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Asymmetric competition in larval amphibian communities: conservation implications for the northern crawfish frog, *Rana areolata circulosa*

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Abstract Asymmetric competition in larval amphibians can influence population dynamics and community structure. This density-dependent regulatory mechanism may be of particular importance for rare or endangered species such as the northern crawfish frog, *Rana areolata circulosa*. Interspecific competition of *R. areolata* with two congeners, *R. blairi* and *R. sphenoccephala*, was examined in artificial ponds. Analysis of covariance (differential mortality covariate) indicated that interspecific competition increased larval period length and decreased metamorphic body mass of *R. areolata*. The number of metamorphs produced was lower for *R. blairi* ponds when reared with *R. areolata* at high density. Body mass at metamorphosis was larger for *R. sphenoccephala* when reared with *R. areolata*, suggesting that *R. areolata* facilitates larval growth in *R. sphenoccephala*. These results indicate that the larval performance of *R. areolata* was reduced in the presence of interspecific competitors. Although many conservation efforts emphasize the preservation of critical habitat or particular rare species, interactive effects of biotic components in the focal community may also be important demographic regulators.

Key words Asymmetric competition · Community structure · Larvae · Performance · *Rana*

Introduction

Understanding species interactions within natural assemblages has long been a fundamental yet elusive goal of community ecologists. Knowledge of these patterns and their underlying mechanisms can be important in determining distributions and abundances of species.

Ecologists in the past half century have recognized interspecific competition as a ubiquitous component of natural systems, but no clear consensus exists regarding the general impact of this mechanism in all communities or its importance relative to other regulatory mechanisms such as predation and disturbance (e.g., Hairston et al. 1960; Connell 1983). Despite this ambiguity, contemporary models of community regulation still incorporate competition as one of the primary regulatory forces in community organization (Menge and Sutherland 1987; Wellborn et al. 1996).

Competition may be particularly important in communities containing rare species. If competitively inferior, rare species were excluded, this could contribute to population declines and local extinctions. This may be especially true for the northern crawfish frog, *Rana areolata circulosa*, which is patchily distributed throughout the central United States and listed as endangered in 5 of the 12 states in which it occurs (Platt et al. 1974; Dundee and Rossman 1989; Busby and Brecheisen 1997). Habitat loss and degradation due to anthropogenic influences have been implicated as primary causes of *R. areolata* decline because throughout its range this species is strongly associated with tallgrass prairie habitats or grasslands (Bragg 1953). However, fundamental life history and demographic information regarding this anuran is lacking due to its fossorial habits and difficulty in locating sufficiently large natural populations. Knowledge of life history traits related to reproduction, viability, and juvenile recruitment can elucidate some of the community-organizing mechanisms important for populations of this rare anuran and therefore be critical in making informed conservation decisions (Pechmann and Wilbur 1994; Semlitsch et al. 1995).

Interspecific competition has important effects on fitness components and community organization in numerous species of larval amphibians (e.g., Morin 1983; Wilbur 1987). It is critical to differentiate between the processes of intraspecific (density dependence) and interspecific competition in drawing conclusions related to the conditions of potential coexistence or exclusion

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in larval amphibian communities (Morin and Johnson 1988; Semlitsch 1993). The design of our experiment therefore separates the per capita effects of density from interspecific competition in order to detect asymmetric competitive differences between species (Underwood 1986). Indeed, it is often the case that larval anuran interspecific competition is asymmetric (reviewed by Morin and Johnson 1988). Asymmetry among competitors can lead to the exclusion of the inferior competitor by the superior one and is therefore of particular concern for the long-term population persistence of rare species such as *R. areolata*.

The maintenance of populations of *R. areolata* depends on the continuous production of larvae capable of reaching metamorphosis. Only metamorphs can contribute to juvenile recruitment and therefore the maintenance of species populations (Semlitsch et al. 1996). Growth rate and developmental time influence the potential for population growth through the timing of and body mass at metamorphosis (Semlitsch 1993). Rapid growth rates allow larvae to metamorphose quickly to escape drying in ephemeral ponds (Newman 1988a, b), whereas slower growth rates allow individuals to maximize body mass at metamorphosis in more permanent ponds (Wilbur and Collins 1973). Larger size at metamorphosis can result in higher juvenile survival, earlier age and larger size at first reproduction, higher fecundity, and better physiological terrestrial performance (Berven and Gill 1983; Smith 1987; Semlitsch et al. 1988; Berven 1990). As a result, larval life history traits related to growth and development function as important indicators of population viability.

We measured the relative strengths of intra- and interspecific competition in artificial pond communities containing species-pair combinations of the northern crawfish frog (*R. areolata*) and two leopard frog species (*R. blairi* and *R. sphenoccephala*). All three of these congeneric species occur sympatrically in portions of their respective ranges (Bragg 1953; Johnson 1987; Dundee and Rossman 1989) and are known to breed syntopically despite slight temporal separation in breeding phenologies and habitat segregation (Busby and Brecheisen 1997; M. Parris, personal observation, R. Sage, personal communication). Thus, the opportunity for interspecific competition among larvae of these three species may be common in natural ponds (Busby and Brecheisen 1997; M. Parris, personal observation). We determined the effects of density-dependent interspecific competition among these three species and interpreted how competition can impact the population persistence of a rare species of anuran.

Materials and methods

Source populations of species and breeding design

We used artificial fertilizations to produce larvae of two leopard frog species, *R. blairi* and *R. sphenoccephala*, and used larvae from

three field-collected egg masses for *R. areolata*. Adult leopard frogs for the fertilizations were obtained on 11–16 April 1997 from ditches along the Missouri River floodplain near Jefferson City (Callaway County), MO., USA. The species identity of each frog was determined morphologically (e.g., Pace 1974) and confirmed by protein electrophoresis using the following diagnostic enzymes: sorbital dehydrogenase, malate dehydrogenase, lactate dehydrogenase, phosphoglucosmutase, and manose phosphate isomerase (Hillis et al. 1983). On 17 April, two female and five male *R. blairi*, and four female and five male *R. sphenoccephala* were used in artificial fertilizations to obtain larvae for each leopard frog species. Eggs were allowed to hatch in the laboratory at 21°C and replicate crosses within species were pooled together. *R. areolata* larvae were obtained from three egg masses collected in Anderson County, KS., USA on 23 March and stored in the laboratory in a cold-temperature incubator (12°C) until leopard frog larvae were obtained. This temperature difference in initial rearing conditions between crawfish and leopard frog larvae likely contributed little to the differential responses of the species to the treatments. Such a situation was necessary, however, to synchronize hatching and the initial developmental stage of larvae, two important life history parameters to standardize for competition studies. Furthermore, even though northern crawfish frog and leopard frog larvae were derived from different geographic areas, all three species are sympatric at both source populations.

Larval performance in artificial ponds

Cohorts of larvae were reared in single- and mixed-species populations at two initial larval densities. This resulted in ten treatment combinations that were replicated two or three times in an array of 25 artificial ponds (Table 1). On 2 May 1997 (day 0), larvae of each species were haphazardly selected and counted into groups of 20 (low density) or 60 (high density), and each group was added to a randomly assigned artificial pond.

We used 1.83-m-diameter polyethylene tanks as artificial ponds. Ponds were positioned in an array in a fenced field at the University of Missouri-Columbia Research Park (Boone County). Ponds were exposed to natural seasonal changes in air temperature and photoperiod. Ponds were filled with tap water to a depth of 50 cm (960 l), and 1.0 kg of air-dried deciduous leaf litter was added to each pond. No additional water was added because rainfall compensated for evaporative water loss during the experiment. Each pond was inoculated six times with 0.5 l of a concentrated plankton solution collected from nearby natural ponds in late March and early April 1997. Immediately following preparation, ponds were covered with lids made of fiberglass window screen (1 mm mesh) to prevent colonization by potential predators and other anurans. Each pond had a drain fitted with an L-shaped standpipe to allow drainage of excess water. Minimum and maximum water temperature at the bottom of two ponds at opposite ends of the array were recorded weekly. There was no difference in temperature between these two ponds on any of the dates, indicating uniform temperature conditions across the array.

Larvae were reared at different initial densities to simulate low- and high-growth environments in which different relative competitive abilities, within and between species, could be expressed (Morin and Johnson 1988). The low initial density was 20 larvae per pond (20.8 larvae per 1000 l) and high density was 60 larvae per pond (62.5 larvae per 1000 l). Constant total numbers of larvae were used in the single- and mixed-species treatments for all three species (Table 1). Previous experiments using similar densities have yielded significant and realistic differences in growth and development (Semlitsch et al. 1997). Natural densities of *R. sphenoccephala* larvae range from 14 to 4238/1000 l water volume (Morin 1983; Petranka 1989).

A constant water depth of approximately 50 cm was maintained in all ponds throughout the 102-day experimental period. A 102-day experimental hydroperiod was used to impose a time-limited environment on competing larvae so that differential performance could be measured, and is within the range of natural

pond hydroperiods. In addition, at least one metamorph was collected from every pond, and in several ponds, 100% of the larvae reached metamorphosis by day 102.

Response variables and statistical analyses

Ponds were checked daily until larvae began to metamorphose. Upon emergence, metamorphs were collected from the ponds every day and held in the laboratory until tail resorption was complete (4–5 days; stage 46, Gosner 1960) and then weighed to the nearest 1.0 mg. Metamorphosis was defined as the emergence of at least one forelimb (stage 42, Gosner 1960). Performance of larvae from each species was measured as: (1) larval period length (days from the start of the experiment to metamorphosis), (2) mass at metamorphosis (body mass after tail resorption), and (3) proportion metamorphosis (proportion of survivors that metamorphosed). On 11 and 12 August (day 101 and 102), we drained and thoroughly searched all ponds for any remaining larvae or metamorphs. Mean values per pond were the unit of analysis because measurements from individuals within ponds were not independent (Semlitsch et al. 1997).

Statistical analyses were performed first on larval responses of the species reared alone at low and high density (Table 1; treatments 1–6), and second on responses to the interspecific competition treatments at low and high density (Table 1; treatments 7–10). The first analysis was used to determine the larval responses of each species reared alone at low and high density. The second analysis was used for testing the effects of interspecific competition in mixed-species populations at low and high density.

Survival differed among the three species, and generally was low for *R. areolata* (Table 2). This could reflect a true biological survival difference among species, or it could be an artifact of different initial rearing conditions between crawfish and leopard frog larvae. To control for the potentially confounding effects of differential mortality on larval responses such as growth rate, survival was used as a covariate in a type III sums-of-squares analysis of covariance

model (SAS 1988). Differential mortality, resulting from either predictable density dependence or the variable and often nonlinear response to interspecific competition (Wilbur 1997), creates different realized densities among surviving larvae, which can influence the precision and obscure the true nature of larval responses to the treatments. Survival values were calculated for each species independently as the proportion of all individuals, larvae and metamorphs, that survived from those initially added to each pond. Mean values per pond for each species were used as units of analysis. Larval responses for all treatments were tested for the main effects of species, density, and interspecific competition (mixed-species treatments), initially with multivariate analysis of covariance (MANCOVA), for all response variables together, and secondly with univariate analyses of covariance (ANCOVA), for each response variable separately. All proportion data were transformed by the arcsine of the square root to reduce skewness and increase additivity of effects and equality of variances (Snedecor and Cochran 1980). Tests of significance for pairwise comparisons were performed using Scheffé's multiple-range tests ($P < 0.05$).

Results

The responses of conspecific groups of larvae to low and high initial densities were used to test the effects of density-dependent growth and the symmetry of responses among species. The multivariate responses of larvae were significantly affected by a species main effect ($F = 3.47, df = 6,8, P = 0.05$), but not by density or their two-way interaction. Univariate analyses indicated that a difference in larval period length was the main contributor to the multivariate species effect ($F = 9.18, df = 2, P = 0.01$).

Table 1 Treatment combinations (1–10) of *Rana areolata*, *R. blairi*, and *R. sphenoccephala* larvae at low and high initial density in single- and mixed-species populations. The number of larvae in each treatment is given as well as the combined total per pond

	Treatments									
	Single						Mixed			
	1	2	3	4	5	6	7	8	9	10
Species										
<i>R. areolata</i>	20	0	0	60	0	0	10	10	30	30
<i>R. blairi</i>	0	20	0	0	60	0	10	0	30	0
<i>R. sphenoccephala</i>	0	0	20	0	0	60	0	10	0	30
Total	20	20	20	60	60	60	20	20	60	60

Table 2 Summary of the treatment means (± 1 SD) of larval period length (days), body mass at metamorphosis (mg), percentage of individuals surviving, and percentage of survivors metamorphosing. Values of *n* represent the number of replicate ponds per treatment

Species	Competition	Total density	<i>n</i>	Larval period	Body mass	Percent survivors	Percent metamorphosis
<i>R. areolata</i>	None	20	1	70.6	3235	25.0	100.0
<i>R. areolata</i>	None	60	2	68.3 \pm 3.3	2509 \pm 320	24.2 \pm 3.5	93.8 \pm 8.8
<i>R. areolata</i>	<i>R. blairi</i>	20	1	87.0	1298	10.0	100.0
<i>R. areolata</i>	<i>R. blairi</i>	60	1	81.0	2461	20.0	100.0
<i>R. areolata</i>	<i>R. sphen.</i>	20	3	69.7 \pm 2.0	2677 \pm 187	36.7 \pm 20.8	100.0 \pm 0
<i>R. areolata</i>	<i>R. sphen.</i>	60	2	68.1 \pm 7.6	2497 \pm 30	28.4 \pm 11.8	59.1 \pm 57.8
<i>R. blairi</i>	None	20	2	60.5 \pm 1.4	2332 \pm 1007	87.5 \pm 3.5	100.0 \pm 0
<i>R. blairi</i>	None	60	2	64.7 \pm 2.1	1273 \pm 369	64.2 \pm 20.0	98.4 \pm 2.3
<i>R. blairi</i>	<i>R. areolata</i>	20	2	58.4 \pm 1.0	3313 \pm 678	70.0 \pm 0	100.0 \pm 0
<i>R. blairi</i>	<i>R. areolata</i>	60	2	64.7 \pm 10.1	1412 \pm 512	61.7 \pm 7.1	100.0 \pm 0
<i>R. sphen.</i>	None	20	3	55.6 \pm 3.2	2129 \pm 821	65.0 \pm 15.0	100.0 \pm 0
<i>R. sphen.</i>	None	60	3	66.7 \pm 7.1	737 \pm 100	61.7 \pm 14.8	97.9 \pm 1.9
<i>R. sphen.</i>	<i>R. areolata</i>	20	3	55.5 \pm 2.3	2628 \pm 134	83.3 \pm 20.8	100.0 \pm 0
<i>R. sphen.</i>	<i>R. areolata</i>	60	2	56.0 \pm 1.3	1611 \pm 919	73.4 \pm 37.7	100.0 \pm 0

Body mass at metamorphosis decreased as larval density increased (ANCOVA: $F = 12.82$, $df = 1$, $P = 0.01$; Fig. 1A). Even though there was not a significant species main effect on body mass at metamorphosis ($F = 3.20$, $df = 2$, $P = 0.11$), Scheffe's tests least-square indicated that *R. areolata* metamorphs were larger than *R. sphenoccephala* at both densities. There was no significant difference in body mass between *R. areolata* and *R. blairi* or between *R. blairi* and *R. sphenoccephala* (Fig. 1A).

Larval period length was affected by both density ($F = 5.36$, $df = 1$, $P = 0.05$) and species ($F = 9.18$, $df = 2$, $P = 0.01$) main effects. Larval period length increased as density increased (Fig. 1B). *R. areolata* had longer larval periods than *R. sphenoccephala* at both densities, but there was no significant difference between *R. areolata* and *R. blairi* or between *R. blairi* and *R. sphenoccephala* (Fig. 1B).

Interspecific competition in two-way combinations had a significant effect on body mass at metamorphosis for *R. areolata* and *R. sphenoccephala* (Table 3). For *R. areolata*, body mass at metamorphosis was significantly larger when they were reared alone than when

reared with *R. blairi*, but only at low density (Fig. 2A). Furthermore, *R. areolata* metamorphs were larger when reared with *R. sphenoccephala* than with *R. blairi*, but only at low density. *R. sphenoccephala* body mass at metamorphosis increased when reared with *R. areolata*, relative to when alone (Fig. 2B).

Competition with *R. areolata* significantly affected the proportion of *R. blairi* survivors that metamorphosed (Table 3). *R. blairi* ponds produced fewer metamorphs when they were reared with *R. areolata* relative to when alone (Fig. 3A). The survival covariate had a significant effect on the proportion of metamorphosing *R. blairi* survivors (Table 3). Interspecific competition did not have a significant effect on metamorphosis for either *R. areolata* or *R. sphenoccephala* (Table 3).

Larval period length was also affected by competition, but only for *R. areolata*, and only after the density \times competition interaction was removed from the analysis of covariance model ($F = 6.32$, $df = 2$, $P = 0.04$). Larval period length was longest for *R. areolata* when reared with *R. blairi* relative to when alone and with *R. sphenoccephala* (Fig. 3B). There was no significant difference in larval period length between

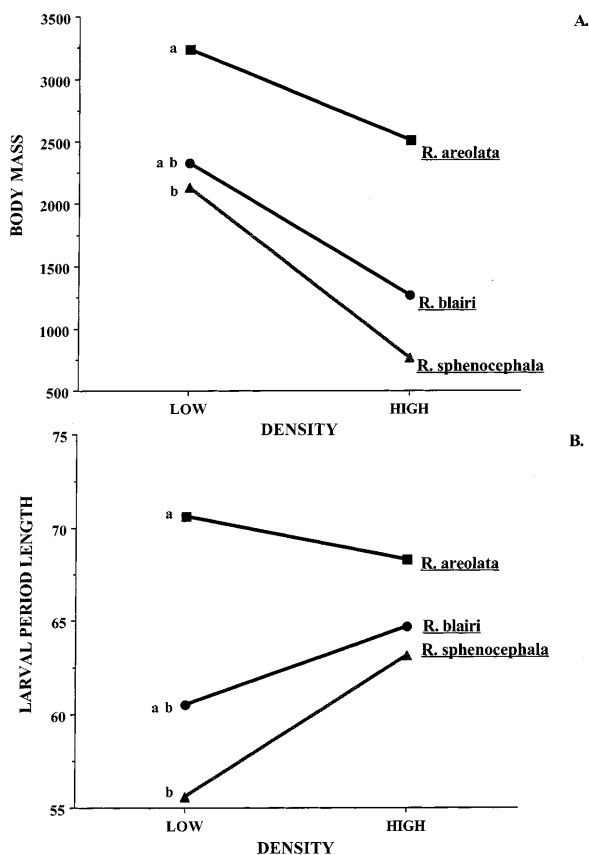


Fig. 1A, B Body mass at metamorphosis (mg) (A) and Larval period length (B) for *Rana areolata*, *R. blairi*, and *R. sphenoccephala* reared separately at low and high densities. Values plotted are least-square means from one to three replicate ponds. Comparisons with different letters indicate significant differences using Scheffe's multiple-range tests

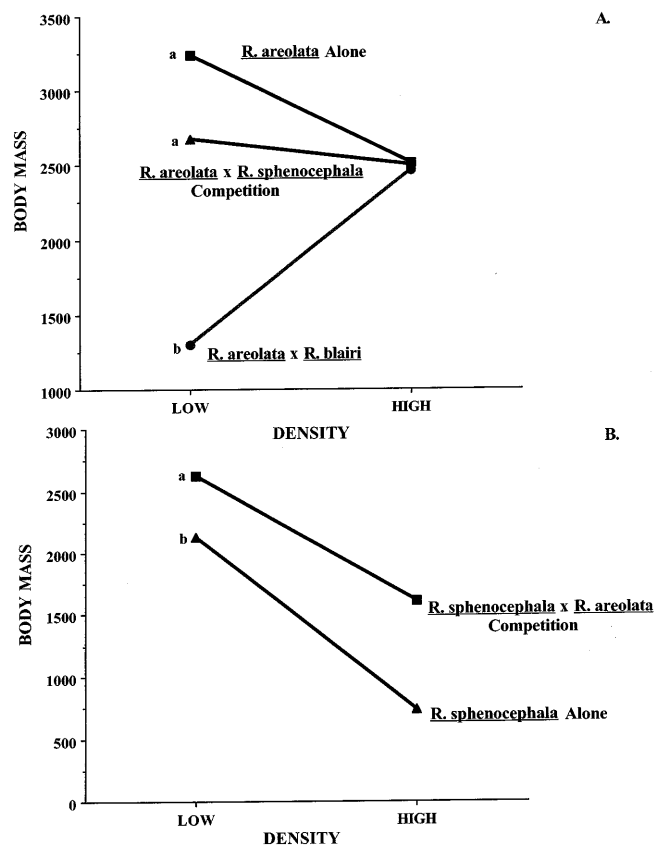


Fig. 2A, B Body mass at metamorphosis (mg) for *R. areolata* when reared in single- and mixed-species treatments with *R. blairi* and *R. sphenoccephala* at low and high densities (A) and for *R. sphenoccephala* when reared in single- and mixed-species treatments with *R. areolata* at low and high densities (B). Values plotted are least-square means from one to three replicate ponds. Comparisons with different letters indicate significant differences using Scheffe's multiple-range tests

Table 3 Summary of the univariate analyses of covariance (survival covariate) of proportion of survivors metamorphosing, body mass at metamorphosis, and larval period length for each species (*R. sphenoccephala*, *R. blairi*, *R. areolata*) reared in two competition treatments at two densities

Response variable	Source of variation	df	Mean square	F-value	P-value
<i>R. sphenoccephala</i>					
Metamorphosis	Competition	1	0.0044	1.29	0.3002
	Density	1	0.0080	2.35	0.1759
	Competition × density	1	0.0089	2.64	0.1554
	Survival (covariate)	1	0.0011	0.32	0.5909
	Error	6	0.0034		
Body mass	Competition	1	0.1623	11.14	0.0157
	Density	1	0.3252	22.31	0.0032
	Competition × density	1	0.0167	1.14	0.3259
	Survival (covariate)	1	0.0580	3.98	0.0930
	Error	6	0.0146		
Larval period	Competition	1	0.0010	2.97	0.1356
	Density	1	0.0022	6.44	0.0443
	Competition × density	1	0.0018	5.29	0.0611
	Survival (covariate)	1	0.0001	0.43	0.5364
	Error	6	0.0003		
<i>R. blairi</i>					
Metamorphosis	Competition	1	0.0138	17.42	0.0250
	Density	1	0.0019	2.34	0.2234
	Competition × density	1	0.00003	0.03	0.8683
	Survival (covariate)	1	0.0128	16.13	0.0277
	Error	3	0.0008		
Body mass	Competition	1	0.0025	0.10	0.7739
	Density	1	0.1452	5.78	0.0956
	Competition × density	1	0.0005	0.02	0.9005
	Survival (covariate)	1	0.0124	0.49	0.5329
	Error	3	0.0251		
Larval period	Competition	1	0.0003	0.18	0.7030
	Density	1	0.0006	0.39	0.5783
	Competition × density	1	0.0002	0.11	0.7650
	Survival (covariate)	1	0.0001	0.08	0.8019
	Error	3	0.0016		
<i>R. areolata</i>					
Metamorphosis	Competition	2	0.0099	0.05	0.9513
	Density	1	0.1095	0.56	0.5074
	Competition × density	2	0.1098	0.57	0.6191
	Survival (covariate)	1	0.1211	0.62	0.4875
	Error	3	0.1943		
Body mass	Competition	2	0.0176	13.35	0.0321
	Density	1	0.0039	2.99	0.1824
	Competition × density	2	0.0199	15.04	0.0273
	Survival (covariate)	1	0.0011	0.81	0.4340
	Error	3	0.0013		
Larval period	Competition	2	0.0042	4.01	0.1422
	Density	1	0.0008	0.74	0.4522
	Competition × density	2	0.00007	0.07	0.9334
	Survival (covariate)	1	0.00001	0.01	0.9232
	Error	3	0.0010		

R. areolata when alone and when reared with *R. sphenoccephala* (Fig. 3B).

Discussion

Asymmetry of interspecific competition

Our results indicate that larvae of three sympatric *Rana* species exhibited asymmetric competition and substantial variation in life history traits directly related to population growth. Such a difference in relative competitive ability can influence the dynamics of natural amphibian communities containing these three species

(Morin and Johnson 1988; Werner 1992). Furthermore, these species demonstrate density-dependent differences that modify the outcome of interspecific competitive interactions.

The performance of *R. areolata* offers some explanations for its low frequency and small population size in natural communities. When reared with *R. blairi*, *R. areolata* metamorphs were smaller than when they were raised alone. This decrease in body mass could have detrimental consequences for the terrestrial life history stage through decreased survival, fecundity, or attainment of sexual maturity at older ages (Berven and Gill 1983; Smith 1987). Body mass at metamorphosis can also affect adult fitness through its influence on terres-

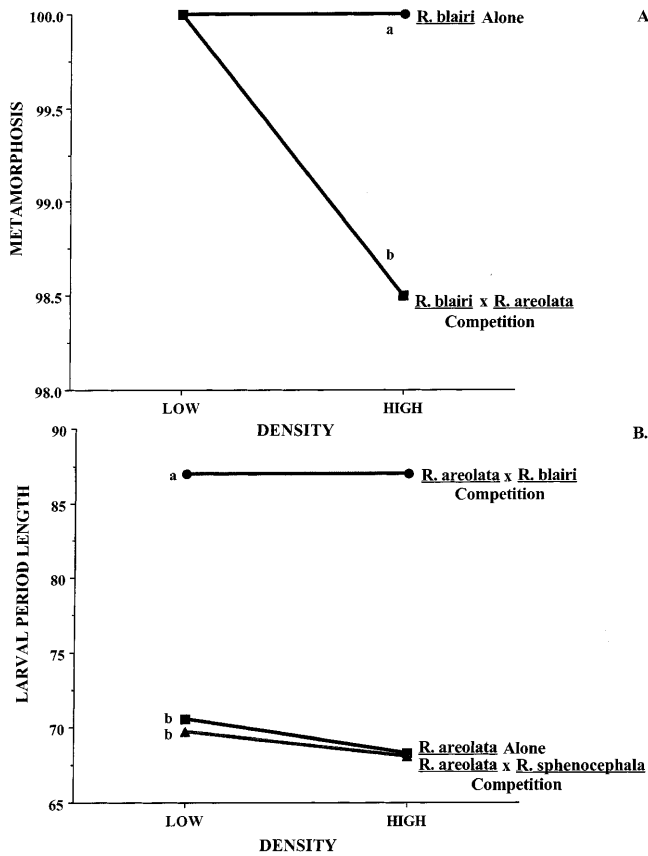


Fig. 3A, B Percentage of *R. blairi* survivors that metamorphosed when reared in single- and mixed-species treatments with *R. areolata* at low and high densities (A) and larval period length for *R. areolata* when reared in single- and mixed-species treatments with *R. blairi* and *R. sphenoccephala* at low and high densities (B). Values plotted are least-square means from one to three replicate ponds. Comparisons with different letters indicate significant differences using Scheffe's multiple-range tests

trial locomotor and physiological performance (Pough and Kamel 1984), as well as predator avoidance, food acquisition abilities, and dispersal efficiency (Dole 1971; Heinen and Hammond 1997). Furthermore, although *R. areolata* did not metamorphose smaller when reared with *R. sphenoccephala*, *R. areolata* metamorphs emerging from ponds with *R. sphenoccephala* were larger than those from ponds with *R. blairi*. Body mass at metamorphosis for *R. areolata* is therefore affected more severely by competition with *R. blairi* than with *R. sphenoccephala*. It is important to note that the decreased body mass at metamorphosis occurred only under low-density conditions (Fig. 2A). At low density, *R. areolata* metamorphosed larger when alone than when reared with *R. blairi*, but interspecific competition did not affect body mass for *R. areolata* at high density. This suggests that *R. areolata* is more susceptible to interspecific competition under low-density conditions and more resistant to a potentially stressful high-density intraspecific environment. Alternatively, this could reflect reduced interspecific competitive ability of *R. blairi* and *R. sphenoccephala* at high densities. Bragg (1953) noted

A. that *R. areolata* larvae often exhibit schooling behavior in natural ponds, which may explain their relative tolerance to high intraspecific density conditions for this larval trait, although we did not observe schooling.

Larval period length was longer for *R. areolata* when reared with *R. blairi* than when alone (Fig. 3B). Larval period length for *R. areolata* did not differ when alone relative to when reared with *R. sphenoccephala*. Nevertheless, *R. areolata* when reared with *R. sphenoccephala* had shorter larval periods than *R. areolata* with *R. blairi*, suggesting a more severe interspecific effect of *R. blairi* on *R. areolata*. In time-limited environments, such as the temporary breeding ponds used by these three species, larval success and population growth are dependent on larval period length relative to pond hydroperiod (Semlitsch et al. 1996). Short larval periods allow larvae to metamorphose quickly and escape a drying pond (Smith 1983; Newman 1988a,b), and avoid exposure to aquatic predators (Woodward 1983). Thus, length of the larval period may be under strong viability selection and can be considered a critical indicator of larval fitness.

R. blairi was affected negatively by competition with *R. areolata*. Ponds with *R. blairi* produced fewer metamorphs when reared with *R. areolata* than when alone at high density (Fig. 3A). High larval density conditions are frequently encountered in natural populations of *Rana* (Morin 1983; Petranka 1989; R.D. Semlitsch, personal observation). Decreased metamorph production by *R. blairi* when reared with *R. areolata* at high density may decrease recruitment of *R. blairi* into adult populations and influence subsequent population growth and persistence (Berven 1990; Semlitsch et al. 1996).

Body mass at metamorphosis was facilitated for *R. sphenoccephala* when reared with *R. areolata* (Fig. 2B), being larger at both densities than when alone. Werner (1992) noted a similar interaction in competition experiments with wood frog larvae facilitating the growth of northern leopard frog larvae. Additionally, *R. sphenoccephala* metamorphs were larger when reared in low- than in high-density ponds, suggesting an important influence of larval density on body mass for this species.

Interspecific differences in body mass are frequently used to explain asymmetric competition in larval amphibians (Morin and Johnson 1988). Large competitors are often superior due to increased foraging ability relative to smaller ones. Although exploitative competition has been found to be the primary mechanism of competition among larval amphibians, interference competition may also be involved in some instances (Lawton and Hassell 1981; Persson 1985; but see Morin and Johnson 1988). Species differed in body mass at metamorphosis, averaging across all treatments 2466 mg for *R. areolata*, 2083 mg for *R. blairi*, and 1776 mg for *R. sphenoccephala* (Table 2). Despite the relatively large body mass of *R. areolata*, it was the inferior competitor in our experiment, indicating that size-dependent competition may not be as important as behavioral mechanisms.

Competitive ability may also be related to larval behavioral activity. Larvae, by spending a large proportion of their time budget foraging, may increase their competitive ability through reducing per capita food availability for competitors (i.e., exploitative competition). This mechanism has been demonstrated in *Scaphiopus holbrooki*, *R. sylvatica*, and *R. esculenta*, all of which show high levels of larval activity and foraging abilities (Woodward 1983; Rist et al. 1997). *R. areolata* may be an inferior competitor due to a decreased foraging rate relative to its competitors. A final alternative is that *R. areolata* may be relatively intolerant to other mechanisms of interference competition, such as increased aggression through interspecific crowding or chemically mediated growth inhibitors (Beebee 1991; Griffiths 1995). Differences in foraging efficiency and activity levels, within and among species, are mediated by larval density in determining competitive outcomes and also likely interact with predation and disturbance to regulate community structure (Werner 1992; Werner and Anholt 1993).

Conservation implications for *R. areolata circulosa*

Although the pattern and process of global amphibian decline remains controversial, recent reports suggest that many amphibian species are experiencing local or regional population declines and range reductions (Blaustein and Wake 1990; Wake 1991; Blaustein et al. 1994). Habitat loss and fragmentation are primary extinction mechanisms of rare or endangered species (Lande 1987). Alternatively, stochastic or deterministic processes may be important for local population dynamics of species with small population sizes. Many amphibian species exist as series of segregated local populations interconnected by migration and colonization allowing for the persistence of the metapopulation (Levins 1970; Pulliam 1988). Strong isolation among populations, perhaps created through severe habitat fragmentation, may increase the probability of regional extinction because immigration and recolonization cannot occur readily (Sjogren 1991). Blaustein and Wake (1990) suggest that this mechanism is relevant in the decline of several species of anurans in the Pacific Northwest. Furthermore, emigration and hence the reestablishment of locally extinct populations depends upon sufficient production of metamorphs (Semlitsch et al. 1996). Decreased juvenile recruitment caused by competitive interactions in the larval life history stage can have drastic impacts on the population persistence of rare or endangered species (Smith 1987; Semlitsch et al. 1988; Berven 1990). Our results indicate that *R. areolata* has reduced success for body mass at metamorphosis and larval period length when reared with *R. blairi* or *R. sphenoccephala*. Because of this reduced success, *R. areolata* may be at a high risk of local extirpation in areas where it is sympatric with *R. blairi* or *R. sphenoccephala*. Furthermore, *R. areolata* may be in particular danger of regional extinction

because it is strongly associated with tallgrass prairies or degraded native grasslands, two habitats which increasingly are being fragmented or converted to cropland (Kuchler 1974; Busby and Brecheisen 1997).

Competitive exclusion is not the rule, however, in all cases of asymmetric competition (Morin and Johnson 1988). Coexistence may occur through differential predation on superior competitors or through interactions with other anuran species (Morin 1983; Wilbur 1987; Werner and Anholt 1993). Furthermore, spatial and temporal heterogeneity in the availability of aquatic habitats may create an open, non-equilibrium situation where not all species are present at the same time. Competitive interactions may also be altered by priority effects, which typically are created by the sequential arrival of different species (Morin 1983; Alford and Wilbur 1985; Wilbur 1987).

The decline of *R. areolata* may be enhanced by predation or competitive interactions with introduced or exotic species (Blaustein and Wake 1990; Kiesecker and Blaustein 1997; Kupferberg 1997). The decline of several western United States ranid frog species has been attributed to the introduction of the bullfrog, *R. catesbeiana* (e.g., Hayes and Jennings 1986; Clarkson and Rorabaugh 1989). Although speculative, the relatively weak interspecific competitive ability of *R. areolata* might extend to interactions with other ranid species or exotics, such as bullfrogs. Such interactions could then compound the already serious problem of weak interspecific competitive ability by forcing dangerously small populations of *R. areolata* into bottlenecks through reduced juvenile recruitment, potentially leading to large-scale patterns of irreversible extinction. Although the impact of exotic species on the northern crawfish frog remains to be tested, it is evident that the population persistence of *R. areolata* is strongly influenced by larval interactions with some ranid species.

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