

Hierarchical competition in a pond-breeding anuran larvae community in a Mediterranean area.

The anuran larval guild is characterised by the co-occurrence of distinct species in the same pond at high densities during development with a high niche overlap. For these reasons anuran larvae have been studied widely as a model system for competition. Body size and activity level are considered the most important factors that influence the outcome of competition between tadpoles. As species from temporary ponds normally show higher activity levels in order to achieve rapid growth and thus escape from the risk of death due to desiccation of the habitat, these species are considered superior competitors. We will test whether body size or activity level determines competition ability among six species from a Mediterranean anuran community. With this objective we designed several laboratory experiments to examine the intra- and interspecific effects on growth rate, mass at metamorphosis and survival to metamorphosis of the six species.

An asymmetric and hierarchical relationship was found among the six species. Larger tadpole species were more successful in competitive interactions than the smaller ones. However, no relationship between activity level and competition effects was found. Species typically found in temporary ponds (*Pelodytes punctatus* and *Bufo calamita*) were considered poor competitors in comparison with others communities studied. Species with low competitive ability can persist by using refuges in which competition is reduced (e.g. drying ponds).

INTRODUCTION

A comparison of the relative strengths of intraspecific and interspecific competition is of interest as a means with which to predict the coexistence and abundance of competitors and the relative roles of these two processes in determining species density (Connell 1983; Schoener 1983). The anuran larval guild is characterised by the co-occurrence of distinct species in the same pond at high densities during development, with high niche overlap between species (Alting & Johnston 1989; Skelly 1997; Alford 1999) since tadpoles are considered non-selective feeders in temperate regions (Diaz-Paniagua 1985, 1989). For these reasons anuran larvae have been studied widely as a model system for competition. Numerous experiments in the laboratory (Smith-Gill & Gill 1978; Steinwascher 1979; Wilbur 1982; Werner 1992; Laurila 2000; Smith et al. 2004), mesocosm (Woodward 1982; Alford &

Wilbur 1985; Wilbur 1987; Morin & Johnson 1988; Griffiths et al. 1991; Pehek 1995) and the field (DeBenedictis 1974; Kupferberg 1997; Bardsley & Beebee 2000) reveal strong asymmetric competition: intra- and interspecific.

Among the several factors that can influence the outcome of competitive interactions between animal species in a freshwater system, two are considered most important: body size of individuals (Steinwascher 1978; Persson 1985) and activity level (Werner 1992; Grill & Juliano 1996). In tadpoles, activity level is often assumed to be correlated with foraging rate (Morin & Johnson 1988; Smith et al. 2004). More active species tend to be competitively superior species because may improving harvesting rate and depletion of the resources (Morin & Johnson 1988; Werner 1992, 1994; Laurila 2000). Large tadpoles have a greater capacity to forage on a per capita basis, due to their size-dependent filtering ability (Wassersug 1975) and consumption rates (Richardson 2002) or perhaps due to physical displacement of small individuals from resources (Richter-Boix et al. 2004). On average, large tadpoles tend to monopolise and consume more resource than smaller ones do. Small tadpoles, however, may be better competitors on a biomass point of view, because they require fewer resources and are generally more abundant (Peters & Wassenberg 1983), with a high impact on system resources, especially where these resources are scarce or competition is intense (Persson 1985).

Pond breeding anurans are normally distributed across a well known hydrological gradient, ranging from ephemeral pools to large permanent lakes (Wellborn et al. 1996; Snodgrass et al. 2000; Babbitt et al. 2003), but local co-occurrence of species in different habitats is not unusual, in part because pond position on the hydroperiod gradient can be dynamic over the years, and thus so can species composition (Semlitsch et al. 1996). The two endpoints of the range differ in many physical and biotic factors. While ephemeral and temporary ponds usually limit the distribution of taxa due to harsh abiotic conditions such as drying, permanent ponds usually limit distribution of taxa through biotic factors (principally predation) (Wellborn et al. 1996; Van Buskirk 2005). Species from the ephemeral end-point of the range normally show higher activity levels with higher growth and development rates than those from permanent ponds, given their need to grow quickly and escape from the risk of death due to desiccation of the habitat (Woodward 1982; Morin 1983; Wellborn et al. 1996). These characteristics

cause species typical of ephemeral and temporary ponds to be considered superior competitors (Woodward 1982; Wilbur 1987; Werner 1992; Dayton & Fitzgerald 2001).

The aim of the present study was to examine the symmetry and intensity of intra- and interspecific competitive effects among tadpole species of a Mediterranean amphibian community which differ in their use of habitats along the hydroperiod gradient. We will test if species from ephemeral ponds are more competitive than more permanent pond species, and determine if competitive ability depends upon activity level or body size.

NATURAL HISTORY AND STUDY SYSTEM

In the natural parks of Garraf and Collserola near the city of Barcelona (NE Iberian Peninsula) the native amphibian community includes a total of 8 species: 1 urodela (*Salamandra salamandra*) and 7 anura (*Alytes obstetricans*, *Pelodytes punctatus*, *Pelobates cultripes*, *Bufo bufo*, *Bufo calamita*, *Hyla meridionalis* and *Rana perezi*). For the present study only 6 anuran species were chosen from the 7 species detected in the region. We excluded *Pelobates* because it is rare in the study area. This zone has a typical Mediterranean climate with hot, dry summers, mild winters and two rainy periods, in spring and autumn. Amount of precipitation varies considerably from year to year. Ephemeral ponds refill after each rainfall period and dry within weeks, with surface water for a maximum of two months. Temporary ponds are flooded by spring or autumn rainfall. The shallower temporary ponds can dry out in winter, whereas the deepest remain flooded until the end of spring or early summer. In some years the deepest temporary ponds can remain as permanent ponds with water in them during the entire summer, but part of them dry up from mid July to August in drought years. With the exception of permanent ponds (mean estimated at 30,320 litres), temporary and ephemeral ponds are small bodies of water (mean of 11,970 litres). However, some of what are considered permanent waters are human-made ponds of relatively small size but with water all year round due to their artificial substrate, which favours occasional colonisation by ephemeral and temporary pond breeder species. In temporary ponds algal blooms occur in the mid spring when rainfall declines, whereas in ephemeral ponds algal blooms are not frequent due to their short duration, and these ponds could be considered in many cases as oligotrophic waters. Species distribution across the freshwater hydroperiod

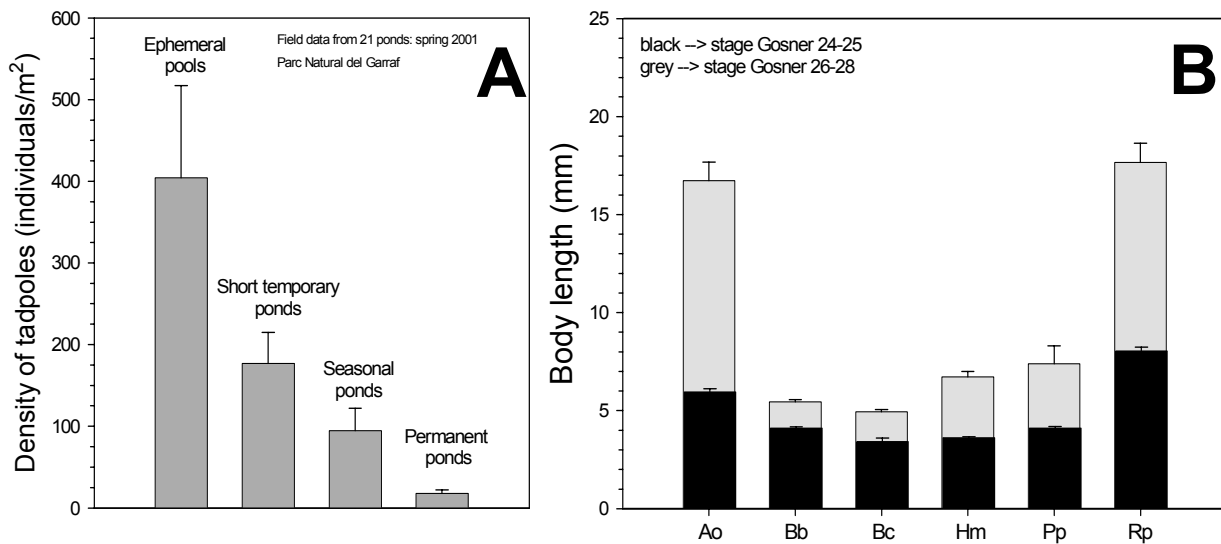


Fig. 1.- (A) Mean and standard error of densities of tadpoles in 21 natural ponds across hydroperiod gradient, (B) mean and standard error of body size of tadpoles from field ponds at different set of development stages. Species abbreviations: Ao = *Alytes obstetricans*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Pp = *Pelodytes punctatus*, Rp = *Rana perezi*.

gradient is as follows: *B. calamita* and *Pelodytes* reproduce in ephemeral and in short-term temporary ponds (Strijbosch 1979; Guyétan et al. 1999), *Hyla* (Diaz-Paniagua 1986) and *B. bufo* use temporary and permanent ponds (Strijbosch 1979; Van Buskirk 2005), whereas *Rana* reproduces almost exclusively in permanent ponds. *Alytes* prefers permanent ponds but is capable of reproducing along the entire hydroperiod gradient, even in oligotrophic waters, from temporary ponds of short duration to permanent ponds. However, species segregation across these habitats is not consistent and all possible combinations of species have been observed in different habitats, at different frequencies and in different years (Richter-Boix et al. unpublished data). Co-occurrence of species is frequent, especially in the middle of the hydroperiod range, in temporary ponds where density of tadpoles could be high. A field survey of 21 natural ponds in Garraf during the spring of 2001 showed higher densities in ephemeral and short-term temporary ponds (mean of 404/m² in ephemeral ponds, 176/m² in short-term temporary ponds, and 14/m² in large temporary and permanent ponds) (Fig 1A). In ephemeral and temporary ponds natural high densities suggest there is some potential for effects of exploitation competition, while this is not likely in permanent ponds with natural low tadpole densities (Loman 2001). Also, larval competition was suggested because preliminary

evaluation of the gut contents of the same species in a similar system has revealed that they have a high dietary overlap (Diaz-Paniagua 1985, 1989). All species consume largely algae, phanerogams and debris (Diaz-Paniagua 1985, 1989).

The breeding phenology of some species (*Pelodytes* and *B. calamita*) follow periods of rainfall, with a main breeding period in spring and a second period in autumn. This temporal segregation is important for interpretation of competition mechanisms and community structure (Toxopeus et al. 1993; Jakob et al. 2003); however, in the present study we focus only on the spring breeding period, when all species coincide in time and competitive effects can only be prevented by spatial segregation. Rainfall pulses and the limited number of ponds limit opportunities to breed; consequently the co-occurrence of several species in space and time is common in the Mediterranean region (Joly & Morand 1994; Morand & Joly 1995).

Differences in size among the six species set the stage for size-structured competition. Total lengths of tadpoles at Gosner's stage 26-30 measured in natural ponds are 7.4 cm for *Alytes* (n=449), 6.1 cm for *Pelodytes* (n=312), 4.2 cm for *B. bufo* (n=627), 3.7 cm for *B. calamita* (n=512), 5.1 cm for *Hyla* (n=144) and 7.2 cm for *Rana* (n=108). These values are consistent with bibliographic data (Nöllert & Nöllert 1995) (Fig. 1B).

MATERIAL AND METHODS

Experimental methods

We conducted a number of laboratory experiments to measure the effects of competition between the tadpole species. Experiments were done in two different years (2001 and 2002). All experiments were performed under the same conditions in laboratories at the University of Barcelona with natural photoperiod and at approximately 21-22 °C from early April to June in both years. For the first year we did 6 replicates of each treatment, and for the second year we repeated all treatments again to increment the number of replicates. The competitive ability was determined from pair-wise competition experiments by estimating the effect of one species upon another by comparing the performance of each species when reared in the same (mixed) environment with performance when reared alone (single treatment). An additive experimental design was used (Underwood 1986): the tadpole density for each species in the mixed and in the corresponding single treatment was the same. Therefore with

this additive design, when species (A) has no competitive effect on species (B), the mass of species (B) at metamorphosis in the mixed environment (A,B) will be the same as in the single treatment.

The experimental design consisted of 27 treatments, each replicated 12 times (6 in 2001 and 6 in 2002):

(1) A low density single species treatment for each species, with 15 tadpoles per experimental unit (6 treatments).

(2) A high density single species treatment for each species, with 30 tadpoles per unit (6 treatments).

(3) All possible two-way mixtures of the six species with 15 tadpoles of each species (15 treatments).

Experimental units consisted of plastic tanks filled with 30 litres of dechlorinated tap water, inoculated with phytoplankton and zooplankton obtained from natural ponds. Tanks were left for two weeks to establish algae and a healthy zooplankton population before tadpoles were introduced. We used a variable number of clutches from the region of study for each species (25 of *Alytes*, 10 of *B. bufo* and *B. calamita*, 28 of *Pelodytes*, 35 of *Hyla* and 20 of *Rana*). In all replicates we used a mixture of an approximately equal number of tadpoles from different clutches per species both years. All individuals started at the same developmental stage (Gosner 25). Tadpoles were fed twice a week with a mixture of ground rabbit chow and fish food (4:1). All treatments received the same amount of food, which was gradually increased throughout the experiment in accordance with tadpole growth and food requirements.

Response variables and statistical analyses

The variables measured were as follows: mass at metamorphosis, larval period, growth rate and survival to metamorphosis. Metamorphosing individuals were collected daily as soon their tails were fully resorbed, and were then weighed to a precision of 0.001 g. Larval period was measured as days between stocking and metamorphosing. Growth rate was expressed as the mass gained each day during the larval period (mass at metamorphosis divided by larval period (g/days)). Survival was expressed as the proportion of larvae that

completed development in each replicate. The experiment for each replicate ended when all individuals reached metamorphosis.

All analyses were done using container means in order to avoid pseudoreplication. Before analysis, mass at metamorphosis and growth rate were \ln transformed, and survivorship proportions were arcsine-square root transformed in order to conform to the assumption of a parametric test. To analyse intraspecific competition we used multivariate analyses of variance (MANOVA) for the three traits together (mass at metamorphosis, growth rate and survival). When statistically significant effects were detected, successive t-tests were done for each variable. Previous analyses including a “year” factor produced the same results as analyses without the “year” factor; therefore, for simplicity we report the analyses without the “year” factor.

To establish whether competition between species was symmetric or asymmetric, and because species differed in baseline responses in the single treatments, we standardised the absolute changes in responses to facilitate interspecific comparison. The model developed by Morin and Johnson (1988) was applied to standardise species response. We estimated the absolute effect of increased intraspecific density for mass at metamorphosis and the other variables by subtracting the value of the mean of the low-density single treatment from the value for each individual in the high-density single treatment. We calculated relative standardised values by dividing the absolute change by the subtracting value (Morin & Johnson 1988).

For interspecific effects we followed the same model (Morin & Johnson 1988). We estimated the absolute influence of the competitor species (B) on (A) for each variable by subtracting the mean of the 12 replicates from (A) high density from the values for each (A) individual in the interspecific treatment (A, B). We also calculated relative standardised values by dividing the absolute change by the mean subtracting value.

The differences between all possible pair-wise tests to determine whether the absolute response differed between species were compared with a t-test, applying a Bonferroni correction for the conservative multiple comparisons test (Rice 1989).

To examine whether there is a relationship between size and competitive effects, we correlated the competitive ability of each species (obtained from the previous analyses) with

Responses to intraspecific competition

species	Mass at metamorphosis	Growth rates	Survival to metamorphosis
Alytes	$t_{1, 22}=-12.89$ $P<0.001$	$t_{1, 22}=-12.89$ $p=0.00848$	$t_{1, 22}=-12.89$ $P<0.001$
B. bufo	$t_{1, 22}=-1.44$ $p=0.16203$	$t_{1, 22}=-0.873$ $p=0.3919$	$t_{1, 22}=-0.901$ $p=0.37723$
B. calamita	$t_{1, 22}=-2.29$ $p=0.03172$	$t_{1, 22}=-3.61$ $p=0.0015$	$t_{1, 22}=-0.54$ $p=0.5905$
Hyla	$t_{1, 22}=-3.51$ $p=0.00199$	$t_{1, 22}=-3.67$ $p=0.00132$	$t_{1, 22}=-9.82$ $P<0.001$
Pelodytes	$t_{1, 22}=-1.74$ $p=0.09428$	$t_{1, 22}=-1.63$ $p=0.11558$	$t_{1, 22}=-2.93$ $p=0.00766$
Rana	$t_{1, 22}=-6.33$ $P<0.001$	$t_{1, 22}=-2.48$ $p=0.02124$	$t_{1, 22}=-8.35$ $P<0.001$

Table 1. t value and p value of t -test of intraspecific effects on the three variables studied (mass at metamorphosis, growth rates and survival to metamorphosis) for the different species.

specific sizes obtained from field measurements. Activity levels for each species were obtained from previous experiments of behavioural response of species to the presence of a predator (Richter-Boix et al. submitted). In this previous study we counted the number of tadpoles active at a precise moment under two conditions: presence and absence of a caged predator. We sampled activity behaviour by counting the number of tadpoles moving in each tub the instant the tub was first viewed (Skelly 1995). Each tub was observed every half hour for a total of 30 replicates during two weeks. This protocol was repeated for all six species. Tadpole densities were the same as in the present study (30 individuals per tank). We used activity level showed under predator-absence conditions as a measure for activity of tadpoles in monoculture. We expected that these values would help explain the outcome of competitive interactions as in previous works (Dayton & Fitzgerald 2001; Morin & Johnson 1988).

RESULTS

Intraspecific, interspecific and asymmetric competition

All species showed a significant response to intraspecific competition for the three variables measured, except *B. bufo* (MANOVA for *Alytes* ($F_{3, 20}=28.48$; $p<0.005$), *B. bufo* ($F_{3, 20}=1.08$; $p=0.38$), *B. calamita* ($F_{3, 20}=4.36$; $p=0.01$), *Hyla* ($F_{3, 20}=37.1$; $p<0.001$), *Pelodytes* ($F_{3, 20}=3.34$; $p=0.04$) and *Rana* ($F_{3, 20}=33.89$; $p<0.001$)). The effects of intraspecific competition were not the same for all species. Some species were affected at the individual level (lost of

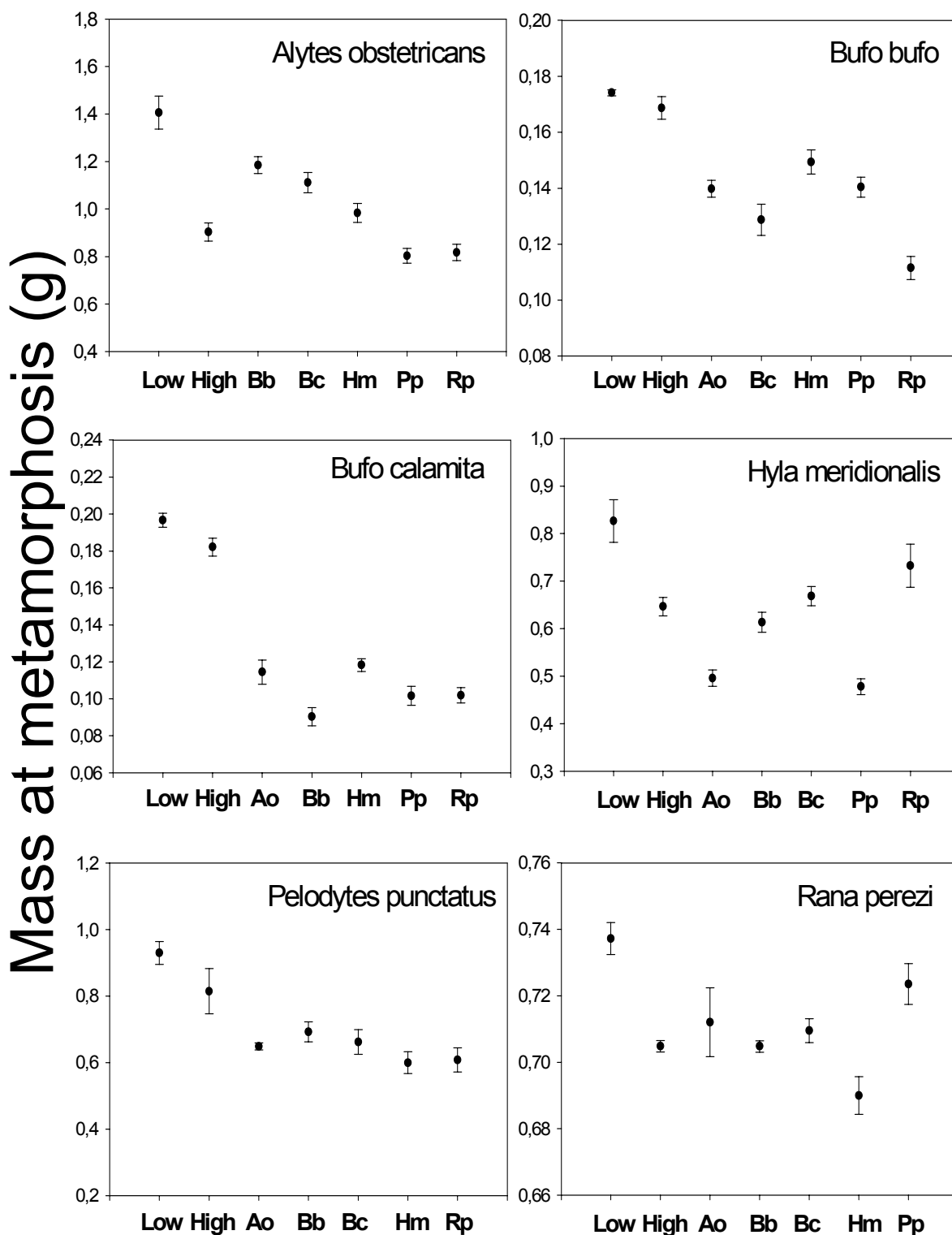


Fig. 2.- Mean and standard error of mass at metamorphosis for each species as a response to intra- and inter-specific competition. Species abbreviations: Ao = *Alytes obstetricans*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Pp = *Pelodytes punctatus*, Rp = *Rana perezi*.

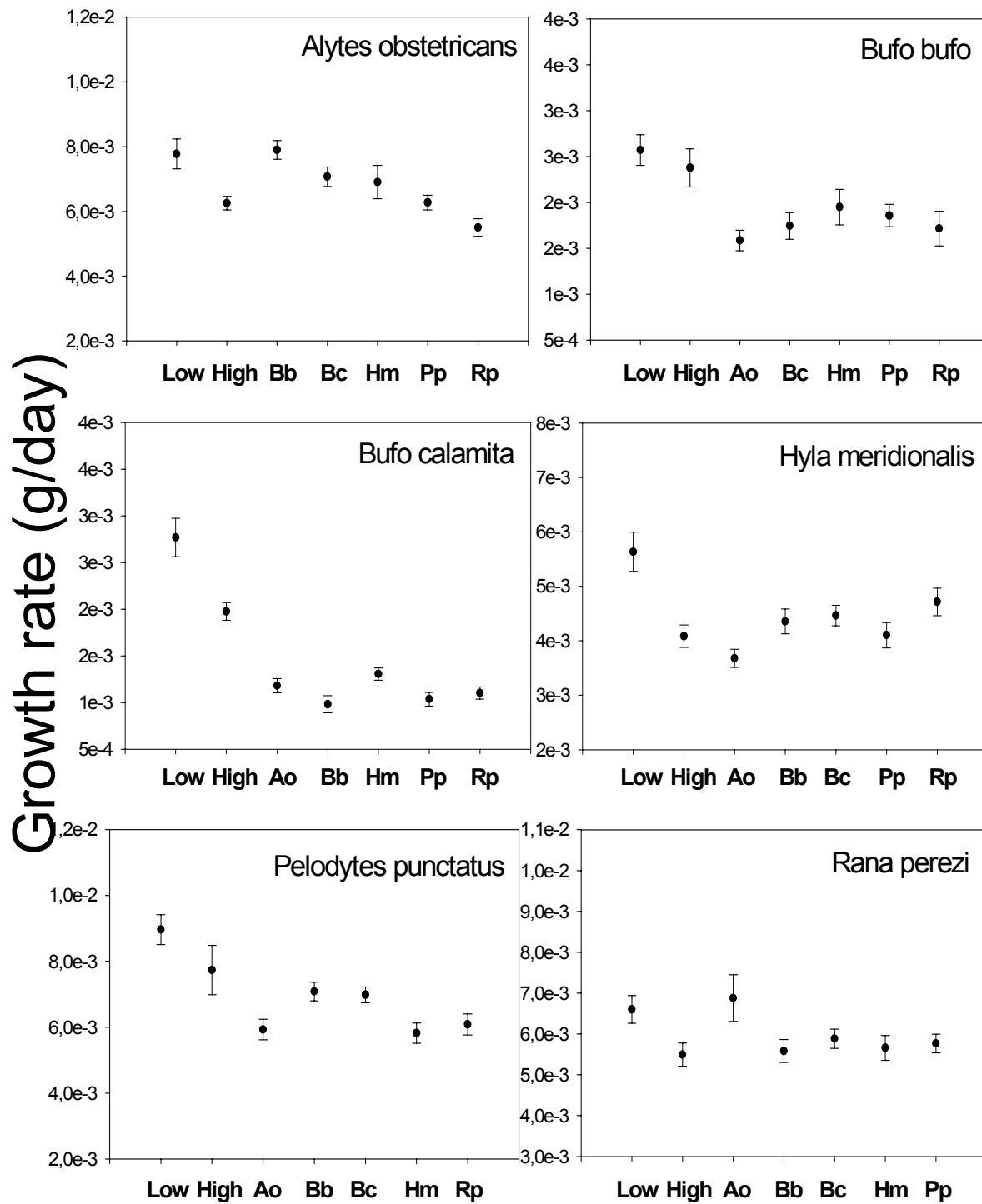


Fig. 3.- Mean and standard error of growth rate for each species as a response to intra- and interspecific competition. Species abbreviations: Ao = *Alytes obstetricans*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Pp = *Pelodytes punctatus*, Rp = *Rana perezi*.

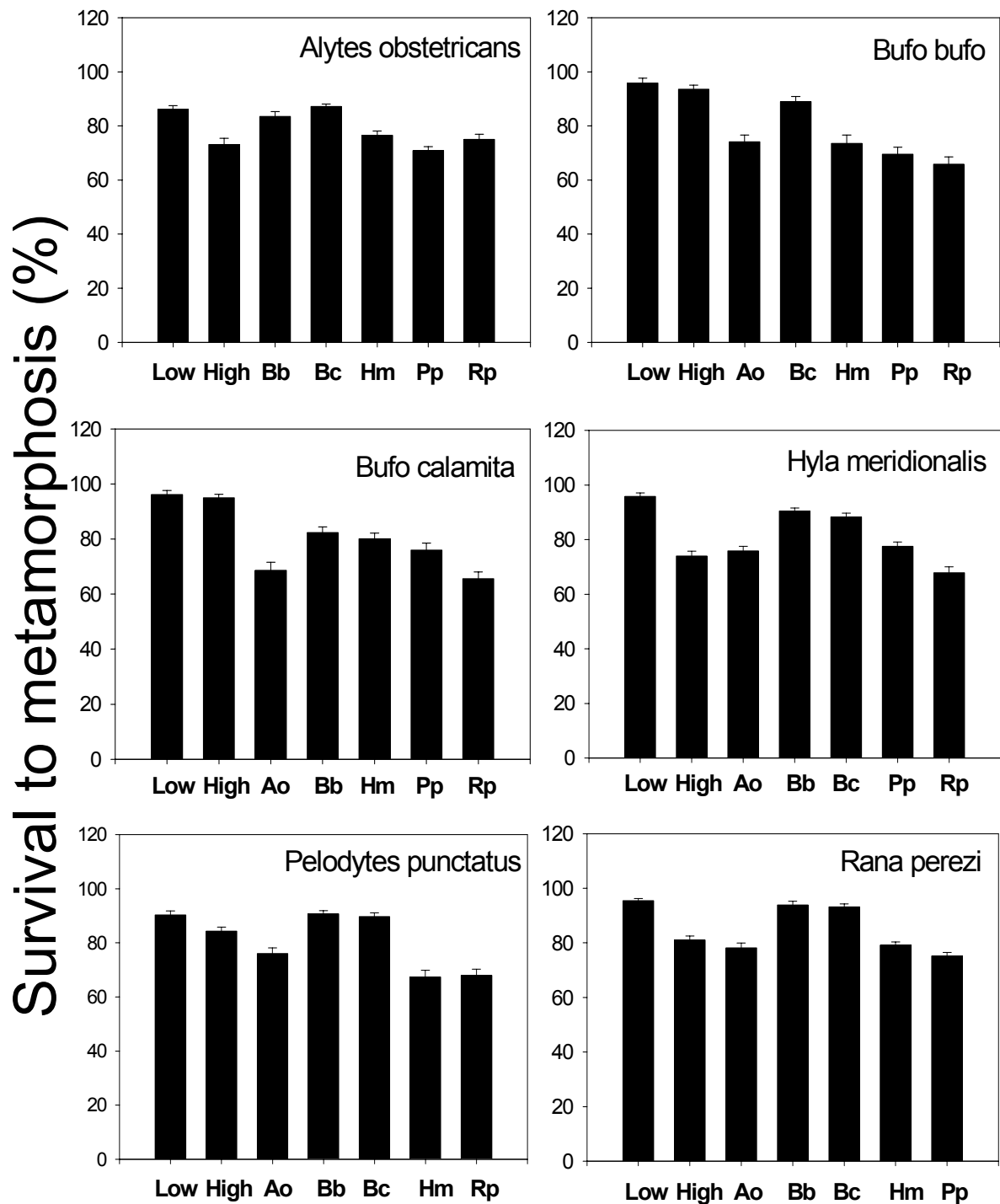


Fig. 4.- Mean and standard error of survival to metamorphosis for each species as a response to intra- and inter-specific competition. Species abbreviations: Ao = *Alytes obstetricans*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Pp = *Pelodytes punctatus*, Rp = *Rana perezi*.

a) Mass at metamorphosis

Target species	Competitor species						Mean response
	Ao	Bb	Bc	Hm	Pp	Rp	
Ao	-0.3577 (0.027)	0.312 (0.039)	0.23 (0.047)	0.089 (0.044)	-0.111 (0.034)	-0.095 (0.038)	0.085
Bb	-0.171 (0.018)	-0.0312 (0.023)	-0.237 (0.033)	-0.114 (0.025)	-0.168 (0.021)	-0.339 (0.025)	-0.2058
Bc	-0.372 (0.036)	-0.504 (0.027)	-0.0738 (0.024)	-0.351 (0.019)	-0.442 (0.028)	-0.441 (0.023)	-0.422
Hm	-0.233 (0.027)	-0.051 (0.033)	0.034 (0.032)	-0.2179 (0.023)	-0.261 (0.026)	0.133 (0.07)	-0.0756
Pp	-0.204 (0.013)	-0.15 (0.037)	-0.188 (0.046)	-0.264 (0.04)	-0.1238 (0.073)	-0.254 (0.044)	-0.212
Rp	0.01 (0.015)	0.0001 (0.002)	0.007 (0.005)	-0.021 (0.008)	0.027 (0.009)	-0.0439 (0.002)	0.00462
Mean effect	-0.194	-0.0785	-0.0308	-0.1322	-0.191	-0.1992	

b) Growth rates

Target species	Competitor species						Mean response
	Ao	Bb	Bc	Hm	Pp	Rp	
Ao	-0.195 (0.027)	0.263 (0.046)	0.131 (0.048)	0.104 (0.083)	0.003 (0.036)	-0.121 (0.043)	0.076
Bb	-0.333 (0.047)	-0.075 (0.081)	-0.266 (0.061)	-0.18 (0.081)	-0.218 (0.052)	-0.278 (0.079)	-0.255
Bc	-0.403 (0.038)	-0.503 (0.047)	-0.286 (0.034)	-0.34 (0.034)	-0.475 (0.037)	-0.443 (0.033)	-0.4328
Hm	-0.099 (0.041)	0.067 (0.056)	0.093 (0.046)	-0.275 (0.036)	0.005 (0.057)	0.155 (0.062)	0.0442
Pp	-0.233 (0.041)	-0.084 (0.037)	-0.097 (0.03)	-0.248 (0.039)	-0.137 (0.083)	-0.213 (0.041)	-0.175
Rp	0.252 (0.103)	0.016 (0.051)	0.071 (0.043)	0.03 (0.055)	0.05 (0.042)	-0.167 (0.043)	0.0838
Mean effect	-0.1632	-0.0482	-0.0136	-0.1268	-0.127	-0.180	

c) Survival to metamorphosis

Target species	Competitor species						Mean response
	Ao	Bb	Bc	Hm	Pp	Rp	
Ao	-0.151 (0.026)	0.141 (0.024)	0.191 (0.013)	0.046 (0.022)	-0.032 (0.02)	0.025 (0.026)	0.0742
Bb	-0.207 (0.026)	-0.023 (0.016)	-0.049 (0.02)	-0.215 (0.033)	-0.257 (0.028)	-0.339 (0.025)	-0.2134
Bc	-0.277 (0.031)	-0.133 (0.022)	-0.012 (0.014)	-0.156 (0.021)	-0.2 (0.027)	-0.309 (0.025)	-0.215
Hm	0.025 (0.022)	0.223 (0.014)	0.194 (0.018)	-0.228 (0.018)	0.047 (0.021)	-0.083 (0.029)	0.0812
Pp	-0.099 (0.025)	0.075 (0.014)	0.063 (0.017)	-0.202 (0.029)	-0.066 (0.017)	-0.194 (0.026)	-0.0714
Rp	-0.035 (0.021)	0.158 (0.017)	0.15 (0.013)	-0.023 (0.014)	-0.072 (0.016)	-0.152 (0.016)	0.0356
Mean effect	-0.1186	0.0928	0.1098	-0.110	-0.1028	-0.180	

Table 2. Matrix of relative standardised competition effects and standard error (in brackets) on mass at metamorphosis (a), growth rate (b) and survival to metamorphosis (c) from the pairwise competition experiments (n = 12 replicates). Column (effect) and row (response) averages are calculated excluding the diagonal elements (intraspecific competition). Species abbreviations: Ao = *Alytes obstetricans*, Pp = *Pelodytes punctatus*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Rp = *Rana perezi*.

mass at metamorphosis and growth rates) but not at the population level (survival to metamorphosis), as for example *B. calamita*. For other species, like *Pelodytes*, intraspecific competition had significant effects on population level but none at the individual level. The intensity and importance of intraspecific competition varied between species (see Table 1 and Figures 2, 3 and 4). For *Alytes*, *Hyla* and *Rana*, standardised intraspecific response values were higher than the standardised interspecific mean response in the three variables considered (Tables 2a, 2b and 2c).

Competitive interactions in multispecies communities can be separated into two processes: the effect of a species on others in the community, and the response of a species to others (Miller and Werner 1987). The overall effect and response are observed as the row and column averages, excluding the diagonal elements (Tables 2a, 2b and 2c). For example, on mass at metamorphosis the mean effect ranged from -0.1992 for *Rana* (indicating that on average *Rana* depressed the performance of other species to 19% of that registered in single treatments) to -0.0308 for *B. calamita*. Competitive response values ranged from -0.422 for *B. calamita* (indicating that on average the other species decreased the performance of *B. calamita* to 42% of its performance in their absence) to 0.0046 for *Rana*. Competitive effect and response were significantly correlated across species for growth rates and survival to metamorphosis ($r = 0.93$, $p = 0.006$ and $r = 0.91$, $p = 0.01$ respectively), but not for mass at metamorphosis whereas showed the same tendency ($r = 0.8$, $p = 0.053$). This observation shows that there was usually asymmetric pairwise competition between the species pairs, with a “winner” and a “loser” (Roxburgh & Wilson 2000).

The extent of the competitive asymmetry was studied further by performing a t-test between each pair of standardised values for the three variables. Of the 15 pairwise comparisons, 9 showed a significant difference between reciprocal standardised values, with a greater capacity for one species of the pair (Tables 3a, 3b and 3c). The pattern of the asymmetric competitive relations among the six species (Tables 3a, 3b and 3c) were arranged into a linear hierarchy of competitive ability, the most competitive at the top and the least competitive at the bottom (Fig. 5A, 5B and 5C). The representations obtained for the three variables were very similar, showing the same hierarchical order.

We used field data for tadpole species size to examine whether there is a relationship between size and competitive effects. Both variables were significantly correlated across species (mass at metamorphosis ($r = 0.96$, $p = 0.01$), growth rates ($r = 0.92$, $p = 0.007$) and survival ($r = 0.87$, $p = 0.02$)), indicating that larger tadpoles are better competitors than smaller ones. Activity was not significantly correlated with competitive effects (mass at metamorphosis ($r = -0.74$, $p = 0.089$), growth rate ($r = -0.8$, $p = 0.052$) and survival ($r = -0.7$, $p = 0.120$)).

DISCUSSION

Our findings on competition are consistent with previous studies that have demonstrated strong asymmetric interspecific effects on the fitness-related parameters of tadpoles (e.g. Smith-Gill & Gill 1978; Wilbur 1982, 1987; Morin & Johnson 1988; Griffiths 1991; Griffiths et al. 1991; Werner 1992; Semlitsch 1993; Kupferberg 1997; Parris & Semlitsch 1998; Bardsley & Beebee 2000; Gurevich et al. 2000; Relyea 2000, Dayton & Fitzgerald 2001; Gómez-Mestre & Tejedo 2002; Smith et al. 2004; Smith 2005). However, our results showed a different pattern from that detected in previous studies from desert communities, where active ephemeral pool species have a competitive advantage over less active species from temporary or permanent ponds (Woodward 1982; Dayton & Fitzgerald 2001). Our data do not support this idea but are coincident with other studies of European temporary pond breeding species (*B. calamita* and *Rana temporaria*), which are less competitive than a permanent pond species (*B. bufo*) (Griffiths 1991; Laurila 2000). One possible explanation for these differences between communities could be that New World desert spadefoot toads are species with ancestral traits adapted to ephemeral pools (e.g. fast development, carnivorous morphs) (Buchholz and Hayes 2002), whereas *B. calamita* and *Pelodytes* probably use ephemeral pools as refuges free of predators and competitors, rather than because of an adaptation characteristic of their respective ancestral traits. This perspective is in concordance with Smith's observations (1983) on *Pseudacris triseriata*, which breed in ephemeral pools to avoid predators in permanent ponds and high competition in temporary ponds. Species with low competitive ability can persist by using refuges in which competition is reduced if heterogeneity exists among patches or if they have a greater capacity to colonise a free environment (Horn & MacArthur 1972; Tilman 1994). Theoretically, in competitive-

hierarchy scenarios, inferior competitors rely on the space left empty by the superior competitors (Wu & Levin 1994; Keymer et al. 2000), and in time habitat segregation among species occurs (“Ghost of Competition Past” (Rosenzweig 1987)). These models suggest that the historical factor that favoured species of the same guild specialising and segregating along the gradient may have been interspecific competition. Such regularity in niche dispersion is often taken as evidence that competition has been at work molding niches in the past, if not in the present (Case 1981; Doebeli & Dieckmann 2003), although it now appears that other factors determine breeding site use by species. Factors related to microhabitat, feeding patterns, ingestion rates, pond duration, and predator densities may also influence distribution of amphibian species across the hydroperiod gradient suggesting that competition is less important than variation in the other parameters which determine quality among habitats for each species (Wellborn et al. 1996; Richardson 2001, 2002; Babbitt et al. 2003; Van Buskirk 2003, 2005). It is possible that in nature differences in larval physiology, period of breeding or other factors reverse the competition observed in our laboratory system. For example, rapid development dependent upon high ingestion rates of suspended nutrients in oligotrophic waters from ephemeral pools enables *B. calamita* to escape quick evaporation of the pools (Viertel 1995), whereas *B. bufo* tadpoles, usually not under pressure to leave their waters soon, were not selected for high suspension feeding efficiency but perhaps for scraping peryphyton or vegetation from the bottom of permanent ponds (Diaz-Paniagua 1989, Viertel 1995). It is possible that competitive abilities and hierarchy do not remain stable but change over a range of hydroperiods, originating a different hierarchy in each habitat depending on morphology, physiology and other factors which could modify species interactions. Thus the system could be considered as a metacommunity in which coexistence is mediated by the existence of different sources and sinks for each species across the hydroperiod gradient (Amarasekare et al. 2004).

In the present study body size differences among species may explain interspecific competitive differences. We found that, at individual and population levels, larger species were more affected by intra- than interspecific competition, while smaller ones were more affected by the latter and normally support high intraspecific densities better. Larger species

a) Mass at metamorphosis						
	Ao	Bb	Bc	Hm	Pp	Rp
Ao	***	<0.0001**	<0.0001**	<0.0001**	0.0552	
Bb		***	<0.0001**		0.0053	
Bc			***		0.0679	
Hm		0.5322	0.0004**	***	0.2175	0.0385
Pp					***	
Rp	0.0016**	<0.0001**	<0.0001**		<0.0001**	***
b) Growth rate						
	Ao	Bb	Bc	Hm	Pp	Rp
Ao	***	<0.0001**	<0.0001**	0.0649	0.0001**	
Bb		***	0.0463		0.6761	
Bc			***			
Hm		0.0285	<0.0001**	***	<0.0001**	0.2466
Pp			0.4572		***	
Rp	0.0025**	0.0375	<0.0001**		0.0004**	***
c) Survival to metamorphosis						
	Ao	Bb	Bc	Hm	Pp	Rp
Ao	***	<0.0001**	<0.0001**	0.5263	0.0281	0.0817
Bb		***	0.0089			
Bc			***			
Hm		<0.0001**	<0.0001**	***	<0.0001**	
Pp		<0.0001**	<0.0001**		***	
Rp		<0.0001**	<0.0001**	0.0921	0.0004**	***

Table 3. Matrix of P values of relative values from t -test between pairwise competitors (see Table 2) for mass at metamorphosis (a), growth rate (b) and survival to metamorphosis (c). Statistically significant P values after Bonferroni correction ($p'=0.003$) are indicated in bold, and show that the row species is competitively superior to the column species. Species abbreviations: Ao = *Alytes obstetricans*, Pp = *Pelodytes punctatus*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Rp = *Rana perezi*.

were better competitors, which is consistent with some previous experiments (Woodward 1982; Wilbur & Alford 1985; Morin & Johnson 1988; Werner & Anholt 1996; Smith et al. 2004). However, for some variables, size does not always explain the asymmetry in the interactions between tadpoles (Werner 1992, 1994; Parrish & Semlitsch 1998; Laurila 2000; Richter-Boix et al. 2004). Activity level may also affect the outcome of competitive interactions

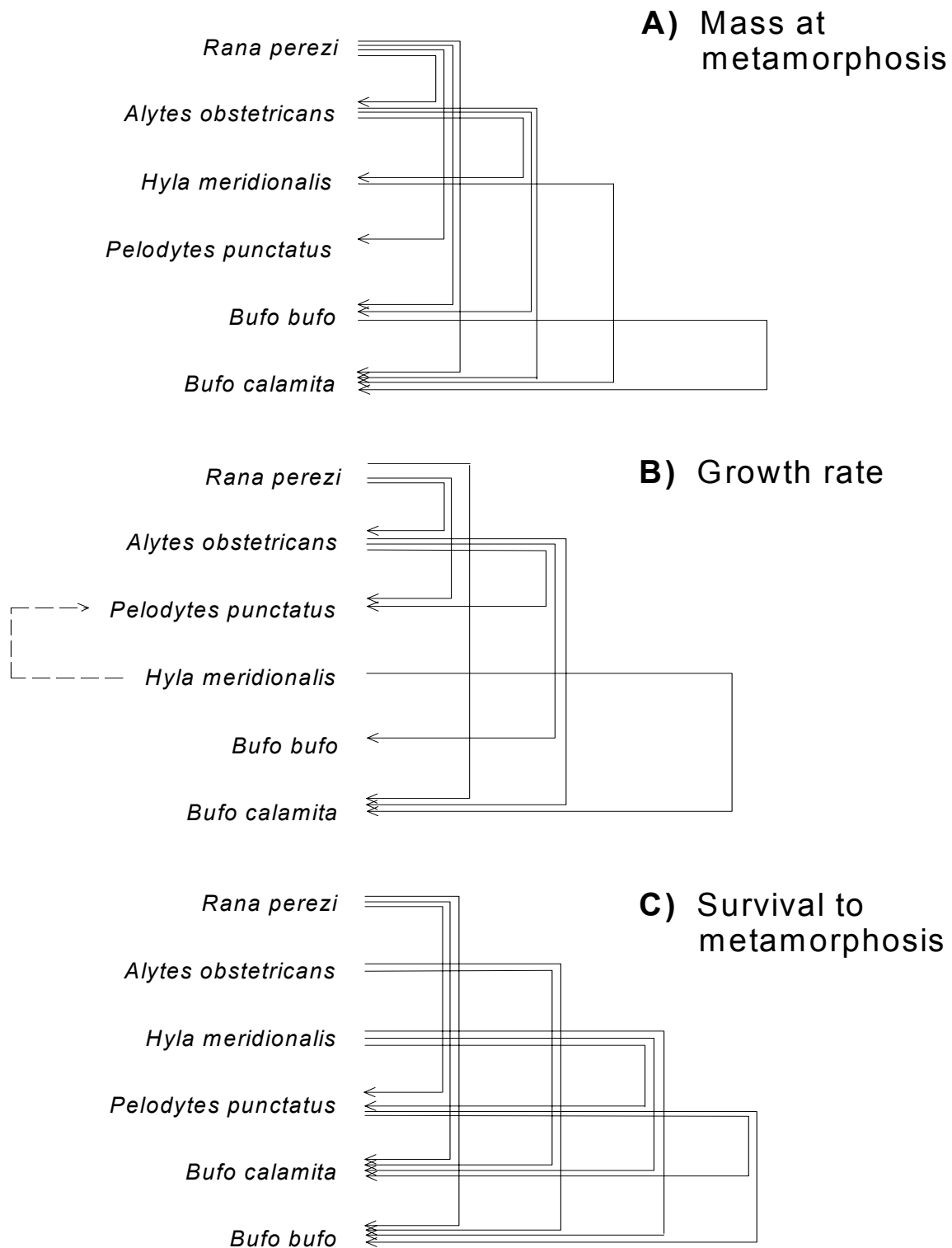


Fig. 5.- Hierarchy of competitive capacity on the basis of the results of the pairwise competition experiment for mass at metamorphosis (A), growth rate (B) and survival to metamorphosis (C). Hierarchies were based on Tables 2a, 2b and 2c respectively. An arrow leaving species A and terminating at species B indicates that species A suppressed B significantly more strongly than vice versa, as defined by the *t*-test in Tables 3a, 3b and 3c before Bonferroni correction. Dashed arrow indicates a statistical countergradient interaction.

(Dayton & Fitzgerald 2001; Werner 1992; Laurila 2000), but in our study we do not find this relationship, and in the community we studied more active tadpoles (those from ephemeral and temporary ponds such as *B. calamita* and *Pelodytes*) are less competitive species. However, we must be cautious with these results, because we used activity levels measured under conditions with no-competition, and studies revealed that the activity level is a plastic variable which can change over time or between treatments (Werner & Anholt 1996; Laurila 2000; Smith et al. 2004; Richter-Boix et al. 2004).

We acknowledge that our experimental conditions place the animals in artificial and over-simplified environments. Current debate is taking place on experimental venue and the estimation of competitive interactions in mesocosm and field experiments (Chalcraft et al. 2005; Skelly 2005). Field experiments allow habitat and abiotic factors to play a role in the outcome of species interactions (Skelly 2002) but often lack precision in testing predictions made by theory and have a high level of variability among replicates with low levels of replication (Morin 2000). Laboratory experiments, on the other hand, allow us to disentangle the effects of abiotic and biotic factors, and by controlling for confounding variables that exist in natural settings we are able to isolate and test specific hypotheses about competition (Dayton & Fitzgerald 2001). We may not be able to say much about what happens in natural conditions beyond the potential for asymmetric competition, because in a more complex natural system the strength of interactions can change and what we observe in laboratory experiment may not coincide with what occurs in natural systems (Laurila 2000; Skelly 2002, 2005). However, our experiment does tell us something about traits that may influence the outcome of interspecific interactions and elaborate hypotheses which will be tested in future field experiments or compared with field observations. From this point of view our results showed that we do not at present have a clear pattern with which to explain tadpole interactions, and that variables other than body size and activity level must be investigated in future studies to help us to explain which mechanisms determine interspecific interactions.

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