ABSTRACT

Evan M. Twomey. LARVAL COMPETITION AND ITS CORRELATES TO SPECIES DISTRIBUTIONS, HABITAT SELECTION, AND INCLUSIVE FITNESS IN PERUVIAN POISON FROGS (Under the direction of Dr. Kyle Summers). Department of Biology, April 2008.

Mechanisms promoting high rates of species turnover over distance have long interested ecologists. In particular, researchers have been interested in abutting distributions of closely related species distributed across an environmental gradient. One proposed mechanism for this phenomenon is differential competitive success as a function of environmental conditions, and that each species excludes the other through competition in its natural environment. The first chapter evaluates competition in the tadpoles of two species of poison frogs, in an attempt to elucidate factors influencing these species' distributions. The second chapter deals with reproductive habitat selection by adult poison frogs in response to risk of tadpole competition. In this study I found that habitat selection by the frog *Ameerega trivittata* is maladaptive in response to a montane competitor, *A. bassleri*. Habitat selection has been a central theme in ecological research, although typically less attention has been paid to the origins and maintenance of maladaptive behavior in natural conditions. Finally, the third chapter deals with the influence of kinship on intraspecific competition in tadpoles of *A. bassleri*. Kin selection theory predicts that kin groups should grow better than mixed groups since cooperation may be favored through the mechanism of inclusive fitness. However, studies testing this hypothesis in tadpoles have shown mixed results. My results for this study were inconclusive, but suggest that cooperative growth in kin groups may be counteracted by inherent genetic (and hence phenotypic) similarities between related individuals.

LARVAL COMPETITION AND ITS CORRELATES TO SPECIES DISTRIBUTIONS, HABITAT SELECTION, AND INCLUSIVE FITNESS IN PERUVIAN POISON FROGS

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CHAPTER 1: EVALUATING CONDITION-SPECIFIC AND ASYMMETRIC COMPETITION IN A SPECIES-DISTRIBUTION CONTEXT

Abstract

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.

Introduction

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, Schoener 1983, Connell 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 (e.g. Tansley 1917) and animals (e.g. 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 *Hyla 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 (see 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*: see 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 (EMT, pers. obs.). 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.

Materials 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 Departamento 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 2 tadpoles per liter, a density comparable to field conditions. Most natural pools range in size from 6 – 47 L (*N* = 7, mean = 28.7 L), 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 to 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 experiments 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 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 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 29.1% of the variation in growth. This contrast does not control for 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. The strengths of interspecific and intraspecific competition are not equal for *A. trivittata.* The addition of *A. bassleri* to a pool more strongly reduces growth in *A. trivittata* than adding the same number of conspecifics (Table 1). There was, however, no interaction between elevation and the equivalence of interspecific and intraspecific competition on tadpole mass, in other words, the difference in strength between inter- and intraspecific competition was 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 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 25.3% of the overall variation in growth. Intraspecific competition did not interact with elevation to influence tadpole growth, nor was there evidence of 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

Even without an explicit test, asymmetric competition was apparent since contrast 4 showed that interspecific competition had a strong effect on growth and survival in *A. trivittata* but not in *A. bassleri* (Table 1). 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 treatments would be parallel. The interspecific density × 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,* 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 strongly 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 (Semlitsch and Caldwell 1982, Wilbur 1972), thus translating directly into numbers of metamorphosing individuals, or by influencing metamorphic 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 congenerics) occur sympatrically with *A. bassleri* in northern San Martín, Peru (R. Schulte, unpubl. data), but only three other species of larval anurans were commonly found with *A. bassleri* larvae (*Osteocephalus taurinus,* *Bufo marinus,* and *B. margaritifer*). 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, multispecies 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, Chalcraft, Morales, and Summers, unpub. data), 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, Pearman 2002, Laurila 2000, Smith et al. 2004), and appears to be the rule rather than the exception (Schoener 1983, Connell 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*.

CHAPTER 2: AMAZONIAN POISON FROGS DEPOSITING TADPOLES WITH ANDEAN COMPETITORS: AN ANCIENT ECOLOGICAL TRAP?

Abstract

Reproductive habitat selection in anurans is an important determinant of an individual's fitness. Although previous studies have shown that anurans select reproductive habitat on the basis of many cues, relatively few have addressed competition risk as a potential cue. We investigate whether a widespread Amazonian frog, *Ameerega trivittata*, selects habitat for tadpole deposition on the basis of intra- or interspecific competition risk. Competition experiments from a previous study allowed us to determine the effects of competition a priori and therefore assess whether habitat selection in response to competitors was adaptive. Our results show that montane populations of *A. trivittata* adaptively select tadpole habitat in response to conspecific competitors. Conversely, their habitat selection in response to a heterospecific competitor (*A. bassleri*) is maladaptive and appears to function as natural ecological trap. We suggest that this ecological trap is maintained by high levels of gene flow from lowland populations that are naïve to the competitor, and the montane population of *A. trivittata* avoids extinction through its connectivity to lowland populations.

Introduction

Habitat selection has been a central focus in ecology, and has broad implications for community organization, population dynamics, patterns of biodiversity, and the evolution of behavior (Pulliam and Danielson 1991, Resetarits 1996, Morris 2003, Resetarits 2005). Effects of habitat selection on an individual's fitness have often been addressed in the context of reproduction, and reproductive success may be strongly dependent on where adults choose to place their offspring (Summers 1999, Murphy 2003). The importance of adaptive reproductive habitat selection has been demonstrated in a wide variety of animal taxa (Gates and Gysel 1978, Mokany and Shine 2003, Citta and Lindberg 2007), including temporary pond–breeding frogs (Resetarits and Wilbur 1989, Binckley and Resetarits 2002, Rudolf and Rödel 2005), which breed in discrete habitats that often vary in quality. The eggs and/or tadpoles of these frogs are faced with risks such as predation, competition, and pool drying—factors which vary between breeding habitats and impact larval survival (Hero et al. 1998, Murphy 2003). Although tadpoles may respond to environmental risks by plastic responses in morphology or behavior (Relyea 2001), adults bear the burden of placing their offspring in habitats conducive to larval survival, metamorphosis, and ultimately recruitment. Adults are therefore presumed to experience strong selective pressure to identify optimal habitats for reproduction.

To make an adaptive choice of habitat, species must recognize reliable cues that indicate habitat quality. Such cues may be indirect correlates of habitat quality that indicate the future condition of a habitat. For example, frogs that breed in temporary ponds cannot directly evaluate the risk of a pool drying at the time of oviposition, but may evaluate cues that correlate to drying risk (Rudolf and Rödel 2005). Other risk factors, such as the presence of predators or competitors, may be evaluated directly at the time of egg or tadpole deposition by detecting visual or chemical cues associated with predator or competitor species (Petranka et al. 1987). Previous studies of larval anurans have shown that competition reduces growth, survival, and mass at metamorphosis

(Wilbur 1977, Semlitsch and Caldwell 1982), all of which are correlates of fitness (Smith 1987, Semlitsch et al. 1988). If the risk of competition is an important indicator of habitat quality, natural selection should favor adults that minimize this risk by placing their offspring in habitats with low densities of potential competitors. Furthermore, tadpole competition is dependent not only on overall competitor density but also on competitor identity (Morin 1988). For pond-breeding anurans, where many species may co-occur in a breeding habitat, a species may alleviate competition risk if it can identify and avoid strong competitors (Resetarits and Wilbur 1989).

Because organisms are adapted to past conditions, rapid environmental changes may break down preexisting correlations between cue and habitat quality. This decoupling of cue and quality can occur when the cue changes, habitat quality changes, or both change simultaneously (Robertson and Hutto 2006). When the relationship between a habitat's cue and quality are altered to yield maladaptive habitat selection, the result is an "ecological trap" (Dwernychuk and Boag 1972). Ecological traps have been the focus of considerable theoretical attention in recent years (e.g. Kokko and Sutherland 2001, Schlaepfer et al. 2002, Kristan III 2003, Battin 2004, Robertson and Hutto 2006) with special regard to their potential consequences on wildlife populations and conservation strategies. Such consequences may include population declines or local extinctions (Kokko and Sutherland 2001), and source-sink population dynamics (Remeš 2000, Kristan III 2003), the latter of which may impose constraints on local adaptation (Garcia-Ramos and Kirkpatrick 1997, Battin 2004). Although most discussions on ecological traps have focused on anthropogenic impacts as instruments of rapid environmental change, natural processes, e.g., rapid dispersal or geographic radiation, may function similarly if an organism moves quickly into a novel environment where established rules of habitat selection are no longer adaptive (Kristan III 2003). However, with a natural ecological trap, maladaptive behavior is not a product of a rapid environmental change but rather an inability to adapt to novel conditions. This somewhat different type of ecological trap may be more common than reported in the literature. For example, Resetarits and Wilbur (1989) found that female gray treefrogs did not discriminate between empty pools and pools containing predatory newts, which they attributed to unpredictability of newts in ponds. However, females responded to cues with relatively weak fitness consequences such as conspecific competitors. Habitat selection rules may therefore be driven not by the forces that have the greatest fitness consequences on individuals, but by weaker forces that may be particularly predictable and to which adults are sensitive (Resetarits 1996).

Though the theoretical framework around ecological traps has been well-developed, empirical examples remain scarce. To demonstrate the existence of an ecological trap, one must (1) provide a measure of habitat preference, (2) estimate habitat-specific reproduction or survival, and (3) demonstrate a preference for the lower-quality habitat (Weldon and Haddad 2005, Robertson and Hutto 2006). Of the 45 studies summarized in a recent review on ecological traps (Robertson and Hutto 2006), just eight provided reasonable measures of preference and only five studies satisfied all three criteria. The generality of ecological traps will only be established by recognizing and investigating diverse empirical examples. This will be critical if we are to seek generality in understanding evolutionary and demographic processes and characteristics of species that can lead to ecological traps in particular and maladaptive behavior in general. Furthermore, examples of natural ecological traps are important since they allow researchers to evaluate conditions in which maladaptive behavior might arise and persist.

Poison frogs (family Dendrobatidae) provide an ideal system to investigate habitat selection strategies since most species deposit their tadpoles in phytotelmata or forest pools which vary greatly in quality (Caldwell and Araújo 1998, Summers and Amos 1997, Murphy 2003). Previous studies of reproductive habitat selection in poison frogs have evaluated cues such as predation (including cannibalism) risk, food availability, and abiotic characteristics of pools (Summers 1999, Poelman and Dicke 2007, von May et al. *submitted*, McKeon and Summers *submitted*). However, the hypothesis that poison frogs select pools by evaluating competition risk has not yet been addressed, and few studies have evaluated whether anurans can distinguish between two competitors which differ in their effects. As part of a separate study (Twomey et al. 2008 *accepted*) we measured intra- and interspecific competition among tadpoles of two poison frog species (*Ameerega trivittata* and *A. bassleri*), and found that for *A. trivittata*, interspecific competition resulted in poor growth and high mortality compared to the effects of intraspecific competition. The two species are sympatric in montane areas of northern Peru, and often use the same pools for tadpole deposition. For this study, we conducted pool-choice experiments using *A. trivittata* in which we manipulated the presence vs. absence of conspecific and heterospecific competitors in experimental pools in order to address the question: Do adults select deposition sites on the basis of the presence or absence of conspecific and/or heterospecific tadpoles? The results of the competition experiments allowed us to make a priori predictions of habitat selection, and address the question: Is reproductive habitat selection in *A. trivittata* adaptive with respect to maximizing larval growth and survival?

Methods

Study system

We chose *Ameerega trivittata* as our study species because it is common, readily deposits tadpoles in artificial pools, and is strongly affected by competition with *A. bassleri*. *Ameerega trivittata* is widely distributed throughout the Amazon basin, inhabiting altitudes up to 1490 m in the Cordillera Oriental. Reproduction occurs year-round at our study sites, and eggs are deposited terrestrially. Males transport a partial or entire brood of tadpoles to a small water body where tadpoles are deposited either simultaneously or in stages (Silverstone 1976). Suitable water bodies include small lentic pools in low-lying areas of the forest and roadside ditches, which range in size from 6–47 liters (N = 7, mean = 28.7 L) based on our field observations. Tadpole density is highly variable in nature, for both species averaging 1.9 tadpoles per liter (counting both species together), but ranging from 0.2–30 tadpoles per liter. The potential for tadpole competition between *A. bassleri* and *A. trivittata* is high, as both species are abundant between ca. 300–600 m elevation, and their tadpoles commonly co-occur in natural pools between 500–600 m elevation (E. Twomey *pers. obs.*). Furthermore, at one of our sites, 45 out of 151 deposition events (267 out of 847 tadpoles) involved *A. bassleri*. In other words, roughly 30% of all deposition activity in this site was attributed to *A. bassleri*. These two species were also the only two that used our experimental pools. Therefore, *A. trivittata* not only encounters *A. bassleri* in nature, but does so far more frequently than with tadpoles of any other species.

Pool choice experiments

Experiments were done in two premontane rainforest sites 23 km apart in the Cordillera Oriental mountains near Tarapoto in central Peru. Site 1 (6° 25' 33" S, 76° 17' 23" W) was located in the Cainarachi valley at 521 m in early-stage secondary forest; site 2 (6° 32' 35" S, 76° 6' 39" W) was located near the town of Chazuta at 318 m elevation in primary forest. In general, the zone of sympatry between our study species is shifted ca. 200 m lower in the Chazuta site.

We conducted two paired-pool choice experiments to evaluate whether male *A. trivittata* use conspecific and/or heterospecific tadpoles as cues for selecting tadpole deposition sites. For experiment 1, a pool pair consisted of one pool containing 10 *A. trivittata* tadpoles and the other pool unoccupied. This experiment allowed us to determine whether *A. trivittata* are capable of detecting conspecific tadpoles. We hypothesized that *A. trivittata* would choose unoccupied pools for deposition and thereby minimize the potential for intraspecific competition. For experiment 2, one pool contained 10 *A. trivittata* tadpoles and the other contained 10 *A. bassleri* tadpoles. This experiment allowed us to determine whether *A. trivittata* can distinguish conspecific versus heterospecific tadpoles occupying a pool, and if they use these cues to select tadpole deposition sites. We hypothesized that *A. trivittata* would choose pools containing conspecific tadpoles, since *A. bassleri* tadpoles are strong competitors (Twomey et al. *accepted*).

In total 112 ten liter plastic pools (each 30 cm in diameter and 15 cm deep) were used in the experiments. Pool size and tadpole densities were designed to match conditions of the competition experiments (see below) so that the competition experiments would be a meaningful representation of what tadpoles experience in our pool-choice experiments. Since male *A. trivittata* are territorial (Roithmair 1994), pools were arranged in widely-spaced clusters in order to sample the ranges of several males, maximizing the number of different males participating in the experiments and minimizing pseudoreplication (i.e., multiple depositions over time from the same male). Each cluster consisted of a single experiment type and clusters were separated by no less than 20 m. Within a cluster, pools were arranged in pairs so that paired pools were ~20 cm apart, and different pairs were located 3-10 m apart.

Site #1 contained 11 pool pairs set along a ~100 m transect and ran from 8-31 July 2006. We consider the pools in this site as one cluster since they were evenly spaced (one pair every ~10 m of transect) and consisted of only experiment 2. Site #2 contained eight clusters, with 5 pairs of pools per cluster, and ran from 6 June 2007 to 3 August 2007. In this site, each cluster was haphazardly assigned to an experiment type, such that each experiment was represented by four clusters. Experiment 2 was replicated in both sites, but experiment 1 was done only in Chazuta due to time constraints in 2006. Pools were dug into the ground and filled with water from a nearby stream. Two sticks were placed in each pool to facilitate egress of adults. Tadpoles used to stock pools were from roadside ditches alongside the Tarapoto-Chazuta and Tarapoto-Yurimaguas roads and from non-experimental artificial pools set up near both sites. When stocking pools of experiment 2, tadpoles of both species were matched for size to control for any effects of tadpole size on deposition preferences.

Pools were sampled 3-5 times per week, removing debris and dip-netting for tadpoles until all were caught. The pools' small size allowed us to be confident that all tadpoles had been captured. Potential predators such as dytiscid beetles were removed from pools. Distinguishing stocked from deposited tadpoles was done on the basis of species identity and/or tadpole size. *Ameerega trivittata* tadpoles can be distinguished from *A. bassleri* tadpoles because the latter species has two white spots lateral to the mouth. *Ameerega trivittata* tadpoles deposited in a pool containing stocked *A. trivittata* could be distinguished by size (stocked tadpoles were always larger) as well as the presence of yolk in their intestinal coils. Deposited tadpoles were counted and moved off-site to non-experimental pools. Stocked tadpoles were counted and, if mortality had occurred, stocks were replaced with new tadpoles.

To analyze our pool-choice data, we must first consider how a tadpole-carrying male might distribute a brood throughout a site. When a male first arrives at a pool cluster, he may deposit tadpoles in one pool or among several pools. Our data support the claim that some *Ameerega* species may deposit a single brood of tadpoles in multiple pools (Silverstone 1976); we observed *A. trivittata* carrying on average 16.8 tadpoles ($N = 5$), but depositing on average 9.5 tadpoles per deposition event ($N = 67$). Because paired pools are in close proximity, males were assumed to be choosing between pools within a pair, even if they moved from one pair to another. Pool clusters for different experiments were widely spaced to reduce the likelihood that males moved between clusters during the deposition of a single brood.

A male's preference for tadpole deposition site can be interpreted as the frequency of deposition in one pool type versus another. However, if males distribute one brood of tadpoles among different pools, how is a deposition event defined? We used four total proxies to estimate deposition activity for our analysis. The first (and most conservative) definition was to score a deposition event for a pool if it received some tadpoles and its counterpart received none (herein referred to as a 'Type I' deposition). In this scenario, the male made an unambiguous choice, but this definition has the drawback of ignoring situations where both pools received tadpoles (52% of total observations were of this type). Therefore, a second definition of a deposition event was used to account for the observation that males are distributing one brood across multiple pools. Here, we scored a deposition event for a pool when it received more tadpoles than its counterpart ('Type II' deposition). This is a less-strict definition and a Type I deposition can be considered a specific type of Type II deposition. Note that in a Type II deposition, both pools could still have received some tadpoles. This accounts for the possibility that if males are depositing tadpoles among pools, they may be doing so non-randomly. Under the null hypothesis that males do not discriminate between pools, one would expect that random sampling of pools by males would not generate systematic differences in deposition frequencies between pool types. Frequencies of deposition events in each pool type were compared using a one-way chi-square test under the null hypothesis that the frequency of deposition events (both Type I and Type II) would be 0.5 in both pools within a pair for both experiments. We applied Yates' correction for continuity in comparisons where the expected number of depositions per cell was five or lower.

Two additional methods were used to analyze deposition preference. We compared the number of tadpoles deposited per pool type during each deposition event. For this analysis, we treated pools within a pair as paired samples and different pairs as independent samples, and compared the number of tadpoles deposited per pool type per deposition event using a paired-samples T-test. Finally, the least conservative proxy of deposition behavior was to sum all tadpoles deposited in one pool type versus another within an experiment type. Tadpole number was square-root transformed to conform to the assumptions of normality.

To estimate whether *A. trivittata* could 'see' *A. bassleri* tadpoles, we counted the total number of tadpoles deposited in experiment 1 clusters vs. the number deposited in experiment 2 clusters in 2007. The two experiments differed only in the presence/absence of *A. bassleri* and were running for equal time and had equal numbers of pools running; therefore, a difference in total tadpoles deposited per experiment type would indicate that *A. trivittata* males did not simply see *A. bassleri* pools as empty pools. Here, we compared tadpole number per experiment type using a chi-square test with the null hypothesis that both experiment types should receive equal numbers of deposited tadpoles.

Results

Experiment 1: Pool choice – Conspecifics vs. empty pools

Pools for this experiment received a total of 162 tadpoles over 10 total (i.e. Type II) depositions; six of the 10 depositions were Type I. Deposition events occurred significantly more frequently in unoccupied pools than occupied pools for both Type I and Type II depositions (Table 3). Unoccupied pools also received a higher number of tadpoles per deposition than pools containing conspecifics (Table 1).

Experiment 2: Pool choice – Conspecifics vs. heterospecifics

Pools received a total of 356 tadpoles over 32 total depositions; fifteen of the 32 depositions were Type I. Contrary to our hypothesis, depositions occurred significantly more frequently in pools containing *A. bassleri* than *A. trivittata* when counting Type II depositions (Table 3). When counting Type I depositions only, this difference was not significant although a trend was apparent (Table 3). For Type II events, there was a significant preference for pools with *A. bassleri* tadpoles. Pools containing *A. bassleri* also received a higher number of tadpoles per deposition than pools containing *A. trivittata* (Table 3).

Detection of A. bassleri

In the Chazuta site in 2007, 162 tadpoles were deposited in clusters consisting of experiment 1 and 66 tadpoles were deposited in clusters consisting of experiment 2. These values deviate significantly ($\chi^2_1 = 40.22$, $P < 0.001$) from the expected tadpole number under the null hypothesis that both experiments would receive an equal number of tadpoles if *A. trivittata* cannot distinguish between *A. bassleri* and an empty pool.

Discussion

We investigated how the presence/absence of conspecific versus heterospecific tadpoles affects reproductive habitat choice by *A. trivittata* using pool-choice experiments in the field. The study was coupled with a previous study in which we assessed the risks *A. trivittata* tadpoles face regarding intraspecific and interspecific competition. The results of that study demonstrate that, in our pool-choice experiments, unoccupied pools represent the highest quality habitat, pools containing conspecific tadpoles are of moderate quality, and pools containing *A. bassleri* tadpoles are of very low quality. Given the results of the competition experiments conducted prior to the pool-choice experiments, we could pose a priori hypotheses about how *A. trivittata* might select deposition sites in light of competition risk. We predicted that *A. trivittata* would choose empty pools over pools containing conspecifics, which was indeed the case (Table 3). Male *A. trivittata* are therefore capable of making an adaptive choice of habitat when selecting between an unoccupied pool versus a pool containing conspecifics. Similarly, Resetarits and Wilbur (1989) demonstrated that gravid gray treefrog females (*Hyla chrysoscelis*) avoided pools containing conspecific tadpoles in an apparent attempt to minimize intraspecific competition. Our results also show that habitat selection by *A. trivittata* in response to *A. bassleri* was decidedly maladaptive. The effect of interspecific competition on growth and survival of larval *A. trivittata* is much stronger than that of intraspecific competition (Twomey et al. *accepted*), yet adult *A. trivittata* were over twice as likely to deposit tadpoles in pools containing *A. bassleri* than pools containing *A. trivittata* (Table 3). However, it does not appear that *A. trivittata* simply cannot detect *A. bassleri*, because there was significantly lower deposition activity in clusters which contained *A. bassleri* compared to those that did not. This suggests to us a three-level decision hierarchy, where *A. trivittata* prefer empty pools over pools with *A. bassleri* over pools with *A. trivittata*.

The clear demonstration of an ecological trap requires satisfying three criteria designed to demonstrate habitat selection and its consequences (Robertson and Hutto 2006). The first is a reasonable measure of preference. Previous studies have been criticized for using indirect proxies of preference (such as nonrandom habitat use or density) which do not necessarily demonstrate a preference (Van Horne 1983, Garshelis 2000). The choice experiments used in our study eliminate confounding factors by isolating specific cues, allowing us to observe behavioral decisions being made in response to these cues. Second, fitness varies by habitat. Our earlier competition experiment shows that larval survival and growth (both components of fitness) vary significantly among our three pool types. Third, we show that *A. trivittata* has the lowest fitness in pools containing *A. bassleri,* yet these pools are preferred over pools containing conspecifics. In this example, the trap is restricted to a reproductive habitat, rather than a habitat used by both adults and offspring, and thus parental fitness is a function of (1) larval survivorship in the pool and (2) the fitness of post-metamorphic frogs. A more complete estimation of parental fitness might therefore include a comparison of post-metamorphic traits such as mass at metamorphosis (Semlitsch 1988). We only witnessed four *A. trivittata* complete metamorphosis in pools containing *A. bassleri*; fitness benefits to these metamorphs would have to outweigh mortality risk in order to cancel out the effects of an ecological trap.

One major question concerning ecological trap theory is whether traps inevitably lead to local extinction or if they can persist (Donovan and Thompson 2001, Battin 2004). In contrast with previous studies documenting anthropogenically-induced traps (e.g. Kriska et al. 1998, Remeš 2003, Weldon and Haddad 2005). we have presented evidence of a natural, presumably ancient ecological trap. Examples of natural traps provide a framework to consider the processes that allow traps to persist in nature, and will help develop more synthetic understanding of the origins of maladaptive behavior. Robertson and Hutto (2006) emphasize that ecological traps are inherently a behavioral and not population phenomenon. While true in a sense, behavioral traits ultimately depend on population-level processes such as local adaptation (Kawecki 2004). If we are to understand the adaptive significance of behavior, we must consider the conditions under which it evolved (Remeš 2000). Consider for example decision-making rules in response to competition for any species. Intraspecific competition, a pervasive risk throughout a species' entire geographic range, can be addressed by the relatively simple habitat selection rule of self-avoidance. In contrast, avoiding interspecific competition requires rules that apply to potentially many species. For example, *A. trivittata* is sympatric with at least 16 congeneric species throughout its range, almost all of which have small ranges in comparison. While the general rule of self-avoidance is relevant throughout its entire range, interspecific rules, relevant only in zones of sympatry, would have to be numerous. Although adult *A. trivittata* may in fact 'see' *A. bassleri* as a potential competitor, they may be unable to evaluate the strength of this competitor in relation the more familiar effect of intraspecific competition. It is important then to consider that our example of an ecological trap is specific to a particular geographic region—in central Peru where *A. trivittata* and *A. bassleri* are sympatric—and that habitat selection rules in response to *A. bassleri* would only be relevant in the context of this montane environment. Furthermore, this trap should become more severe with increasing elevation as *A. bassleri* becomes more common. But why have montane *A. trivittata* not evolved habitat selection rules that allow them to minimize larval contact with *A. bassleri*?

The answer may lie in population dynamics linking lowland and montane populations of *A. trivittata*. Battin (2004) outlined several characteristics of landscapes and organisms that increase vulnerability to an ecological trap, including rapid environmental change, high ratio of trap to source habitat, low capacity for learning, low level of knowledge about a landscape, among others. Additionally, we propose that when an ecological trap arises within a small part of a species' geographic range, migration load from adjacent populations may allow the ecological trap to persist. This hypothesis relies on the idea that migration acts as an opposing force to local adaptation (Freeman and Herron 2004). If gene flow between populations is asymmetrical, this can counteract the potential for one population to adapt locally through accumulation of a migration load (Lenormand 2002). That peripheral populations are susceptible to migration load has been promoted in theoretical work (Garcia-Ramos and Kirkpatrick 1997, Lenormand 2002), which suggests that local adaptation in peripheral populations may be inhibited by gene flow from the center of a species' range. For example, Camin and Ehrlich (1958) attributed the persistence of a banded phenotype in an island population of water snakes as a consequence of emigration from a mainland population, despite negative fitness consequences (King 1993). The balance between migration and selection may become further skewed if low fitness in a trap habitat causes that habitat to act as a sink (or pseudosink), where emigration is low and immigration from adjacent populations is high. Some authors have suggested that ecological traps may in fact lead to source-sink population dynamics (Remeš 2000, Kristan III 2003), although empirical examples are lacking. In general, one would expect trap habitats to be net importers of individuals due to low productivity; thus, net gene flow would be directional—from a source habitat to the trap habitat—and promote migration load while constraining local adaptation. In our study system, *A. trivittata* from lowland Amazonia are unlikely to carry alleles that are adaptive in response to competition with *A. bassleri,* therefore, migration load from lowland populations may be preventing montane populations from evolving an appropriate response to *A. bassleri* tadpoles.

CHAPTER 3: THE EFFECT OF KINSHIP ON INTRASPECIFIC COMPETITION IN LARVAE OF THE POISON FROG *AMEEREGA BASSLERI* (ANURA: DENDROBATIDAE)

Abstract

According to inclusive fitness theory, cooperation between related individuals should ameliorate the effect of intraspecific competition. However, close relatedness is also thought to increase similarity between individuals and therefore increase the risk of exploitative competition. Studies of the effects of kinship in larval amphibians have often yielded mixed results concerning these two hypotheses. We examined the effect of kinship on the mean and variation of growth in groups composed of either pure siblings or a mixture of five different sibships in a species of poison frog, *Ameerega bassleri*. We found no significant difference in growth in sibling and mixed treatments with respect to growth or variation in growth. Our results are consistent with certain other studies in larval anurans which have found no differences between sibling and mixed treatments, suggesting that the effects of kin selection and genetic similarity between competitors may in some cases cancel each other out.

Introduction

Hypotheses of how relatedness affects the intensity of intraspecific competition have important implications for the evolution of social behavior, reproductive ecology, and habitat selection in many organisms, but debate exists as to what these effects are. The theories of kin selection and heterogeneous advantage produce opposing predictions about how relatedness affects intraspecific competition (Hamilton 1964), and both have received empirical support in certain taxa (Griffiths and Armstrong 2001). On one hand, kin selection theory predicts that groups of closely related individuals should compete less intensely than unrelated individuals. Behaviors that reduce aggression and interference between kin may increase an individual's inclusive fitness and therefore be favored by natural selection. On the other hand, heterogeneous advantage predicts that because siblings are genetically similar, the potential for exploitative competition is higher because individuals in a group will overlap more in their resource use (Sammeta and Levins 1970). Consequently, intraspecific competition is predicted to be stronger between siblings than unrelated individuals.

Larval amphibians are valuable model organisms in studies of kin selection (see Waldman 1991) as they often form aggregations which may be composed of kin or non-kin, and larval success is often density dependent (Wilbur 1977). Although larval amphibians may preferentially associate with kin (Halverson et al. 2006), the adaptive significance of this behavior is complex and varies depending on the species or experimental conditions. For example, several studies (Jasieński 1988, Waldman 1991, Saidapur and Girish 2001, Girish and Saidapur 2003) have shown that individuals reared in sibling groups grow faster and/or achieve a larger mass at metamorphosis than those raised in mixed groups, results which support kin selection theory. Conversely, other studies have found that certain species grow better in mixed groups (Shvarts and Pyastolova 1970, Hokit and Blaustein 1994), supporting the heterogeneous advantage hypothesis, while others have found no difference in growth between sibling and mixed groups (Walls and Blaustein 1994, Gramapurohit et al. 2004).

In addition to affecting growth, some authors have suggested that genetic relatedness can influence variance in growth within a cohort. Waldman (1991) argued that sibling groups should experience higher variation in growth than mixed groups due to competitive restraint on the part of slow-developing ‘runts’. If runts have a low probability of metamorphosis or survival, they may be able to facilitate growth of larger siblings by restraining their foraging intensity, redirecting predation risk, and, in extreme cases, sacrificing themselves to cannibalism. However, empirical studies testing this hypothesis have shown varying results. While some studies on fish and amphibians have found higher variation in growth in sibling groups (Beacham 1989, Waldman 1991), others have found the opposite result (Hokit and Blaustein 1997, Anderson and Sabado 1999, Pakkasmaa and Aikio 2003, Saidapur and Girish 2001, Girish and Saidapur 2003).

We explored the effects of genetic relatedness on larval growth and variation in a species of poison frog, *Ameerega bassleri* (family Dendrobatidae). Like other species of *Ameerega,* this species deposits eggs in leaf litter and subsequently transports tadpoles to small pools that form in low-lying areas of the forest. Pool size in nature is highly variable, although pools are generally small, ranging from 6–46 L, and tadpole growth in this species is strongly affected by intraspecific competition (Twomey et al. *in press*). Although schooling behavior of tadpoles has not been observed, adult *A. bassleri* are free to deposit their tadpoles in pools which may be occupied by kin or non-kin. Bearing that in mind, kinship effects on intraspecific competition could have ramifications not only for tadpole growth and fitness, but also for habitat selection behavior in adults. The goal of the present study was to determine whether tadpoles raised in sibling groups grew faster than those raised in mixed-brood groups and to compare variances in growth between groups.

Materials and Methods

To evaluate the effect of relatedness on the mean and variation in the growth of larval *A. bassleri*, we set up a competition experiment in artificial pools where we manipulated relatedness of the competing tadpoles while maintaining a constant density of ten tadpoles per pool. We used two treatments in this experiment, a high-relatedness (sibling) treatment where all tadpoles in a pool were full siblings, and a low-relatedness treatment which contained two tadpoles from five different cohorts. In the low-relatedness treatment, any one tadpole had only one sibling present in the pool and was presumed to be unrelated to the other eight tadpoles. The sibling treatment and the low-relatedness treatment were replicated five and four times, respectively.

For this experiment, a total of 90 larval *A. bassleri* were collected from artificial pools set up in a field site near the town of Chazuta in Departamento San Martin, Peru (6° 32' 35" S, 76° 6' 39" W) in June and July of 2008. While collecting egg clutches as opposed to tadpoles would have been ideal for kinship experiments, eggs are deposited in leaf litter and difficult to find. We were, however, able to confidently identify sibling and non-sibling tadpoles by frequently monitoring deposition activity in our artificial pools and taking into account time and place of deposition. Our artificial pools were arranged in eight distinct clusters which were spaced minimum 20 m apart; within a cluster pools were arranged in five pairs, so that paired pools were less than 1 meter apart but different pairs were spaced 3-10 m apart. If tadpoles appeared in a single pool within a day of the time the pool was last checked, and were of the same stage, they were collected as siblings. It is unlikely that tadpoles collected from a single pool were of multiple parents because pools were checked frequently (3-5 times per week) and only freshly-deposited, early-stage tadpoles were used. Additionally, if two pools within a pair each received tadpoles, they were collected as siblings but only if the pools had been checked very recently, the tadpoles were of the same stage, and the sum of the tadpoles in both pools did not exceed the typical brood size for this species (~17 tadpoles, unpub. data.). We never considered tadpoles as siblings if they were collected from different pairs of pools or from different clusters. To collect unrelated tadpoles, we collected two putative siblings from a single cluster of pools, and repeated this in five different clusters to make a total of ten tadpoles. We never considered tadpoles as unrelated if they came from the same cluster. It is unlikely that tadpoles from different clusters were siblings, since clusters were widely spaced.

Once tadpoles were collected from the field site, they were transported to a nearby field station, assigned to the appropriate treatment, and reared in the experimental pools. These pools were ten liter plastic washtubs ~ 30 cm in diameter and 15 cm deep. Tadpole density was therefore 10 tadpoles per liter, a density which is comparable to estimated field densities (Twomey et al. *in press*). An experimental pool was initiated by filling it with dechlorinated water and three dried *Cecropia* leaves. Tadpoles were fed commercial rabbit chow ad libitum and weighed weekly to the nearest 0.01 g for 30 days. Fifty percent water changes took place weekly.

Growth data were analyzed by taking mean tadpole mass per pool after 30 days of growth, and performing a one-way ANOVA on these values between the two treatments. Due to the limited time frame for this study, pools were not run long enough to record metamorphosis data. However, rapid growth facilitates a short larval period, which may allow tadpoles to reduce risk of predation and desiccation (Wilbur 1980). We compared variation in growth after 30 days between the two treatments using two methods. First, we performed a Levene's test for homogeneity of variances. Second, we calculated the coefficient of variation for each pool and compared these values using a one-way ANOVA.

Results and Discussion

At the start of the experiment, there was no significant difference in tadpole mass in the two treatments ($F_{1,7} = 0.223$, $P = 0.65$). After 30 days of growth, there were no significant differences between treatments with respect to tadpole mass or coefficient of variation (Table 4). A Levene's test showed homogeneous variances in tadpoles at both the start of the experiment (Levene's $W = 1.48$, $P = 0.227$) and after 30 days of growth (Levene's $W = 1.71$, $P = 0.196$). Distribution of tadpole masses is shown on Fig. 4.

Previous studies in tadpoles on the effect of relatedness on growth have shown mixed results. While some studies have found no differences between sibling and mixed groups (Walls and Blaustein 1994, Gramapurohit et al. 2004), several studies have shown that siblings tend to grow better than mixed groups. For example, Girish and Saidapur (2003) found that sibling groups of *Rana temporalis* had a higher proportion of metamorphosing froglets and shorter larval periods than mixed groups, and that these differences were more pronounced in higher density treatments. Likewise, Waldman (1991) found that sibling groups of *Bufo americanus* reached larger mass at metamorphosis than mixed groups. Kin selection theory provides an eloquent explanation of these results, where cooperation is predicted to evolve so long as the cost of the behavior for the actor is less than the product of the benefit to the recipient and their relatedness (Hamilton 1964). Cooperative behaviors may entail sharing reproductive duties (Emlen and Wrege 1988), predator-warning (Sherman 1977), or assistance in acquiring mates (Krakauer 2005). In tadpoles, mechanisms for cooperation may include competitive restraint (reducing exploitative competition), decreased interference with competitors (thereby increasing time available for foraging), or beneficial behaviors such as stirring up more periphyton than they can consume (Waldman 1991, Hokit and Blaustein 1997). However, these beneficial behaviors may be counteracted by genetic similarities between kin by increasing the potential for exploitative competition, potentially canceling out effects of cooperation (Griffiths and Armstrong 2001).

In contrast with previous studies that have shown higher variation in growth in sibling groups (Waldman 1991), we found that variation in mass after 30 days was not significantly different between sibling and mixed tadpole groups. Previous studies that have addressed the effect of kinship on growth variation have shown varying results. For example, in *Rana temporaria,* full-sib treatments had lower variation in growth rate and mass at metamorphosis (Pakkasmaa and Aikio 2003), while Hokit and Blaustein (1997) found that mass was more skewed towards small tadpoles in mixed groups compared to kin groups. Our results are more consistent with the idea that inherent genetic similarities among related competitors should homogenize differences in growth rates and hence, variation.

Theory suggests that if the scale of competition is such that altruistic behavior benefits some relatives only at the expense of other relatives, increased relatedness should have no effect on the evolution of cooperation (West et al. 2002). In the case of *A. bassleri* tadpoles, it seems likely that the scale of competition is such that it includes non-relatives, although the precise level of competition with non-relatives compared to relatives is not known. Deposition in the same pool by different adults has been observed in the field (N = 4), and thus it is likely that tadpoles within pools face a mix of both kin and non-kin with some frequency. In this scenario, any cooperation between kin that enhances their growth at the expense of non-kin in the same pool should be favored. When considering competition at a larger scale (i.e. via recruitment success across different pools), one can consider kin groups within pools to be in competition with kin groups in other pools to exploit the resources available with the maximum efficiency and thoroughness. In this sense, cooperative traits that enhance the ability of all members of a kin group to exploit the available resources in an efficient manner should be favored by kin selection.

Under the first scenario, we might expect traits such as aggression toward non-relatives, or protection of resources from non-relatives to be favored. Under the second scenario, we might expect traits such as restraint in the rate of consumption of resources to be favored. This could enhance the efficiency with which resources are processed, providing an advantage to the entire kin group. In the experiment presented here, the experimental design creates a situation that reflects the second level of competition described above, in which kin groups compete with groups composed of non-kin across pools. We predicted that, if kin selection is operating at this level, we would see higher growth rates in pools containing only kin. However, this prediction was not supported by our results.

From the standpoint of an adult frog depositing tadpoles, differential performance of kin vs. non-kin groups would, on one hand, drive *A. bassleri* to preferentially deposit tadpoles in pools containing related individuals. However, this behavior would also increase the relatedness between competitors, which opposes evolution of cooperative behavior (West et al. 2002). While increased relatedness of competitors may oppose kin selection, kin groups may also be more effective at exploiting resources (Foster 2005) and in the global sense of competition, may be advantageous.

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. 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 #1, and mixed-species, highland treatments would be #6.

A. trivittata		Tadpole mass				30-day mortality		
Contrast	*df*	*F*	*P*	Effect size	*df*	*F*	*P*	Effect size
1. Elevation effects (1,2,3 vs. 4,5,6)*	1	0.07	0.791	—	1	36.99	< 0.001	0.597
2. Intraspecific density (1,4 vs. 2,5)	1	25.80	< 0.001	0.117	1	0.015	0.903	—
3. Elevation × intraspecific density**	1	2.16	0.143	—	1	0.04	0.844	—
4. Interspecific density (1,4 vs. 3,6)	1	47.97	< 0.001	0.291	1	1.74	0.207	—
5. Elevation × interspecific density**	1	0.71	0.402	—	1	0.481	0.499	—
6. Species equivalence (2,5 vs. 3,6)	1	14.48	< 0.001	0.070	1	1.338	0.263	—
7. Elevation × species equivalence**	1	0.05	0.831	—	1	0.193	0.666	—

A. bassleri		Tadpole mass				30-day mortality		
Contrast	*df*	*F*	*P*	Effect size	*df*	*F*	*P*	Effect size
1. Elevation effects (1,2,3 vs. 4,5,6)*	1	0.81	0.369	—	1	86.44	< 0.001	0.769
2. Intraspecific density (1,4 vs. 2,5)	1	68.50	< 0.001	0.253	1	0.007	0.933	—
3. Elevation × intraspecific density**	1	0.53	0.817	—	1	0.101	0.756	—
4. Interspecific density (1,4 vs. 3,6)	1	0.85	0.358	—	1	0.045	0.834	—
5. Elevation × interspecific density**	1	1.24	0.267	—	1	0.141	0.713	—
6. Species equivalence (2,5 vs. 3,6)	1	47.20	< 0.001	0.184	1	0.091	0.767	—
7. Elevation × species equivalence**	1	2.59	0.109	—	1	0.648	0.434	—

*Growth data compared using ANCOVA
**Interaction tested using factorial ANOVA

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.

A. trivittata	Lowlands		Highlands	
Contrast	χ2	*P*	χ2	*P*
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

A. bassleri	Lowlands		Highlands	
Contrast	χ2	*P*	χ2	*P*
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

Table 3. Results of pool-choice experiments.

	Pool choice (exp. 1)				Pool choice (exp. 2)			
	A. trivittata	No tadpoles	Test statistic	*P*	*A. trivittata*	*A. bassleri*	Test statistic	*P*
Type I deposition events	0	6	$\chi^2 = 4.16$	0.041	4	11	$\chi^2 = 3.27$	0.071
Type II deposition events	1	9	$\chi^2 = 6.40$	0.011	7	25	$\chi^2 = 10.13$	0.001
Tadpoles per deposition*	4.4	9.1	$T_{11} = 4.17$	0.002	3.7	7.5	$T_{31} = 3.48$	0.001
Total tadpoles deposited	53	109	$\chi^2 = 19.36$	< 0.001	117	239	$\chi^2 = 35.87$	< 0.001

* Means compared using paired-samples T-test

Table 4. ANOVA table for the effects of kinship on mass and growth variation.

Response variable	Source	*df*	SS	*F*	*P*
Mass	Between groups	1	9.17	2.26	0.176
	Within groups	7	28.36		
	Total	8	37.53		
Coefficient of variation	Between groups	1	0.014	2.50	0.157
	Within groups	7	0.039		
	Total	8	0.053		

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 standard error. 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).

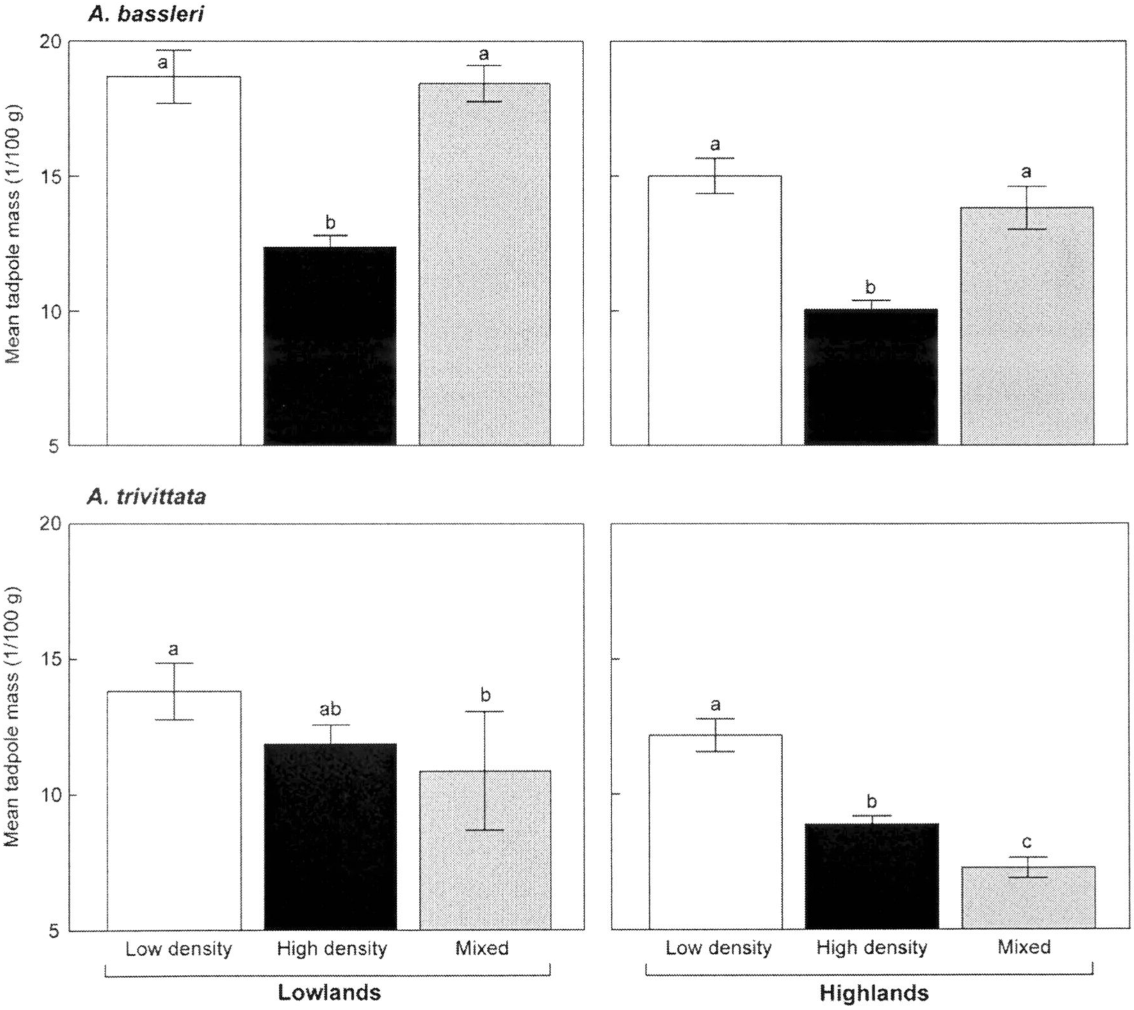


Figure 2. Interaction diagram showing asymmetric competition in *A. bassleri* and *A. trivittata*. This figure compares per capita effects of interspecific competition in both species. The positive slope of the line connecting *A. bassleri* means indicates that intraspecific competitors exert a stronger 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 × species identity, $F = 11.32$, $P = 0.001$) indicating that the strengths of interspecific competition in these two species are not equal.

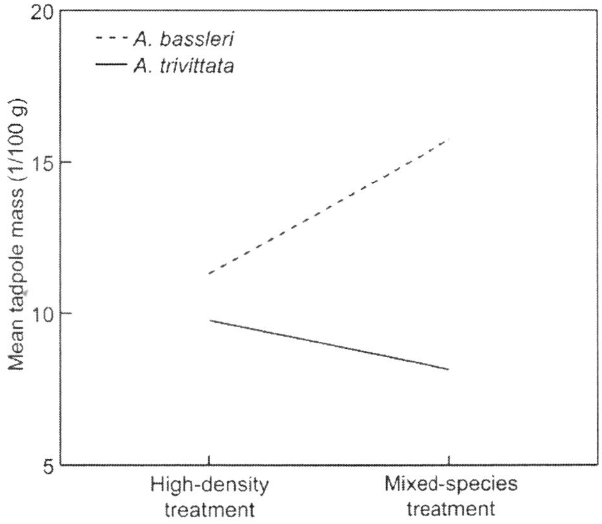


Figure 3. Survival functions drawn with the Kaplan-Meier estimator; open circles represent a censorship event. Each quadrant represents treatments for a single species and elevation. Significance tests for pairwise comparisons are given in Table 2.

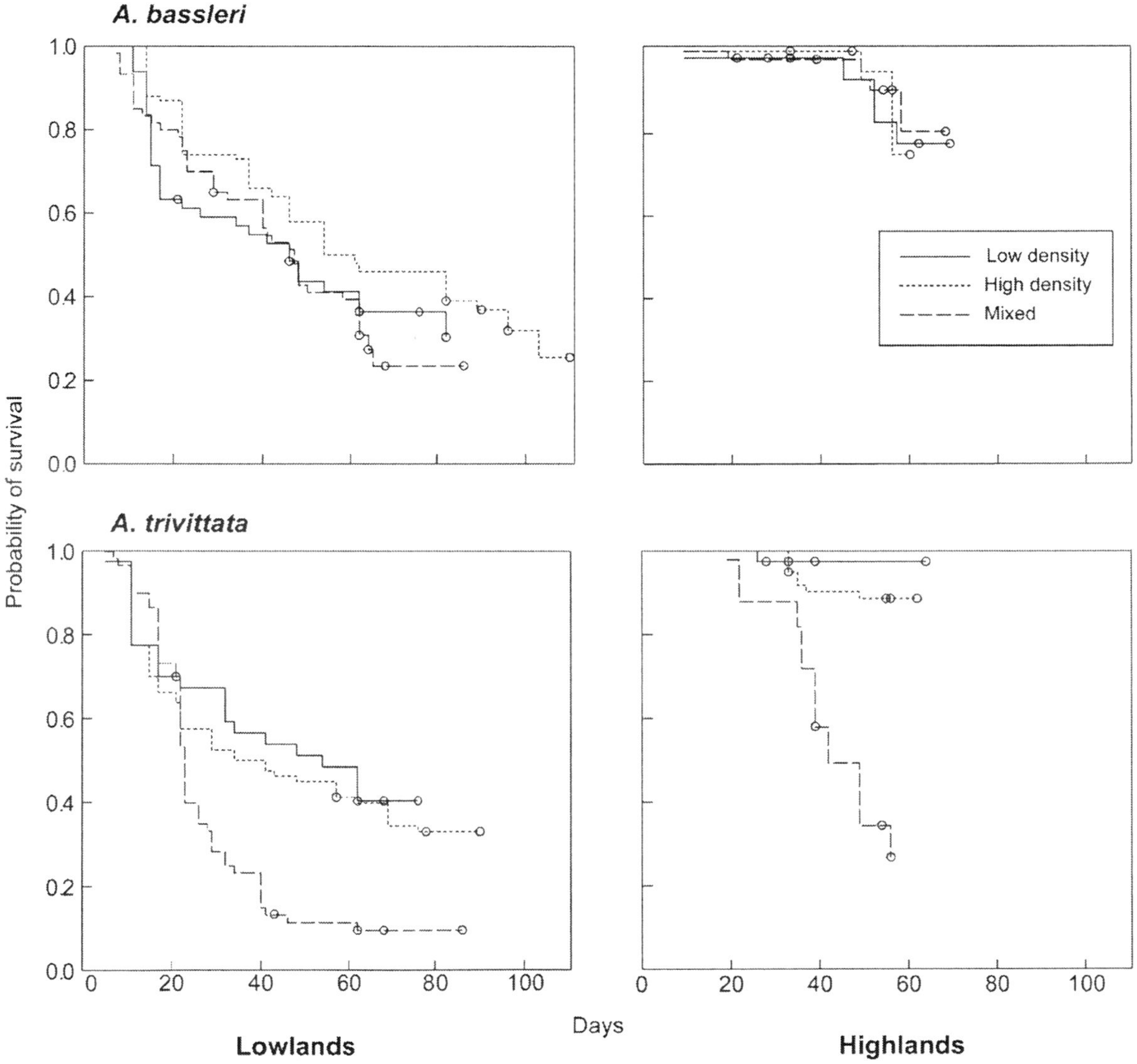
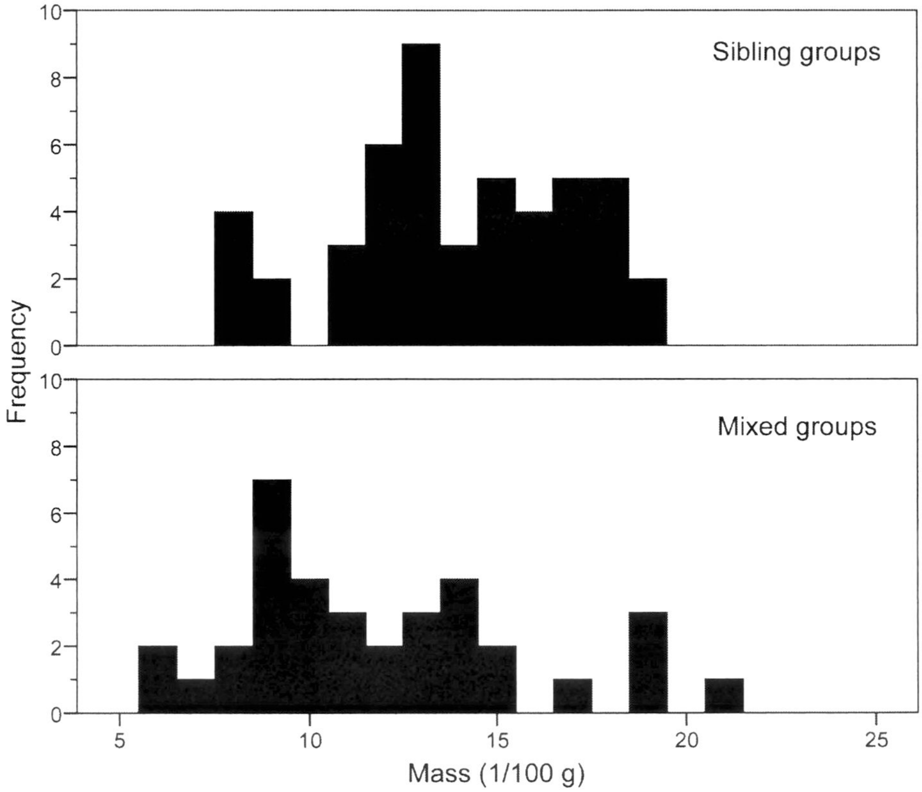


Figure 4. Distribution of tadpole masses after 30 days of growth in sibling vs. mixed group treatments.



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