



# Evaluating condition-specific and asymmetric competition in a species-distribution context

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Mechanisms resulting in parapatric distributions of closely related taxa have long interested ecologists. If two species are distributed across an environmental gradient, and differ in their ability to cope with environmental conditions, the outcome of competitive interactions may be dependent on prevailing abiotic conditions. Two closely related species of poison frogs in north-central Peru were observed to occupy parapatric distributions across an elevation gradient. *Ameerega bassleri* is a highland endemic restricted to a small region of Peru, and *A. trivittata* is distributed throughout lowland Amazonia. The goal of this study was to examine the effect of an abiotic factor (elevation) on two biotic factors (intraspecific and interspecific competition), by measuring growth and survival in the larvae of *A. trivittata* and *A. bassleri*. Using mesocosm experiments arranged in a fractional factorial design, we found that (1) *A. bassleri* had a strong negative effect on the growth and survival of *A. trivittata* regardless of elevation, (2) *A. trivittata* had no effect on the growth of *A. bassleri* at either elevation, but did appear to reduce the survival of *A. bassleri* more strongly in the lowlands than highlands, (3) lowland conditions uniformly reduced survival in all treatments and in both species, and (4) competition was strongly asymmetric between *A. bassleri* and *A. trivittata*. We conclude that the perceived low density of *A. trivittata* in highland sites may be influenced by the presence of *A. bassleri*, but the lower limit to the distribution of *A. bassleri* cannot be explained by competition with *A. trivittata* and may be due to physiological constraints imposed by lowland conditions.

Factors that influence community structure can ultimately define a species' distribution (Brown 1984), a theme uniting ecology and biogeography. As MacArthur (1972) states, "The ranges of single species would seem to be the basic unit of biogeography". Factors influencing community structure and species ranges may include biotic interactions (Connell 1961, Hairston 1980), abiotic constraints (Grinnell 1917, Freda and Dunson 1986, Dunson and Travis 1991, Halverson et al. 2003), and interactions between the two (Dunson and Travis 1991, Warner et al. 1993, Chalcraft and Andrews 1999, Taniguchi and Nakano 2000). More specifically, the distribution or population viability of a species can be constrained by unfavorable biotic interactions such as competition (Connell 1961), predation (Wilbur 1972, Morin 1983), or parasitism (Minchella and Scott 1991, Poulin 1999), or increased by favorable interactions such as increased food availability (Gawlik 2002) or mutualisms such as mycorrhizae in plants (Hartnett and Wilson 1999). Competition has long been held as a key factor influencing species distributions, particularly among closely related or ecologically similar species distributed across an environmental gradient (Hairston 1951, Jaeger 1971, Terborgh and Weske 1975). Hairston (1980) provided strong support for this idea through competitor-removal experiments on plethodontid

salamanders, in which the removal of one species resulted in a range expansion by its close competitor.

When potential competitors occur together, competition may be symmetric, where both species are affected equally by the other, or asymmetric, where one species is more affected by competition than the other. Asymmetric competition has been proposed as an interaction that may influence community structure by resulting in competitive exclusion and potentially allopatric distributions of taxa (Wiltshire and Bull 1977), and has been shown to be common in many taxa (Lawton and Hassell 1981, Connell 1983, Schoener 1983). Previous studies have documented asymmetric competition in larval anurans (Morin and Johnson 1988, Laurila 2000, Smith et al. 2004, Lehtinen 2005), but these studies have typically attempted to identify properties of species that make competition permanently asymmetric (such as tadpole size or foraging efficiency), rather than attempting to identify factors that cause a switch in which species is the dominant competitor.

Interactions between abiotic conditions and competitive interactions may modulate (or in extreme cases switch) competitive abilities. There has been a long history of studies examining the influence of abiotic conditions on biotic interactions in both plants (Tansley 1917) and animals (Ayala 1966, Warner et al. 1993, Taniguchi and

Nakano 2000, Thomas and Holway 2005). One study in larval anurans (Warner et al. 1993) found that pH and interspecific competition interacted to affect survival and larval period in the tree-frog *Hyla gratiosa* and size at metamorphosis in *H. femoralis*, but in both species these interactions were only apparent at high densities and high pH levels. Taniguchi and Nakano (2000) found evidence of temperature-mediated competitive dominance in salmonid fishes, with a high-elevation species being dominant in cool water and a low-elevation species dominant in warmer water. Other, more recent studies in amphibians have also demonstrated these types of effects due to pesticides (Relyea et al. 2005, Boone et al. 2007).

Condition-specific competition, where the outcome of competitive interactions is modulated by abiotic factors, has been proposed as a mechanism explaining how competition may shape community structure (Dunson and Travis 1991) and species distributions (Taniguchi and Nakano 2000) by resulting in the competitive exclusion of a subordinate species when it occurs in the presence of a dominant species (Morin 1999). A few researchers have invoked condition-specific competition as an explanation for parapatric (largely allopatric but slightly overlapping) distributions of closely related taxa, on the basis that if two species are adapted to two different environments, neither species is a competitive superior outside of its optimal habitat. Jaeger (1971) noted that the salamander *Plethodon richmondi* was restricted to talus habitats while *P. cinereus* lives in deep-soil habitats outside the talus, and found that in the presence of interspecific competition, each species had reduced survivorship outside of its natural habitat. Taniguchi and Nakano (2000) used their results to explain species distributions in two salmonids, but on a larger geographic scale (i.e. Japan's north island). In both studies, each species was physiologically capable of persisting in either habitat in the absence of competition, but differential success at the range edge of either species was the proposed mechanism leading to their parapatric distributions.

The purpose of this study was to evaluate asymmetric and condition-specific competition in a species-distribution context in two species of tropical anurans in north-central Peru. Poison frogs (family Dendrobatidae) of the genus *Ameerega* are a potentially valuable system for evaluating competition in this context, as many (up to six) species of *Ameerega* occur near Tarapoto, Peru, and species of this genus utilize small, terrestrial breeding pools for tadpole development. Two of the more common species, *A. trivittata* and *A. bassleri*, are parapatric across an elevation gradient near Tarapoto and share breeding resources in zones of sympatry, so interspecific competition in the larval stage is likely. To our knowledge this study is only the second to address asymmetric competition in tropical amphibians (Lehtinen 2005), the first to address condition-specific competition in a tropical system, and the first to address both asymmetric and condition-specific competition in a species-distribution framework in tropical taxa.

## Study system

*Ameerega trivittata* (previously called *Epipedobates trivittatus*; Grant et al. 2006) is widely distributed throughout the

Amazon basin in Peru, Colombia, Brazil, Bolivia and the Guiana Shield (Silverstone 1976). Most of its range lies in the Amazon lowlands (30–180 m elevation), but in Peru this species is common up to approximately 600 m elevation, and has been observed as high as 1490 m, though it does not appear to be common at such high elevations. A closely related species, *Ameerega bassleri*, is restricted to montane habitats of the east-Andean versant of north-central Peru (Roberts et al. 2006). This species is most common between 500 and 1100 m elevation, though individuals have been found as high as 1262 m and as low as 180 m. In low-elevation populations, these frogs occur exclusively in association with small, enclosed streambeds at the base of mountains (Ewomey unpubl.). All species of *Ameerega* lay terrestrial eggs which are tended by the male, and upon hatching, tadpoles are transported by the male to a suitable water source (Silverstone 1976). Reproduction in both *A. trivittata* and *A. bassleri* takes place year-round, and tadpoles are deposited in lentic bodies of water such as roadside ditches, forest pools, or pools formed alongside small streams. Tadpoles were commonly found in sympatry between 500 and 600 m elevation, thus there was potential for interspecific competition between these two species.

We constructed the following verbal model to explain the observed distribution of these two species. We hypothesized that, because *A. bassleri* is a montane endemic, it should be adapted to highland conditions and should thus dominate in competition experiments in the highlands, whereas *A. trivittata* should be more adapted to lowland conditions and therefore dominate competition experiments in the lowlands. Temperature and insolation have been shown to be important determinants of tadpole performance (Skelly and Freidenburg 2000, Skelly et al. 2002, Halverson et al. 2003) and likely differ between our sites, with lowland sites having higher temperatures and in general higher solar insolation. Site-specific dominance would suggest that the distributional segregation observed in these two species could be in part due to competitive exclusion through condition-specific competition.

## Material and methods

### Experimental design and procedures

To evaluate the effect of elevation on intraspecific and interspecific competition in the larvae of these species, we conducted a reciprocal transplant experiment where we measured competition in two sites (highlands and lowlands). We manipulated intraspecific and interspecific density in artificial pools, so that in each site we had three treatments for each species: a low-density, single-species treatment (10 tadpoles per vessel), a high-density, single-species treatment (20 tadpoles per vessel), and a mixed-species treatment (10 tadpoles of each species per vessel). These treatments allow us to compare the per-individual effects of conspecific and heterospecific competitors by controlling for overall tadpole density while manipulating species composition, and therefore allow us to explicitly test for asymmetric competition by disentangling density-dependent effects from per-capita differences between

species. Each treatment was replicated 3–6 times, and treatments were split between sites so that there were 25 experimental pools in the lowlands and 23 in the highlands. Treatments were set up in two sites in northern Depto San Martin, Peru. Based on interpolated WORLDCLIM data (Hijmans et al. 2005), the climatic conditions in our site in the Cordillera Oriental differ from those in the nearby Amazonian lowlands (~180 m elevation, mean annual temp. 25.7°C, annual precip. 2778 mm) with respect to temperature and precipitation. The highland site (505 m elevation, mean annual temp. 24.8°C, annual precip. 1772 mm) was located in the Cainarachi valley, a steep valley situated in the northern Cordillera Oriental of Peru. The lowland site (330 m elevation, mean annual temp. 25.1°C, annual precip. 1303 mm) was located in the city of Tarapoto. This area is sparsely forested and more arid, and consequently receives more solar radiation than the Cainarachi valley. The WORLDCLIM data predicted only a small temperature difference between these sites, although the temperatures measured in the experimental pools were substantially different between the two sites (Cainarachi valley, mean daily max/min = 30/18.5°C; Tarapoto, mean daily max/min = 33/19°C). Solar insolation may also be higher in Tarapoto than in the Amazonian lowlands, however our pools were set up under artificial cover and comparable to pools set up in forested sites.

Ten liter plastic washtubs were used for competition experiments. Tubs were ≈30 cm in diameter and 15 cm deep. Maximum tadpole density in an experiment was two tadpoles per liter, a density comparable to field conditions. Most natural pools range in size from 6–47.1 (n = 7, mean = 28.71), though we have found tadpoles of both species in depressions formed by cattle hoof prints (approx. 100–300 ml). Densities in natural settings are highly variable, but based on tadpole collection data in measured natural pools, we estimate field densities to range from 0.2–7.6 (mean = 1.9) tadpoles per liter, although we have observed on several occasions 10–15 tadpoles occurring in pools smaller than half a liter.

Tadpoles used in the competition experiments came from three sources: 1) from the backs of tadpole-carrying males, 2) free-living tadpoles collected along the Tarapoto–Yurimaguas road, and 3) free-living tadpoles collected from artificial pools being used for another study. Sites for tadpole collection were found by walking along the road between km 14 and km 40 and dip-netting in roadside ditches. Tadpoles were identified to species in the field based on snout pattern and transported to the experimental sites. Free-living tadpoles are problematic in that they vary in developmental stage, for that reason only tadpoles stage 30 or smaller were used for experiments. Due to the difficulties of collecting large numbers of small-stage tadpoles at one time, tadpole collection was continuous throughout the field season (May–August of 2005 and 2006) and replicates were started as tadpoles became available. When tadpoles were available, we distributed them across different treatments to control for effects of seasonal variation. For example, tadpoles collected early in the season were not all allocated to one treatment but rather distributed across as many treatments as possible. The result was that replicates lasted for different lengths of time; those set up early in the season lasted up to 110 days, while

those set up late in the season in some cases lasted as short as 21 days.

An experimental pool was started by grouping tadpoles by size and stocking them in tubs; these tubs were then filled with dechlorinated tap water and three dried *Cecropia* leaves. Tadpoles were fed commercial rabbit chow ad libitum, and weighed weekly with a digital scale to the nearest 0.01 g for the duration of each experiment. Fifty-percent water changes took place weekly. Metamorphosing tadpoles were removed from the tubs at stage 44 to prevent drowning; at stage 46 (Gosner 1960) metamorphs were weighed to the nearest 0.01 g and measured (snout–vent) to the nearest 0.1 mm with mechanical calipers.

## Data analysis

We measured three variables in order to evaluate larval performance: mass of surviving tadpoles at day 30, percent mortality after 30 days, and an estimated survival function over time. Rapid growth of tadpoles has been suggested to contribute to a faster larval period, which may allow tadpoles to alleviate predation and desiccation risk (Wilbur 1980). We could not analyze mass at metamorphosis because some replicates did not last long enough for metamorphosis to occur for most larvae. Mass and mortality data were log transformed to conform to assumptions of parametric tests. Replicates varied in how long they ran depending on when they were set up, but mass after 30 days was chosen as an arbitrary cutoff since most pools were still running and differences in tadpole growth and survival were already apparent.

We used planned contrasts between particular sets of treatments to test specific hypotheses about the effects of elevation, intraspecific competition, and interspecific competition. To test hypotheses about interactions between elevation and competition, we used a factorial ANOVA. All analyses were run separately for each species. To test the hypothesis that elevation affects the growth of species A, we performed a planned contrast that compares the growth of species A in all lowland treatments to all highland treatments (contrast 1). There was a significant negative correlation between tadpole mass and number of tadpoles remaining in the experiment in both lowland experiments ( $R^2 = 0.157$ ,  $p < 0.001$ ) and highland experiments ( $R^2 = 0.143$ ,  $p < 0.001$ ); therefore, ANCOVA was used for this contrast with tadpoles remaining at day 30 as the covariate. This contrast confounds all other factors (i.e. interspecific and intraspecific density), but tells us whether or not there were any differences between the two levels of the abiotic factor. To test the hypothesis that intraspecific density influences growth in species A, we performed a planned contrast comparing low-density, single-species treatments and high-density, single-species treatments, pooled across site (contrast 2). To test for an interaction between elevation and intraspecific effects, we performed a factorial ANOVA on low-density, single-species and high-density, single-species treatments with elevation (highland/lowland) as the factor (contrast 3). To test the hypothesis that the presence of species B influences growth of species A, we performed a planned contrast that compares single-species, low-density treatments in species A to mixed species

treatments in species A, pooled across site (contrast 4). An interaction between elevation and interspecific competition was tested with a factorial ANOVA using low-density, single-species treatments and mixed-species treatments with elevation as the factor (contrast 5). To test the hypothesis that the strengths of interspecific and intraspecific competition in species A are equal, we performed a planned contrast comparing high-density, single-species treatments in species A with mixed-species treatments in species A, pooled across site (contrast 6). Finally, to test for an interaction between elevation and species equivalence, we performed a factorial ANOVA on high-density, single-species and mixed-species treatments with elevation as the factor (contrast 7). This final contrast fixes total density and is thus a more informative test for condition-specific competition than contrast 5 which does not fix tadpole density. While a significant result for the latter would suggest condition-specific competition, it does not tell us whether the interaction is due to increased competitor density or simply an increase in overall tadpole density (per capita differences of species vs density-dependent effects).

In addition to analyzing 30-day mortality, we analyzed survival as a function over time using the Kaplan–Meier product-limit estimator. Because of the difficulties of starting many replicates at one time, the duration of each experiment varied substantially (21–110 days across all replicates), resulting in many instances where a treatment regime was represented by replicates of varying duration. The resulting functions were compared using the Mantel–Cox log rank test, a nonparametric test designed to compare hazard functions containing censorship events. Both the Kaplan–Meier estimator and the Mantel–Cox log rank tests have been widely used in clinical trials to account for censorship events, where a patient drops out of a study before the final outcome is observed. Pairwise contrasts were made separately for each species and site, and across all three treatments to determine effects of intraspecific

density, interspecific density, and per capita interspecific effects on survival.

To test for asymmetric competition (whether the effect of species A on B is equivalent to the effect of species B on A), we used a factorial ANOVA with the factors species equivalence and species identity, with mass at day 30 as the response variable. For this contrast we crossed high-density, single-species and mixed species treatments of one species with high-density, single-species and mixed species treatments of the other species. An ANCOVA showed no effect of site in either species (Table 1, contrast 1), so highland and lowland treatments were pooled within a species.

## Results

### *Ameerega trivittata*

Growth trends for *A. trivittata* were similar in the lowlands and highlands, with low-density, single-species having grown the most after 30 days, and high density and mixed-species treatments having grown the least (Fig. 1). For 30-day mortality, only contrast 1 (which tests for the main effect of site) was significant. Mortality after 30 days was significantly higher in the lowlands, so we used analysis of covariance with tadpoles remaining at day 30 as a covariate for contrast 1. Tadpole growth was not significantly affected by site (Table 1). Though tadpoles were on average 33% larger after 30 days in lowland conditions, this difference was attributable to covariance with decreased density due to mortality. Intraspecific competition was evident in this species; increasing conspecific density resulted in a marginally significant reduction of tadpole mass after 30 days of growth, but intraspecific competition did not interact with elevation to influence tadpole mass (Table 1). Interspecific competition was the strongest factor reducing growth in this species and accounted 26.6% of the variation in growth. This contrast does not control for

Table 1. Results of significance tests for planned contrasts and factorial ANOVAs for both species. Tadpole mass was treated with an ANOVA unless indicated otherwise. Effect size is reported as partial eta-squared ( $SS_{\text{hypothesis}}/(SS_{\text{hypothesis}} + SS_{\text{error}})$ ) only if the contrast was significant at the 0.05 level (one marginally significant value reported). Numbers in parentheses in the contrast column refer to the treatments that were used for that contrast, treatment numbers following Fig. 1 left to right within a species, so that low-density, lowland treatments would be no. 1, and mixed-species, highland treatments would be no. 6.

| Contrast                                   | Tadpole mass |       |       |             | 30-day mortality |       |        |             |
|--|--------------|-------|-------|-------------|------------------|-------|--------|-------------|
|  | DF           | F     | p     | Effect size | DF               | F     | p      | Effect size |
| <i>Ameerega trivittata</i>                 |              |       |       |             |                  |       |        |             |
| 1. Elevation effects (1, 2, 3 vs 4, 5, 6)* | 1            | 0.09  | 0.758 | –           | 1                | 36.99 | <0.001 | 0.597       |
| 2. Intraspecific density (1, 4 vs 2,5)     | 1            | 4.14  | 0.061 | 0.117       | 1                | 0.015 | 0.903  | –           |
| 3. Elevation × Intraspecific density**     | 1            | 0.23  | 0.163 | –           | 1                | 0.04  | 0.844  | –           |
| 4. Interspecific density (1, 4 vs 3, 6)    | 1            | 5.44  | 0.034 | 0.291       | 1                | 1.74  | 0.207  | –           |
| 5. Elevation × Interspecific density**     | 1            | 0.56  | 0.470 | –           | 1                | 0.481 | 0.499  | –           |
| 6. Species equivalence (2, 5 vs 3, 6)      | 1            | 1.21  | 0.286 | 0.070       | 1                | 1.338 | 0.263  | –           |
| 7. Elevation × Species equivalence**       | 1            | <0.01 | 0.969 | –           | 1                | 0.193 | 0.666  | –           |
| <i>Ameerega bassleri</i>                   |              |       |       |             |                  |       |        |             |
| 1. Elevation effects (1, 2, 3 vs 4, 5, 6)* | 1            | 0.37  | 0.551 | –           | 1                | 86.44 | <0.001 | 0.769       |
| 2. Intraspecific density (1, 4 vs 2,5)     | 1            | 11.25 | 0.004 | 0.253       | 1                | 0.007 | 0.933  | –           |
| 3. Elevation × Intraspecific density**     | 1            | 0.01  | 0.940 | –           | 1                | 0.101 | 0.756  | –           |
| 4. Interspecific density (1, 4 vs 3, 6)    | 1            | 0.23  | 0.635 | –           | 1                | 0.045 | 0.834  | –           |
| 5. Elevation × Interspecific density**     | 1            | 0.21  | 0.656 | –           | 1                | 0.141 | 0.713  | –           |
| 6. Species equivalence (2, 5 vs 3, 6)      | 1            | 5.88  | 0.028 | 0.184       | 1                | 0.091 | 0.767  | –           |
| 7. Elevation × Species equivalence**       | 1            | 0.37  | 0.553 | –           | 1                | 0.648 | 0.434  | –           |

\*growth data compared using ANCOVA

\*\*interaction tested using factorial ANOVA

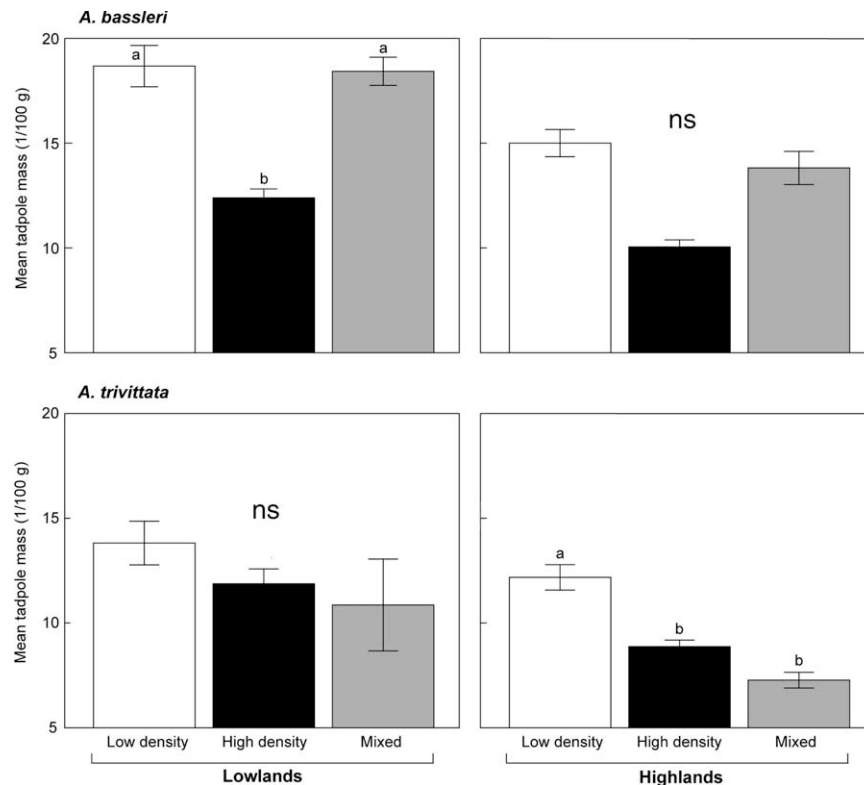


Figure 1. Mean mass of surviving tadpoles after 30 days of growth in *A. bassleri* and *A. trivittata* for each treatment. Error bars represent 1 SE. Post-hoc pairwise comparisons were made using Tukey's HSD. Pairs of means that do not differ significantly are joined by a common letter. Pairwise comparisons were only made within quadrants of the figure (i.e. within species and within site). ns = non-significant difference.

density effects, but if interspecific competition does not exist, then by definition there should be no difference between these treatments. Elevation did not interact with interspecific competition to influence tadpole growth. This contrast does not, however, account differential effects of conspecifics and heterospecifics. Per capita effects of *A. bassleri* on *A. trivittata* are addressed by the final two contrasts. When comparing growth, we found no significant difference between the strengths of inter- and intraspecific competition in *A. trivittata* (Table 1). There was no interaction between elevation and the equivalence of interspecific and intraspecific competition on tadpole mass, in other words, the effects of inter- and intraspecific competition were equal in both lowland and highland conditions.

When comparing survival functions (Table 2, Fig. 3), increasing intraspecific density had no effect on survival at either elevation, while increasing interspecific density significantly reduced *A. trivittata* survival in both the highlands and lowlands. The per capita effects of intra- and interspecific competitors were not equal; survival of *A. trivittata* was more strongly reduced by *A. bassleri* on a per capita basis in both highland and lowland environments.

#### *Ameerega bassleri*

Trends for tadpole growth were similar in both highland and lowland settings. In neither site did low density and mixed species treatments differ significantly, but in the lowlands high density treatments grew less than both other

treatments (Fig. 1). As with *A. trivittata*, mortality in *A. bassleri* was consistently higher in lowland treatments, so ANCOVA was used for contrast 1 to control for density effects. Results of contrasts for growth and mortality are shown in Table 1. Thirty-day mortality was significantly higher in the lowlands than the highlands, but no other contrast for mortality was significant. An ANCOVA showed no significant difference between sites with respect to growth (Table 1). The strongest factor influencing tadpole growth in *A. bassleri* was intraspecific competition, which explained 42.9% of the overall variation in growth. Intraspecific competition did not interact with elevation to influence tadpole growth, nor was there evidence of

Table 2. Comparisons of survival functions to examine the effects of intraspecific competition, interspecific competition, and per capita interspecific competition on survival throughout the duration of the experiments. Pairwise comparisons of functions were done with the Mantel-Cox log rank test.

| Contrast                   | Lowlands |       | Highlands |        |
|----------------------------|----------|-------|-----------|--------|
|                            | $\chi^2$ | p     | $\chi^2$  | p      |
| <i>Ameerega trivittata</i> |          |       |           |        |
| Intraspecific density      | 0.26     | 0.612 | 0.96      | 0.327  |
| Interspecific density      | 11.90    | 0.001 | 18.08     | <0.001 |
| Per capita effects         | 10.36    | 0.001 | 40.64     | <0.001 |
| <i>Ameerega bassleri</i>   |          |       |           |        |
| Intraspecific density      | 2.63     | 0.105 | 0.06      | 0.801  |
| Interspecific density      | 0.15     | 0.697 | 0.24      | 0.627  |
| Per capita effects         | 4.99     | 0.026 | 0.11      | 0.742  |

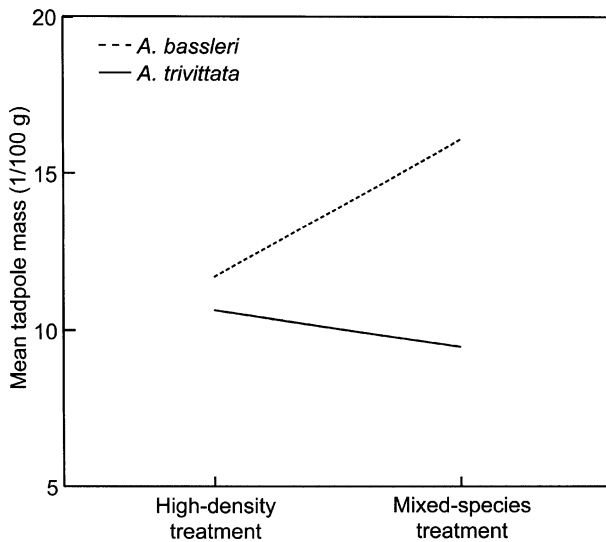


Figure 2. Interaction diagram showing asymmetric competition in *A. bassleri* and *A. trivittata*. This figure compares per capita effects of interspecific competition in both species. The positive slope of the line connecting *A. bassleri* means indicates that intraspecific competitors exert a stronger per capita effect than interspecific competitors in *A. bassleri*, while the negative slope for *A. trivittata* suggest the opposite is true for this species. The slopes of these lines are not parallel (factorial ANOVA for interspecific density  $\times$  species identity,  $F = 5.24$ ,  $p = 0.029$ ) indicating that the strengths of interspecific competition in these two species are not equal.

interspecific effects on *A. bassleri* with respect to growth. Tadpole growth in low density experiments was roughly equal to growth in mixed-species treatments, despite the fact that overall tadpole density in mixed-species treatments was twice that of low density treatments. Interspecific competition did not interact with elevation to influence growth. The contrast for species equivalence was significant, which indicates that the magnitudes of the effects of intraspecific and interspecific were different, but this difference was not influenced significantly by elevation (Table 1).

When comparing survival functions (Table 2, Fig. 3) in highland conditions, no treatment had a significant effect on *A. bassleri* survival. In the lowlands, survival responses were more complex. Increasing intraspecific density had no significant effect on survival, but there was a weak trend for slightly higher survival in high density than low density treatments. Interspecific density had no effect on survival when confounding overall tadpole density, but interspecific density significantly reduced survival on a per capita basis (Table 2, Fig. 3).

### Asymmetric competition

Asymmetry can be visualized by comparing the slopes of the lines in Fig. 2. Symmetrical competition would predict that each species would be equally affected by the presence of the other, and if this were the case than the slopes of the lines connecting means of single species and mixed species

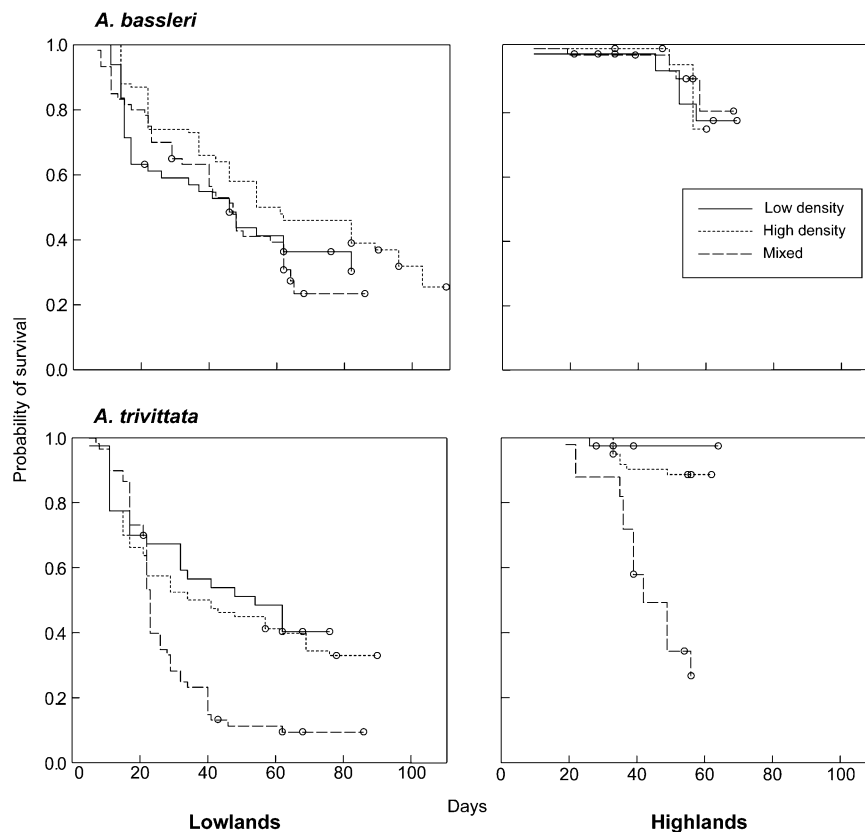


Figure 3. Survival functions drawn with the Kaplan–Meier estimator; open circles represent a censorship event. Each quadrant represents treatments for a single species and elevation. Significance tests for pairwise comparisons are given in Table 2.

treatments would be parallel. The interspecific density  $\times$  species identity factorial ANOVA tells us whether or not these lines are indeed parallel. There was an interaction between interspecific density and species identity, indicating these lines are not parallel, and that interspecific competition did not affect both species equally. Per capita effects of *A. bassleri* on *A. trivittata* were qualitatively different from the per capita effects of *A. trivittata* on *A. bassleri*, as indicated by the difference in sign of the slopes of the lines in Fig. 2.

## Discussion

We used mesocosm experiments in the field to examine the effect of elevation on intraspecific and interspecific competition in the larvae of two species of poison frogs distributed across an elevation gradient. The main effect of elevation was that it increased mortality in the lowlands in both species; any effects of elevation on competitive interactions were small in comparison. Intraspecific competition was present in both species, but the intensity of intraspecific competition did not change as a function of elevation in either species. Interspecific competition between these species was strong in *A. trivittata* when measuring survival but weak or absent in *A. bassleri* depending on the response variable measured. *Ameerega bassleri* had a strong negative effect on the growth and survival of *A. trivittata*, but these effects were not modulated by elevation. Conversely, the presence of *A. trivittata* had no effect on the growth of *A. bassleri* at either elevation (despite increased overall tadpole density), but did have a significant negative effect on survival of *A. bassleri* in the lowlands on a per capita basis. Per capita effects of heterospecifics were asymmetric in both species. Replacing conspecifics with an equal number of heterospecifics facilitated growth in *A. bassleri*, but reduced growth and survival in *A. trivittata*. These results suggest that larval *A. bassleri* are competitively superior to larval *A. trivittata*, regardless of elevation. This may be attributable to an inherent difference in growth rates and/or size of the tadpoles of these species. If we compare growth of these species under 'good' conditions (low density), *A. bassleri* tadpoles are consistently larger than *A. trivittata* after 30 days, suggesting that *A. bassleri* may be dominant simply because it grows faster, attains a larger size, and presumably exploits resources (such as periphyton) more efficiently than *A. trivittata*.

Inferring causality with regard to species distributions is difficult and requires the removal of a competitor and observing a range shift in another species. To our knowledge this has only been done in one study (Hairston 1980), which focused on plethodontid salamanders. Removing abundant and vagile species (such as these frogs) would be very difficult. We can, however, measure interactions between two competitors occupying parapatric ranges and interpret these results in a species-distribution framework. Competition in larval amphibians is thought to be a major factor regulating overall population sizes (Wilbur 1980), by influencing survivorship (Wilbur 1972, Semlitsch and Caldwell 1982), thus translating directly into numbers of metamorphosing individuals, or by influencing meta-

morphic traits, which can affect fitness of adults (Semlitsch et al. 1988, Altwegg and Reyer 2003).

The absence of *A. bassleri* from lower elevations cannot be explained by larval competition with *Ameerega trivittata* based on our results. Though *A. trivittata* did reduce the survival of *A. bassleri* in the lowlands, these effects were small compared to the general effect of lowland conditions, which was to drastically reduce survival in all treatments. Furthermore, competition with respect to survival appeared to be asymmetric in the lowlands, so that the effect of *A. trivittata* on *A. bassleri* was weak compared to the effect of *A. bassleri* on *A. trivittata*. Competition with other species not included in this study may influence the distribution of *A. bassleri*, as an estimated 119 species of anurans (five of which are congeners) occur sympatrically with *A. bassleri* in northern San Martín, Peru (R. Schulte, pers. comm.), but only three other species of larval anurans were commonly found with *A. bassleri* larvae (*Osteocephalus taurinus*, *Bufo marinus* and *B. margaritifera*). These three species occur in both lowland and highland habitats, and thus cannot explain the absence of *A. bassleri* from the lowlands. Competition between adult anurans may also play a role in shaping anuran communities, though few studies have examined this possibility (but see Lehtinen 2005), and fewer still have found evidence of competition in adult anurans (Wilbur 1980).

If *A. bassleri* was derived from a montane ancestor, it would be possible that radiation into the lowlands simply has not occurred yet, but phylogeographic evidence suggests that the ancestor to *A. bassleri* was a lowland species that radiated into montane habitats (Roberts et al. 2006), so this seems unlikely. However, climatic changes in the more recent past (i.e. post-Pleistocene) may have imposed physiological constraints on *A. bassleri*, excluding them from the lowlands. Conditions during the Pleistocene are thought to have been cooler and drier than current conditions (Bush 1994), and subsequent warming would presumably have caused *A. bassleri* populations to shift towards the highlands. Current abiotic conditions may therefore play an important role in limiting the current distribution of *A. bassleri* by imposing physiological constraints on both adults and larvae. This idea is supported by our experimental results, where larval mortality is high in lowland conditions, and by our field observations, where adult *A. bassleri* in lower altitudes have been observed to occur exclusively in deep-cut streambeds characterized by cooler temperatures than the surrounding forest, whereas in higher altitudes they appear to be less habitat-specific and can be found throughout the forest. The idea that amphibian community structure may be strongly regulated by abiotic factors has been supported by recent studies (Halverson et al. 2003, Werner et al. 2007), which have found that certain environmental parameters (such as canopy cover or pond hydroperiod) are strongly correlated to patterns of species occurrence and richness.

The reduced abundance of *A. trivittata* in highland areas may be at least partially attributed to the presence of an abundant and dominant competitor, *A. bassleri*. When two species compete over a limited resource, one possible result is that the subordinate species becomes excluded from the habitat in dispute (Hardin 1960). Reproductive resources have been shown to limit population sizes in another

dendrobatid frog, *Oophaga pumilio* (Donnelly 1989), and are likely to be a limiting factor for *A. bassleri* and *A. trivittata*. Theory predicts that in two species that compete asymmetrically, the dominant species will exclude the weaker species unless the dominant becomes self-limited (Lawton and Hassell 1981, Connell 1983). Self-limitation can occur when the effect of intraspecific competition is stronger than interspecific competition (Morin 1999). Based on our results, *A. bassleri* might be predicted to exclude *A. trivittata* in the highlands, since interspecific competition is stronger than intraspecific competition in *A. trivittata* when measuring both growth and survival. How then can *A. trivittata* persist in sympatry with *A. bassleri*?

In more complex competitive relationships, competitive exclusion is not inevitable (Scheffer et al. 2003). Because species do not compete in pairs, any one species may experience different intensities of competition in natural communities, and complex associations of species can produce results that are difficult to predict. For example, Wilbur (1987) found that in an experimental community composed of four larval anuran species, predators selectively targeted the competitively dominant species, which allowed competitively weaker species to perform better, and that these effects were modulated by abiotic factors such as pond hydroperiod. Relyea (2000) found that threat of predation (as opposed to direct predation) reversed the outcome of interspecific competition in two species of larval anurans by inducing the weaker species to increase mouth width and tail length.

An unstable environment may also promote species coexistence (Hutchinson 1961, Connell 1978) by creating conditions where a single species cannot remain dominant for long enough to exclude weaker competitors. Subsequent theoretical work (Huisman and Weissing 1999, 2001) demonstrated that even under stable conditions, multi-species systems with competition over multiple resources can generate oscillations of species abundance which are impossible to predict. Thus, while competitive exclusion is one possibility based on the results of our experiment, complex interactions within an entire community may alter interspecific competition in these two species in such a way that sustains their coexistence.

Defense of territories against heterospecifics has also been proposed as a mechanism by which competing species can overlap across an elevation gradient. For example, Robinson and Terborgh (1995) found that closely related bird species in the Andes tended to segregate spatially and interact aggressively. Previous work in poison frogs has demonstrated territoriality in a number of species (Roithmair 1992, Pröhl 1997, Caldwell and Oliveira 1999), including *A. trivittata* (Roithmair 1994). *Ameerega trivittata* males defend territories against conspecifics, but the cue for attacking an intruder is vocalization and thus may be a species-specific signal (Roithmair 1994). Furthermore, Roithmair (1994) found that territories defended by *A. trivittata* did not contain tadpole deposition sites; therefore, even if *A. trivittata* does defend territories against encroaching *A. bassleri*, reproductive resources are shared by both species. Thus, although it is possible that adults could segregate by defending territories, interspecific competition in shared reproductive habitats should still manifest a

response by reducing the abundance in the competitively inferior species. However, on a larger scale, habitat heterogeneity may promote intraspecific aggregation and thus species coexistence (Morin 1999). At lower altitudes, *A. bassleri* are more confined to areas of low solar insolation, which should free up habitat for *A. trivittata*.

Persistent influx of *A. trivittata* from lowland populations into highland habitats may play an important role in maintaining highland populations, if we assume that the lowlands (where *A. trivittata* is widely distributed) represent high-quality source habitat and the highlands represent low-quality sink habitat (due to the presence of *A. bassleri*). Tadpole deposition data suggest that adult *A. trivittata* actively avoid depositing tadpoles in pools containing conspecifics, to the point that they will deposit tadpoles in pools with *A. bassleri* more frequently than in pools with *A. trivittata* (Twomey et al. unpubl.), an observation which suggests that *A. trivittata* may be caught in an ecological trap (Robertson and Hutto 2006). Avoidance of conspecific competitors may therefore drive *A. trivittata* to disperse from source populations towards the highlands. The radiation of *A. trivittata* across Amazonia appears to have occurred both recently and rapidly (Roberts et al. 2006), and may explain why adult *A. trivittata* actually prefer to place tadpoles with *A. bassleri* tadpoles, in spite of the fact that this results in lower growth and survival.

Asymmetric competition has been demonstrated in a diverse array of animal taxa such as birds (Török and Tóth 1999), mammals (Luo et al. 1998), insects (Lawton and Hassell 1981), and amphibians (Morin and Johnson 1988, Laurila 2000, Pearman 2002, Smith et al. 2004), and appears to be the rule rather than the exception (Connell 1983, Schoener 1983). Asymmetric competition is thought to be a major force regulating community structure, potentially resulting in competitive exclusion (Morin 1999), and thus reducing the amount of species a community can contain (Rummel and Roughgarden 1983). Additionally, theoretic work suggests that asymmetric competition can cause the extinction of a species over evolutionary time (Law et al. 1997). Factors influencing the distributions of *A. bassleri* and *A. trivittata* are complex and appear to be different for each species, but interspecific competition is likely to be an important one. Asymmetric competition between these frogs imposes certain constraints on their coexistence, but despite this they are sympatric in some areas of their ranges. We argue that *Ameerega bassleri* is restricted to montane habitats due to physiological constraints associated with adaptation to a montane habitat, whereas the highland *A. trivittata* populations are limited due to larval interspecific competition with *A. bassleri*, and that persistent influx of *A. trivittata* from the lowlands may be allowing this species to co-occur with *A. bassleri*.

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