *H. andersonii* and *H. versicolor* from ponds in the New Jersey Pine Barrens between 31 May and 6 June 1992. I held the pairs in plastic dishpans overnight for egg deposition, after which they were returned to the ponds from which they were collected. *Rana sphenocephala* egg masses were collected from Pine Barrens ponds on 7 June 1992. Hatchlings produced by all pairs from a particular species were thoroughly mixed before counting tadpoles for introduction to minimize genetic differences among tanks. On 13 June 1992 I introduced 200 *H. andersonii* tadpoles to each tank, 200 *H. versicolor* to *Hyla* competition tanks, and 200 *R. sphenocephala* to *Rana* treatment tanks.

Response variables and statistical analyses

I collected all metamorphosed froglets and measured wet mass after tail resorption. Many untransformed tadpoles of *R. sphenocephala* and a few each of the two *Hyla* species remained in the tanks until late October. No metamorphs had emerged for over a month, and the declining temperature made it unlikely that any more tadpoles would metamorphose before winter. On 24 and 27 October 1992 I removed all remaining tadpoles from the tanks and measured their wet mass. For froglets I calculated length of larval period as date of metamorphosis minus date of introduction, and growth index as mass at metamorphosis divided by length of larval period. For unmetamorphosed tadpoles I calculated a tadpole growth index as the mass when tadpoles were removed from tanks divided by the number of days elapsed since introduction. Response variables for mass, tadpole mass, larval period, and metamorph and tadpole growth indices are tank means. The response variable for survival is percent surviving to metamorphosis. For purposes of analysis I counted tadpoles with metamorphs as survivors, but kept tadpole mass and growth as separate response variables. The values of all of the response variables used in this experiment may affect adult fitness or population dynamics of anurans (Smith 1987, Berven 1990). Data for all response variables were non-normally distributed, and thus the following transformations were employed: arcsine square root (survival); log (mass); log (larval period); and log (growth index).

I was interested in the responses of *H. andersonii* to competition and pH, and the interaction of competition with pH. *H. versicolor* and *R. sphenocephala* were exposed to potential competition from *H. andersonii* in all cases, and therefore I could only look at their responses to pH. Analyses were done using Multivariate Analysis of Variance (MANOVA) to show whether treatments had a significant overall effect, and Analysis of Variance (ANOVA) to determine which variables contributed to any significant overall effects (SAS Institute 1985). I adjusted significance levels for ANOVA using a multistage Bonferonni correction (Rice 1990). I performed orthogonal contrasts related to my hypotheses on the responses of *H. andersonii.* Specifically, contrasts explored the pH main effect, the competition main effect, and the interaction of pH and competition. Further contrasts determined whether *R. sphenocephala* and *H. versicolor* had different effects on *H. andersonii,* and whether the effects of the two competitor species were affected differently by pH. These analyses were done on the data set containing metamorphs alone for the two *Hyla* species and on the data set containing metamorphs plus tadpoles remaining at the termination of the experiment for *R. sphenocephala. Rana sphenocephala* tadpoles may overwinter and metamorphose the next spring or summer, so unmetamorphosed tadpoles may be counted as survivors. Tadpoles of *H. andersonii* and *H. versicolor* do not overwinter, so any remaining in late October would not survive to metamorphose the next spring.

RESULTS

Four tanks were contaminated with fish fry introduced inadvertently with the zooplankton. Each of these tanks contained one *Enneacanthus obesus.* In three of these tanks anuran survival was extremely low and these tanks were dropped from the experiment. A fourth tank had good survivorship and was used in the analysis. The tadpoles in this tank apparently obtained a size refuge from fish predation early in the experiment.

Effects of pH on tadpole survival and larval performance

Contrary to my initial hypothesis, low pH had no effects on tadpoles of any of the three anuran species studied. The results of MANOVA and ANOVA indicated that pH had no significant effect on survival, mass, length of larval period, or growth index of *H. andersonii* tadpoles (Wilks' lambda = 0.789521, df = 4, 10, $F = 0.6665$, $P = 0.6296$. See Fig. 1 and Table 1).

MANOVA and ANOVA showed that reduced pH did not affect survival, mass at metamorphosis, length of larval period, or growth index for either *H. versicolor* or *R. sphenocephala* (*H. versicolor*: Wilks' lambda = 0.759704, df = 4, 2, $F = 0.1582$, $P = 0.9423$; *R. sphenocephala*: Wilks' lambda = 0.053713, df = 4, 1, $F = 4.4043$, $P = 0.3414$. See Tables 2 and 3 for means and Tables 4 and 5 for ANOVA results). Tadpole mass and growth were not significantly different between ambient and low pH tanks for *R. sphenocephala* (Tables 3 and 5).

Effects of competition on H. andersonii

Results of MANOVA supported my second hypothesis, that interspecific competition would have significant negative effects on *H. andersonii* (Wilks' lambda = 0.077274, df = 8, 20, $F = 6.4934$, $P = 0.0003$). Results of ANOVA showed a significant effect of competition on survival of *H. andersonii* tadpoles (Fig. 1, Table 1). When the extremely conservative Bonferroni correction was applied, the effect of competition was significant on mass at metamorphosis, but not on growth and larval period (Rice 1990). Orthogonal contrasts, however, showed a significant effect of competition on both mass and growth of *H. andersonii* (mass: $F = 11.47$, $P = 0.0049$; growth: $F = 8.44$, $P = 0.0123$).

My third hypothesis, that low pH would lessen the effects of competition on *H. andersonii,* was not supported by my results. MANOVA and ANOVA indi-

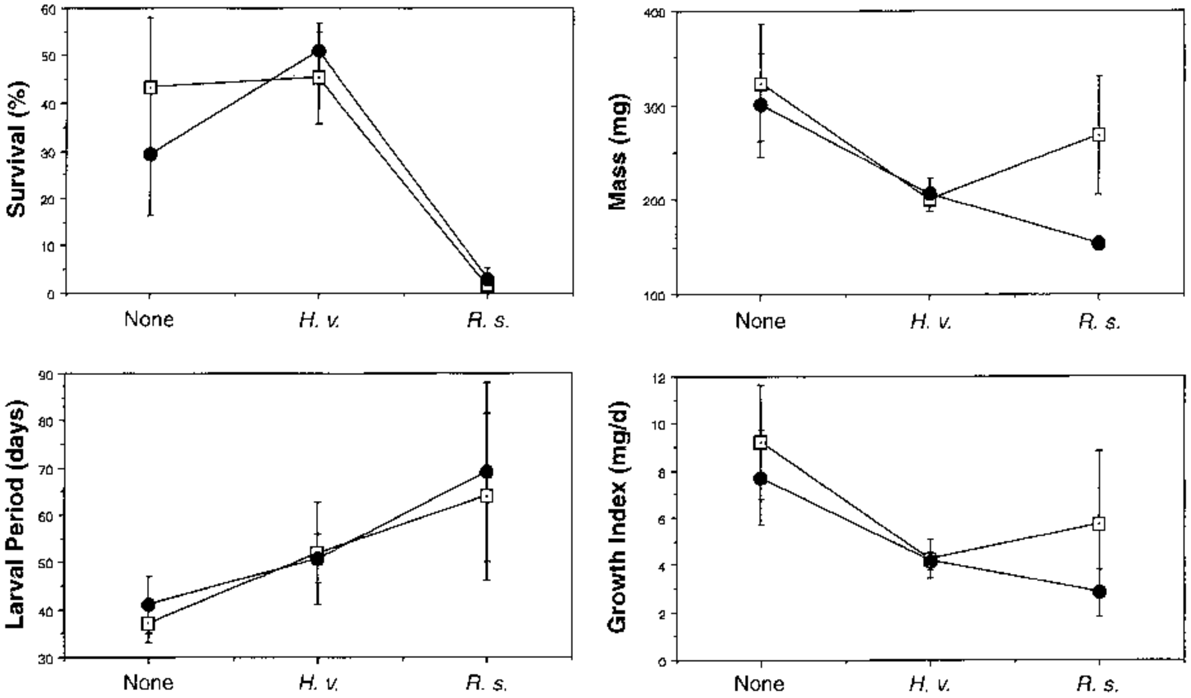

FIG. 1. Plots of means of the four response variables for *Hyla andersonii* by competition and pH treatments. On the x axis, None = tanks with no competitors, *H. v.* = tanks with *Hyla versicolor* competitors, and *R. s.* = tanks with *Rana sphenocephala* competitors. Open squares indicate means for low pH tanks and solid circles indicate means for high (ambient) pH tanks.

cated that there was no interaction between pH and competition in this experiment (Wilks' lambda = 0.439805, df = 8, 20, F = 1.2697, P = 0.3129. See Fig. 1, Table 1). This result strongly suggests that *H. andersonii* does not use low pH ponds as a refuge from competition with the two anuran species used in this experiment.

TABLE 1. Summary of ANOVA for responses of *Hyla andersonii* tadpoles to pH and competition. Values in bold are significant using the sequential Bonferroni procedure.

Source	df	Sum of squares	F	P
Survival				
pH	1	0.00018431	0.01	.9399
Competition	**2**	**1.64248402**	**26.17**	**.0001**
pH × competition	2	0.05749409	0.92	.4213
Error	15	0.47065627		
Mass				
pH	1	0.16454665	2.71	.1238
Competition	**2**	**0.69677395**	**5.73**	**.0164**
pH × competition	2	0.25043379	2.06	.1669
Error	13	0.78979307		
Larval period				
pH	1	0.01460482	0.11	.7484
Competition	2	0.00710141	2.28	.1412
pH × competition	2	36.90871086	0.04	.9565
Error	13	1.76922682		
Growth				
pH	1	0.27808958	1.01	.3340
Competition	2	2.44594243	4.43	.0342
pH × competition	2	0.26300072	0.48	.6317
Error	13	3.59159402		

Contrasting the effects of R. sphenocephala *and* H. versicolor *on* H. andersonii

My results showed, in contrast to my prediction, that *R. sphenocephala* had a stronger competitive effect on *H. andersonii* than did *H. versicolor*. Orthogonal contrasts showed that the competitive effects of *R. sphenocephala* and *H. versicolor* on *H. andersonii* were not significantly different for mass and growth, but a contrast comparing the effects of these two competitors on survival of *H. andersonii* was highly significant (F = 28.96, P = 0.0001, Fig. 1). This reflects the depression of *H. andersonii* survival by *R. sphenocephala*, but not by *H. versicolor*. Once again, pH did not alter the outcome of competitive interactions. Contrasts examining whether the competitive effects of *H. versicolor* and *R. sphenocephala* were differentially affected by low pH were non-significant for all response variables.

I compared the growth rates and masses at metamorphosis of the three tadpole species in an effort to determine what factors contributed to competitive superiority in this experiment. On average, *R. sphenocephala* grew over four times faster than either *H. andersonii* or *H. versicolor*. The average mass at meta-

TABLE 2. Means and standard deviations for *Hyla versicolor* response variables, listed by pH treatment.

Level of pH	*N*	Survival (%)	Mass (mg)	Larval period (d)	Growth (mg/d)
		Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD
Low	4	70.63 ± 12.20	261.34 ± 64.88	51.43 ± 13.60	5.30 ± 1.11
High	3	64.17 ± 23.69	261.99 ± 27.77	47.77 ± 18.92	6.28 ± 2.43

morphosis of *R. sphenocephala* was over four times greater than that of either of the *Hyla* species.

DISCUSSION

Early workers believed that the association of *Hyla andersonii* with acidic ponds was caused by a dependence on acid waters for the larval habitat. Results of my work and that of other authors has shown that *H. andersonii* can reproduce successfully in waters ranging up to pH 7 or 8 (Gosner and Black 1957, Freda and Dunson 1986, Pehek 1994). As an alternate explanation, I proposed that less acid-tolerant competitors exclude *H. andersonii* from all but the most acidic ponds in the New Jersey Pine Barrens. The results of the present experiment show that competition from tadpoles of other anuran species can have a significant impact on *H. andersonii* tadpoles, reducing mass, growth, and even survival, but, contrary to my expectations, acidity did not appear to reduce this impact.

It is possible that other competitor species are responsible for limiting *H. andersonii* to low pH ponds. Most other syntopic anurans, however, are either nearly ubiquitous on a local scale (such as *Bufo woodhousei fowleri*, or *Pseudacris crucifer*), limited to the most permanent ponds (*Rana catesbeiana, R. virgatipes*), or have extremely patchy local distributions, either temporally or spatially (*Scaphiopus holbrooki*). *Hyla andersonii* would have been eliminated from breeding in the New Jersey Pine Barrens if competition from the ubiquitous species was intense enough to cause competitive exclusion in the larval stage. Although *H. andersonii* does not breed in most permanent ponds (presumably due to predation), it is also absent from many temporary ponds and streams, eliminating the possibility that competition with permanent pond breeders has determined its distribution. Anurans with patchy distributions probably have limited impact on other pine barrens anurans because they are seldom encountered. One anuran species whose impact on larval *H. andersonii* should be investigated is the green frog, *Rana clamitans*. Within the Pine Barrens I have not found *R. clamitans* tadpoles or adults in or around the extremely acidic ponds, referred to locally as spongs, where *H. andersonii* reproduction appears to be strongest.

I examined the effects of pH on the larval stage only. Competitors may be eliminated or reduced in abundance during the egg stage. Embryos of many species of larval anurans suffer lethal and sublethal effects at low pH in laboratory assays (Gosner and Black 1957, Tome and Pough 1982, Pierce et al. 1984, Clark and LaZerte 1985, Freda and Dunson 1986, Leuven et al. 1986). *Hyla versicolor* and *R. sphenocephala* suffer death of embryos at pH below 3.8 and 3.7, respectively (Freda 1986). In contrast, embryos of *H. andersonii* may survive at a pH as low as 3.4. Results found in laboratory assays, however, cannot be assumed to occur in natural ponds. For example, I have found *R. sphenocephala* reproducing successfully in ponds supposedly below the critical or lethal pH for embryonic development.

The association of *H. andersonii* with low pH in natural ponds may be related to other indirect effects of pH. Predation by aquatic insects, salamanders, or fish, themselves excluded from low pH ponds, might also limit the distribution of *H. andersonii*. In a previous study I examined the question of whether pH affects the impact of insect predation on tadpoles of *H. andersonii* (Pehek 1994). I found that densities of insect predators falling within the natural range could eliminate 200 tadpoles of *H. andersonii* from 1000-L artificial ponds within 1–2 d. However, I did not find that pH lessened the impact of insect predation on *H. andersonii*.

The distribution of *H. andersonii* might be explained by looking at factors acting on the adult, terrestrial stage. Predation on metamorphs may have a major impact on population dynamics of anurans (Berven 1990).

TABLE 3. Means and standard deviations for *Rana sphenocephala* response variables, listed by pH treatment.

Level of pH	*N*	Survival (%)†	Mass (mg)	Larval period (d)	Growth index (mg/d)	Tadpole mass (mg)	Tadpole growth index (mg/d)
		Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD	Mean ± 1 SD	Mean ± SD	Mean ± SD
Low	3*	63.88 ± 39.91	1777.21 ± 1798.18	53.94 ± 10.80	37.98 ± 43.40	1369.99 ± 439.06	10.15 ± 3.18
High	3*	64.00 ± 32.57	1343.15 ± 1061.70	53.65 ± 9.52	27.82 ± 25.45	1559.97 ± 203.98	11.59 ± 1.49

* N for the variable "Survival" was 4.

† Tadpoles that were alive at the end of the experiment were also counted as survivors.

The ponds where I have observed the greatest numbers of metamorphic *H. andersonii* share the characteristic of dense mats of *Sphagnum* spp. along the shore, as well as the lowest pH values. In my surveys of these ponds, nearly all metamorphs were found underneath these mats of *Sphagnum*. I have observed green frogs, *R. clamitans*, preying on newly emerged metamorphs near ponds with little *Sphagnum* growth. Although it is clear that some species of *Rana* actively prey on metamorphs of other anuran species, it is unknown whether this predation has a significant impact on adult populations of any anuran species (Moyle 1973, Hayes and Jennings 1986, Schwalbe and Rosen 1988).

Another aspect of the terrestrial habitat that has been suggested as limiting for *H. andersonii* is the availability of shrub borders around ponds, used by males for calling perches and perhaps by both sexes for cover during the move towards water (Means and Longden 1976, Means and Moler 1979, Cely and Sorrow 1982). The spongs mentioned above do have a dense shrub border, but many other ponds in the Pine Barrens share this characteristic.

In reverse of expectations based on allopatry/sympatry, the species that *H. andersonii* encounters more often in nature (*Rana*) had more of a competitive effect than did the species that *H. andersonii* seldom encounters in the larval stage (*H. versicolor*). The factors that are implicated in competitive superiority of tadpoles are unknown, but growth rate and activity level may be important factors (Warner et al. 1991, 1993, Werner 1992). *Rana* tadpoles reach a much larger size than *H. andersonii* and grow much faster. *H. versicolor* tadpoles reach a somewhat larger size than do those of *H. andersonii* and grow slightly faster. In laboratory observations, *H. versicolor* was consistently more active than *H. andersonii*, but no data are available for activity levels of *R. sphenocephala* (Lawler 1989). Although *H. versicolor* is a weaker competitor than *R. sphenocephala* in the larval stage, the two species of *Hyla* would compete more in the adult stage due to differences in microhabitat.

TABLE 4. Summary of ANOVA for responses of *Hyla versicolor* tadpoles to pH.

Source	df	Sum of squares	*F*	*P*
Survival				
pH	1	0.00567834	0.17	.6948
Error	5	0.16426050		
Mass				
pH	1	0.00076541	0.02	.8961
Error	5	0.20261895		
Larval period				
pH	1	0.01548492	0.16	.7081
Error	5	0.49238212		
Growth				
pH	1	0.02722369	0.24	.6419
Error	5	0.55651977		

TABLE 5. Summary of ANOVA for responses of *Rana sphenocephala* tadpoles to pH.

Source	df	Sum of squares	*F*	*P*
Survival				
pH	1	0.00104734	0.00	.9501
Error	6	0.94327707		
Mass				
pH	1	0.03240410	0.04	.8434
Error	4	2.91818750		
Larval period				
pH	1	0.00000801	0.00	.9887
Error	4	0.14084089		
Growth				
pH	1	0.02414252	0.02	.8836
Error	4	3.96941233		
Tadpole mass				
pH	1	54140.5004167	0.46	.5340
Error	4	468762.0138667		
Tadpole growth				
pH	1	3.12761332	0.51	.5154
Error	4	24.62525671		

Several factors may explain why relatedness did not determine competitive strength in this experiment. Closely related species would be expected to compete more strongly than distantly related species only if relatedness was associated with increased dietary overlap. As most tadpole species are generalist feeders, partitioning of resources may be minimal (Jenssen 1967, Heyer 1973, Seale 1980, Morin 1983). In this experiment the increased growth rate of the ranid lineage may have overshadowed any greater dietary overlap that exists between the two hylid species. In addition, the two species of *Hyla* share characteristics that may increase the likelihood of competitive interactions. They are both terrestrial in the postmetamorphic stages and thus would compete with each other, but not with *R. sphenocephala*, as juveniles and adults. In addition, the genus *Hyla* appears to be constrained to warm-weather breeding (John-Alder et al. 1988), whereas *R. sphenocephala* often breeds in early spring, before *Hyla* begin calling.

On the whole-pond level, *R. sphenocephala* is found with *H. andersonii* more often than is *H. versicolor*, despite its greater competitive effect on *H. andersonii*. This finding cautions against using co-occurrence as a gauge of competitive strength. The inverse, that strength of competition seen in experimental studies cannot always be used to predict whether species will be found together, is also instructive. In addition, relatedness was not a good predictor of competitive strength in this experiment. These findings reinforce the idea that interactions between species cannot be looked at in isolation from other aspects of their environment, both biotic and abiotic. In addition, in organisms with complex life cycles, all life stages must be examined in order to determine the overall effect of competition on population dynamics.

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