

The effects of competition on pre- and post-metamorphic phenotypes in the common frog

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Many species express different phenotypes when reared under different environmental conditions. However, few studies have considered the possible post-metamorphic effects associated with the induction of particular larval phenotypes in organisms which undergo metamorphosis. In this study, we manipulated both larval density and food availability to create the conditions likely to induce high and low competition morphs in the common frog *Rana temporaria* and examined the resulting pre- and post-metamorphic phenotypes. Tadpoles reared in a high competition environment took longer to reach metamorphosis, were smaller in terms of both mass and total length and possessed relatively narrow bodies and mouths and short, narrow tails compared to low competition tadpoles. Competition level also influenced swimming ability with high competition tadpoles swimming slower and less far than low competition tadpoles. The effects of high levels of larval competition persisted through metamorphosis; high competition froglets were initially shorter and lighter than those reared under a lower level of competition. In addition, froglets reared under a high level of competition as larvae developed relatively short femurs. However, differences in froglet morphology did not significantly affect performance. These results suggest that factors influencing the phenotype in the larval stage will also have post-metamorphic fitness consequences through influences on post-metamorphic morphology.

Key words: developmental trade-offs, phenotypic plasticity, swimming ability, *Rana temporaria*, life history

INTRODUCTION

Organisms that undergo radical habitat shifts across life-history stages are often subjected to different selection pressures at different stages of their life cycle (Wilbur, 1980). For example, many insects and amphibians metamorphose from aquatic larvae to terrestrial adults. A particular set of conditions in the larval habitat might be associated with a high prevalence of a specific morphology, either through phenotypic plasticity, where development is adjusted in response to prevailing environmental circumstances, or as a consequence of selective mortality of those individuals not displaying appropriate phenotypic traits (Quinn & Buck, 2001; Laurila et al., 2002; Taborsky et al., 2003; Yeh & Price, 2004). However, physiological and functional interrelationships within an organism might constrain an individual's ability to tailor phenotypic development to environmental conditions across all life-history stages (Phillips, 1998).

The finding that traits are not necessarily independent of one another across life-history stages (Ray, 1999) suggests that metamorphosis does not always provide the chance to "start again" (Pechenik et al., 1998). The duration of the larval period is known to influence the post-metamorphic phenotype (Relyea, 2001; Relyea & Hoverman, 2003) and several studies have demonstrated that the manipulation of some larval tissues particularly affects those post-metamorphic traits developing in relatively close anatomical proximity to the manipulated larval trait (Hirano & Nishida, 1997; Nijhout & Emlen, 1998). Furthermore, where metamorphosis occurs via the

remodelling of larval structures to form adult structures, such as occurs in the majority of amphibian traits (Alberch, 1987), greater linkage between larval and adult traits would be expected than in cases of compartmentalization, where adult structures are formed from undifferentiated cell lineages (Moran, 1994). This phenotypic non-independence means that trade-offs are likely to occur across life-history stages, although the nature of these trade-offs and the way in which larval environment affects future fitness has yet to be fully investigated.

Despite numerous studies describing the morphology of several species of anuran tadpoles reared under varying levels of inter- and intraspecific competition (e.g. Murray, 1990; Goater, 1994; Relyea, 2002), few have considered the possible carry-over effects of larval morphology to post-metamorphic size and shape (Relyea, 2001; Relyea & Hoverman, 2003). Tadpoles reared under high levels of competition have been shown to possess relatively larger bodies and smaller tails than tadpoles from low competition environments (Relyea, 2002; Relyea & Hoverman, 2003). This differential allocation of resources is thought to be beneficial to competing individuals as the larger body houses a longer digestive tract, which presumably allows the more efficient processing of food (Relyea & Auld, 2004). However, if structures in close anatomic proximity are positionally linked across metamorphosis, it seems likely that, in anurans, resources arising from the absorption of the tail will be allocated to the hind limbs of post-metamorphic individuals. Therefore, tadpoles that develop relatively long bodies, and consequently short tails, would be expected to metamor-

phose into froglets with relatively short hind limbs, a potentially disadvantageous trait in terms of locomotion in the terrestrial environment (Gillis & Biewener, 2000; Phillips et al., 2006). This hypothesis is in direct contrast with the finding that tadpoles that undergo a prolonged larval period, as has been demonstrated for tadpoles reared in a high competition environment, develop into froglets with larger hind limbs (Ficetola & de Bernardi, 2006; Gomez-Mestre & Buchholz, 2006; Richter-Boix et al., 2006).

Few studies have considered the effect of tailoring the larval phenotype to prevailing environmental conditions on locomotor performance at any stage of the life cycle. The relatively small tails of high competition tadpoles will have a reduced area available for the generation of thrust (Doherty et al., 1998) and the associated smaller muscle mass could reduce swimming speed and/or the distance over which swimming is maintained. In addition, individuals reared in high competition environments are usually smaller than those reared at higher levels of competition (Relyea, 2002) and it has been demonstrated in several taxa that larger individuals can swim faster for longer than smaller individuals (e.g. fish, Ojanguren & Braña, 2003; ducks, Anderson & Alisaukas, 2001; snakes, Webb et al., 2001). If this size difference is maintained through metamorphosis then the potentially poor locomotor ability of high competition tadpoles compared to their low competition conspecifics may persist in the terrestrial phase of the life cycle. Here, using the common frog *Rana temporaria*, we experimentally test the hypothesis that larval phenotypes prevailing under conditions of high and low competitor density give rise to post-metamorphic phenotypes with different hind limb size, and examine the consequences of this for locomotion.

METHODS

Tadpoles

On 10 March 2003, three clumps of *R. temporaria* spawn, each comprising several egg masses, were collected from Killearn near Glasgow (56°02'N, 42°02'W) and maintained at ambient temperature in the laboratory until hatching. Larval density and food quotas were then manipulated to create conditions likely to favour high and low competition morphs (Relyea & Werner, 2000). Hatchlings (stage 23; Gosner, 1960) from all three clumps were combined to ensure mixing of genotypes and assigned to 24 tanks (559 × 370 × 310 mm) divided equally between high (150 tadpoles per tank; 4.69 tadpoles per litre) and low (50 tadpoles per tank; 1.56 tadpoles per litre) levels of competition. These densities were comparable to those observed in the source population.

Tanks were arranged in three covered outdoor enclosures each containing two blocks of four tanks, two from each treatment group, to minimize tank and enclosure effects. Tanks contained 32 litres of water, a bottom covering of clean gravel, a length of drainpipe to provide shelter and an air supply. Tadpoles were exposed to natural light and temperature and were fed a 3:1 mix of rabbit chow and fish flakes. The mass of food provided was calculated as 6% of the mean body mass of 100 stock

tadpoles, maintained at an intermediate density of 100 tadpoles per tank, per day (Relyea & Werner, 2000). All tanks received the same amount of food; therefore low competition tadpoles received three times more food than high competition tadpoles. Although food was not always completely consumed between feedings food was not provided *ad libitum* and the food ration per tank was reduced on a *pro rata* basis as individuals reached metamorphosis or were observed to have died.

Due to the expected differences in the developmental rates of high and low competition tadpoles, morphology and swimming ability were assessed at specific stages during development, rather than at a given age. At Gosner (1960) stages 28 and 39 two tanks per treatment group were removed from the experiment and a sub-sample of 20–30 tadpoles per tank was removed for sampling; tanks were considered ready for sampling when 80% of tadpoles were at the appropriate stage. Entire tanks were removed, rather than a subsample of tadpoles from each tank, as large numbers of individuals were also required for a separate study and consequently the density of tadpoles in each tank would have been substantially reduced throughout the duration of the larval period.

Swimming trials occurred in a constant temperature room at 16 °C and were digitally recorded. At the start of a trial, a single tadpole was placed at one end of a tank (1500 × 20 × 50 mm) filled with water to a depth of 30 mm and with a bottom scale graduated at 1 mm intervals, gently prodded at the base of the tail with a thin wire to elicit an escape response, and allowed to swim until it came to a complete stop. Tank dimensions minimised the movement of tadpoles in the water column and encouraged them to swim in a straight line. Distance swum was measured as the position of the tip of the snout to the nearest mm immediately before the first movement of the tail to the position of the tip of the snout after the last movement of the tail. The swimming speed of tadpoles was calculated as the distance swum divided by the time spent swimming, recorded in minutes, seconds and milliseconds, to give swim speed in terms of cm/s. Each tadpole was tested three consecutive times and as there was no evidence of habituation (repeated measures ANOVAs, all *P* values >0.200) the average speed and distance of the three trials were used in analyses.

Once tested, tadpoles were sacrificed in a lethal dose of benzocaine (10 ml of 1% stock solution/1000 ml water), preserved in buffered formalin and weighed to the nearest mg. A dissecting microscope was used to measure the snout–vent length, body width, mouth width, tail length, maximum tail height, tail muscle height, tail muscle width and dorsal and ventral tail fin height to 0.1 mm. Total length was measured to 0.1 mm from the tip of the snout to the distal tip of the tail using digital callipers.

Froglets

Each remaining individual was transferred to a semi-terrestrial tank (250 × 250 × 300 mm; six individuals per tank) on emergence of its forelimbs, signalling the onset of metamorphosis (stage 42), according to treatment group and date of metamorphosis. Each tank contained clean gravel, wetted daily, a pool of water, a length of drainpipe

for shelter, and was constructed with mesh sides to aid air circulation. Froglets were fed *Drosophila melanogaster ad libitum*.

To assess the effect of the larval phenotype on morphology post-metamorphosis, froglets were weighed to the nearest mg and their snout–vent length and femur length measured to 0.1 mm using digital callipers every two weeks from the completion of metamorphosis. To minimise potential tank effects froglets were rotated between tanks but remained grouped according to date of metamorphosis. The experiment was terminated once the last individual had reached eight weeks post-metamorphosis due to difficulties in maintaining froglets beyond this stage.

In addition, a sample of 30 froglets was removed every four weeks from the completion of metamorphosis to measure either swimming or jumping ability before being weighed and measured as described above. Swim testing was carried out as described for tadpoles, with movement of the hind limbs indicating the start and end of swimming. The jumping ability of froglets was assessed in a constant temperature room at 16 °C by placing an individual on an ink pad at the end of a length of damp lining paper (1000 × 1000 mm) and touching it at the tip of the urostyle to elicit an escape response. The ink allowed accurate tracking of the froglets' movements to give distance jumped (mm). The average distance of the first three jumps was used in analyses. The proportion of individuals not showing an escape response, and thus from which measurements could not be recorded, did not differ between treatments (four weeks post-metamorphosis, swimming $df=1$, $\chi^2=2.44$, $P>0.05$, jumping $df=1$, $\chi^2=0.545$, $P>0.05$; 8 weeks post-metamorphosis, swimming $df=1$, $\chi^2=0.208$, $P>0.05$, jumping $df=1$, $\chi^2=0.948$, $P>0.05$).

Statistical procedures

Data were tested for normality and homogeneity of variances and transformed as necessary. Tank was nested within treatment for each analysis of the tadpole data. The mass, total length and swimming ability (average speed and distance) of tadpoles were analysed using multivariate GLMs followed by univariate analyses for significant effects. Relative snout–vent/tail length was assessed by entering tail length into a univariate GLM with competition level as a factor and snout–vent length as a covariate. Relative morphology and swimming ability of tadpoles were analysed using MANCOVAs with total length, as a measure of size, as a covariate. ANCOVAs were then conducted for significant effects. Model simplification was used to determine the effect of relative morphology on the performance of tadpoles. The full model (measure of swimming ability as the response variable, competition level as a factor, tank nested within competition level, total length, body width and all measures of tail morphology as covariates and the interaction between treatment and each morphological variable) was simplified using both ANOVA and AIC scores (Crawley, 2005). The morphology and swimming ability of froglets were analysed as above with the inclusion of date of metamorphosis as a covariate and the substitution of total length for snout–vent length as a measure of size. Froglet

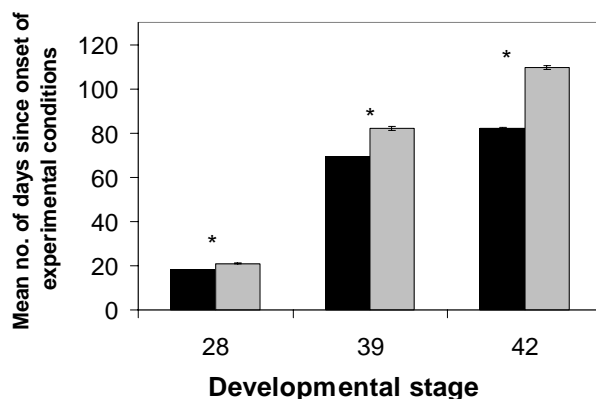


Fig. 1. The time taken for tadpoles (\pm S.E.) reared under high (grey bars) and low (black bars) levels of competition to reach three developmental stages. * indicates a significant difference at the Bonferroni corrected α level.

jumping ability was analysed using univariate GLMs. Two-way interactions were initially included in all analyses and removed if non-significant. A sequential Bonferroni correction was conducted to estimate a new α value for each statistical test (Rice, 1989). The statistical packages JMP (v. 5.0.1) and R (v. 2.5.1) were used for all analyses.

RESULTS

Development time and mortality

As expected, competition level had a significant effect on the developmental rate of tadpoles. From the onset of experimental conditions (stage 23), tadpoles from the high competition environment took significantly longer to reach stage 28 ($t_{57.35}=19.6$, $P=0.001$), stage 39 ($t_{46.00}=21.5$, $P=0.001$) and the onset of metamorphosis ($t_{676.98}=27.4$, $P=0.001$) than those reared in a low competition environment (Fig. 1).

Competition level also influenced mortality rates with 2.60% (S.E. ± 0.99) mortality between hatching and metamorphosis in the low competition group compared to 42.67% (S.E. ± 4.52) in the high competition group ($df=1$, $\chi^2=164.0$, $P<0.05$). However, the mean number of tadpoles per high competition tank remained substantially higher throughout the larval period than that of the low competition tanks (mean initial densities: high competition tanks 150 tadpoles per tanks, 4.69 tadpoles per litre; low competition tanks 50 tadpoles per tank, 1.96 tadpoles per litre; mean densities at metamorphosis: high competition tanks 86 tadpoles per tank, 2.69 tadpoles per litre; low competition tanks 49 tadpoles per tank, 1.53 tadpoles per litre). Mortality rates in the juvenile phase of the life cycle were difficult to estimate as a number of froglets could not be accounted for; presumably these individuals either escaped or died and decomposed before they were found. Estimates suggest a mortality rate of approximately 35% in the low and 60% in the high competition froglets ($t_{514}=3.8$, $P=0.0002$).

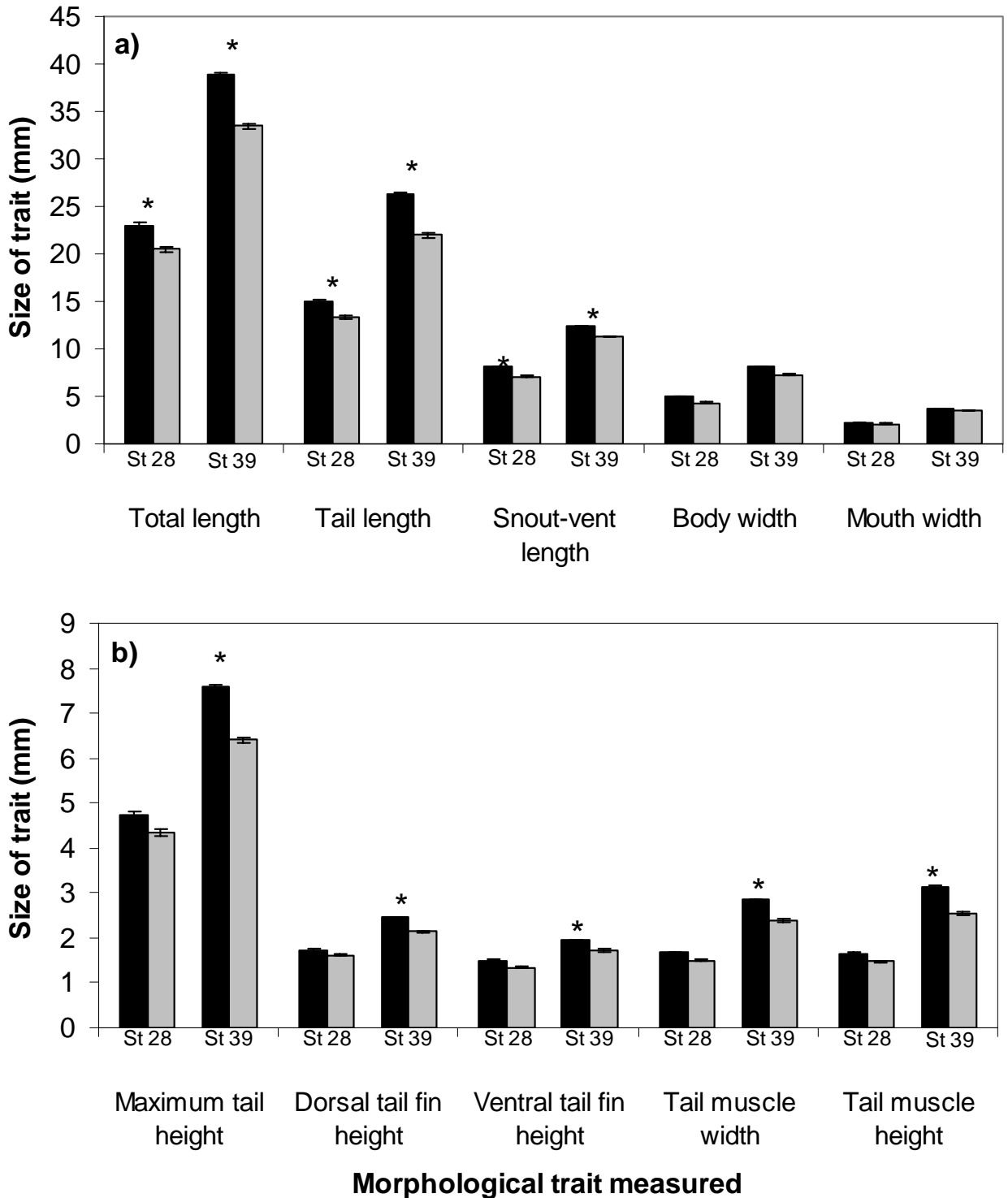


Fig. 2. The mean (\pm S.E.) for each morphological variable measured from tadpoles reared under high (grey bars) and low (black bars) levels of competition at developmental stages 28 and 39. * indicates a significant difference at the Bonferroni corrected α level (GLM with morphometric variable as a dependent factor, competition level as the fixed factor and total length as a covariate).

Phenotype favoured in the larval environment

Tadpoles reared in the high competition environment were noticeably smaller than those from the low competition environment (MANCOVA, $F_{1,73}=95.6$, $P<0.0001$; mass \pm S.E.: high competition tadpoles 0.079 ± 0.003 g, low competition tadpoles 0.111 ± 0.003 g, $F_{1,73}=102.9$,

$P<0.0001$; total length: $F_{1,73}=102.9$, $P<0.0001$, Fig. 2a) just three weeks after the onset of experimental conditions (stages 23–28). The shape of tadpoles also differed, with high competition tadpoles possessing significantly shorter tails for a given snout–vent length than low competition tadpoles ($F_{1,72}=18.4$, $P<0.0001$) as reported in other studies (Relyea, 2002; Relyea & Hoverman, 2003). There was no other detectable difference in the relative

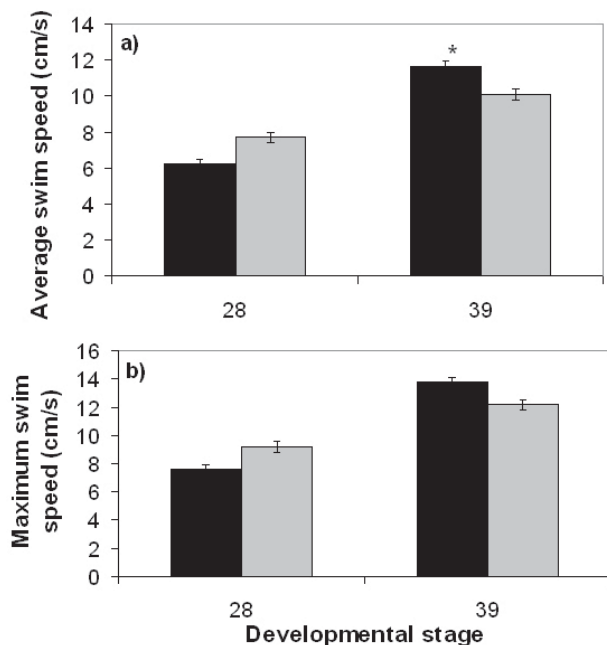


Fig. 3. a) Mean swim speed and b) distance swum (\pm S.E.) for tadpoles reared under low (black bars) and high (grey bars) levels of competition at different stages of larval development. * indicates a significant difference at the Bonferroni corrected α level (GLM with swim speed or distance swum as a dependent factor, competition level as the fixed factor and total length as a covariate).

morphology of tadpoles from the two treatment groups at this stage (MANCOVA, $F_{6,67}=1.9, P=0.1027$; Fig. 2a,b). As expected, all morphological variables increased with total length.

Competition level was found to have a much greater effect on tadpole phenotype towards the end of the larval period. At stage 39, high competition tadpoles were again

smaller than those from the low competition environment (MANCOVA, $F_{1,103}=143.3, P<0.0001$; mass \pm S.E.: high competition tadpoles 0.299 ± 0.008 g, low competition tadpoles 0.423 ± 0.008 g, $F_{1,103}=158.5, P<0.0001$; total length $F_{1,103}=148.3, P<0.0001$, Fig. 2a) and again possessed significantly shorter tails than low competition tadpoles for a given snout–vent length ($F_{1,72}=18.4, P<0.0001$). There was also a significant difference in the shape of tadpoles independent of total length, however (MANCOVA, $F_{6,96}=6.4, P<0.0001$). Tadpoles from the high competition group had shallower dorsal and ventral tail fins, shallower and narrower tail muscles and a shallower maximum tail height than low competition tadpoles for a given total length (Fig. 2a,b).

All morphological variables measured, with the exception of ventral tail fin height, increased with total length. The relationship between ventral tail fin height and total length was positive for high competition tadpoles but negative for low competition tadpoles (interaction between competition level and total length: $F_{1,101}=8.0, P=0.0057$).

The effect of phenotype on larval performance

Despite the morphological differences between tadpoles from different treatment groups at developmental stage 28 there was no significant difference in their swimming ability (MANCOVA, $F_{1,72}=0.2, P=0.6865$).

At developmental stage 39, however, differences in morphology translated into a difference in swimming ability (MANCOVA, $F_{1,102}=4.5, P=0.0356$). Low competition tadpoles swam approximately 13.25% faster than those from the high competition group ($F_{1,102}=6.36, P=0.0132$; Fig. 3a). Model simplification indicated that only competition level explained a significant amount of the variation in swim speed ($t_{103}=2.8, P<0.0054$). Thus, low competition tadpoles swam faster than those reared under a high level of competition independent of both total length and relative morphology.

Table 1. Mean \pm S.E. for mass, snout–vent length and femur length of froglets reared under different levels of competition. * indicates a significant difference in absolute mass and snout–vent length, and relative femur length at the Bonferroni corrected α level (see text for F values).

Weeks post-metamorphosis	Competition level	<i>n</i>	Mass (g) (\pm S.E.)	Snout–vent length (mm) (\pm S.E.)	Femur length (mm) (\pm S.E.)
2	Low	98	0.156 (0.003)*	11.666 (0.095)*	4.911 (0.037)*
	High	108	0.094 (0.004)*	9.239 (0.133)*	3.856 (0.069)*
4	Low	68	0.162 (0.005)	11.593 (0.129)*	5.169 (0.060)*
	High	63	0.134 (0.008)	10.287 (0.192)*	4.433 (0.106)*
6	Low	40	0.188 (0.010)	12.296 (0.271)*	5.365 (0.135)
	High	30	0.206 (0.017)	11.690 (0.370)*	5.185 (0.182)
8	Low	35	0.245 (0.015)	13.273 (0.279)	5.996 (0.149)
	High	24	0.265 (0.023)	13.046 (0.400)	6.006 (0.191)

Low competition tadpoles also swam further than high competition tadpoles at stage 39, by an average of 50.67% ($F_{1,102}=8.5$, $P=0.0043$; Fig. 3b). Model simplification indicated that while competition level was significant ($t_{100}=3.3$, $P=0.0015$), the shape of the tail also influenced the average distance swum. Distance swum increased with dorsal tail fin height for both treatment groups ($t_{100}=2.3$, $P=0.0224$) and increased with tail muscle width and ventral tail fin height for low competition tadpoles but decreased for high competition tadpoles (interaction between competition level and tail muscle width: $t_{100}=2.3$, $P=0.020$; interaction between competition level and ventral tail fin height: $t_{100}=2.2$, $P=0.033$). Thus, low competition tadpoles swam significantly further than those from the high competition treatment group independent of size, but this was influenced by tail shape.

Post-metamorphic consequences of variation in larval phenotype

Two weeks post-metamorphosis, froglets from the high competition environment were smaller than their low competition conspecifics (MANOVA, $F_{1,200}=6.0$, $P=0.003$) in terms of both mass ($F_{1,202}=140.0$, $P<0.0001$) and snout-vent length ($F_{1,202}=9.8$, $P=0.002$; Table 1). Date of metamorphosis also influenced froglet size. Individuals that metamorphosed earlier in the season were heavier ($F_{1,201}=7.5$, $P=0.007$) than later metamorphs while snout-vent length decreased with date of metamorphosis for low competition froglets but increased for high competition froglets (interaction between competition level and snout-vent length: $F_{1,202}=4.1$, $P=0.045$). High competition froglets also had shorter femurs for their body length than low competition froglets (Table 1); this effect became more marked in large animals (interaction between competition level and snout-vent length: $F_{1,199}=7.5$, $P=0.007$).

The difference in snout-vent length ($F_{1,128}=11.5$, $P=0.001$) and relative femur length ($F_{1,127}=8.1$, $P=0.005$) remained four weeks post-metamorphosis although there was no longer a significant difference in mass (Table 1) or any effect of date of metamorphosis. By six weeks post-metamorphosis, however, only the difference in snout-vent length remained ($F_{1,66}=4.8$, $P=0.032$; Table 1) and at eight weeks post-metamorphosis there was no detectable difference in the morphology of surviving froglets from different treatment groups (all P values >0.05 ; Table 1).

Despite the observed differences in froglet morphology there was no significant difference in the swimming or jumping ability of froglets reared under high or low levels of competition at four or eight weeks post-metamorphosis (all P values >0.05). At eight weeks post-metamorphosis, however, the duration of the larval period influenced the jumping ability of froglets and did so differently for each treatment group. Distance jumped increased with date of metamorphosis for froglets reared under a low level of competition but decreased for those reared in a high competition environment (interaction between competition level and date of metamorphosis: $F_{1,27}=9.98$, $P=0.004$), mirroring the pattern observed for snout-vent length and hind limb length, although these were not significant.

DISCUSSION

The level of competition experienced during the larval stage of the life cycle influenced the phenotype of both tadpoles and froglets. Tadpoles reared under a high level of competition took longer to reach metamorphosis, were shorter and lighter than low competition tadpoles and possessed relatively narrow bodies and mouths and short, shallow tails. Consequently, the emerging froglets were smaller than those from the low competition environment and initially had relatively shorter femurs. These results demonstrate that there are consequences of the adaptation of larval phenotypes to intra-specific competition beyond the end of metamorphosis. Several studies have reported effects of predator-induced larval defences immediately after completion of metamorphosis (Relyea, 2001; Van Buskirk & Saxer, 2001; Nicieza et al., 2006) but few have focused either on the consequences of larval competition or longer term effects of the larval phenotype (Relyea & Hoverman, 2003). As we did not take repeated measures of individuals reared in isolation, we cannot distinguish between larval morphology and other factors associated with competition as the cause of the observed differences in post-metamorphic morphology. The fact that high competition tadpoles had smaller tails and metamorphosed into froglets with relatively short femurs, as also reported by Relyea & Hoverman (2003), is in agreement with predictions made by the theory that resources are allocated to areas in relatively close anatomical proximity during the restructuring that occurs through metamorphosis (Hirano & Nishida, 1997; Nijhout & Emlen, 1998). However, this is in direct contrast to previous findings that tadpoles that take longer to reach metamorphosis develop longer hind limbs (Gomez-Mestre & Buchholz, 2006; Ficetola & de Bernardi, 2006).

As predicted, high competition tadpoles had relatively short, shallow tails with shallow, narrow tail muscles, supporting previous reports that tadpoles reared in a high competition environment invest more in the body at the expense of the tail (Relyea, 2002; Relyea & Hoverman, 2003; Relyea & Auld, 2004). Competition level also influenced swimming ability, although this effect was not consistent through ontogeny. Early in the larval period (stage 28) there was no significant difference in the swimming ability of tadpoles from the two treatment groups, contrary to the expectation that larger individuals should swim faster than smaller ones (Gillis & Biewener, 2000; Wilson & Franklin, 2000; Ojanguren & Braña, 2003). While the faster growth and developmental rates of low competition tadpoles are likely to confer an advantage in terms of overwintering survival (Werner, 1986), accelerated growth rates are associated with the development of less efficient muscle fibres, supporting evidence of a trade-off between growth rate and swimming speed in larval anurans (Arendt, 2003). Additionally, at this stage in their development high competition tadpoles may invest in somatic maintenance at the expense of growth (Alford & Harris, 1988; Arendt, 2000) since current conditions may yet improve; therefore they are small but have not compromised their physiological condition and swimming ability. These potential differences in physiology could

explain the lack of a significant difference in swimming ability at this stage.

Towards the end of the larval period low competition tadpoles swam both faster and further than high competition tadpoles. The difference in speed could not be explained either by size or by differences in relative morphology, again suggesting that there are physiological differences between high and low competition tadpoles that influence performance. The efficiency of muscle fibres in faster growing individuals may improve through ontogeny as growth rates slow (Arendt, 2000), potentially leading to an improvement in the swimming speed of low competition tadpoles compared to high competition tadpoles. In addition, high competition tadpoles must switch investment from somatic maintenance to growth at some point during development to attain the minimum size for metamorphosis (Wilbur & Collins, 1973; Morey & Reznick, 2004; Lind et al., 2008). This could result in a reduction in speed compared to low competition tadpoles if their condition is compromised. Tail morphology did explain some of the variation in the distances swum by tadpoles, however, suggesting that swim speed and distance swum are influenced differently by morphology. Many studies consider only burst swim speed when assessing the effect of predators and competitors on larval performance (Van Buskirk & McCollum, 2000a,b; Watkins, 1996), but our data suggest that other aspects of performance might also be influenced by changes in morphology.

We are unable to determine whether the differences in tadpole phenotypes observed in this study are a result of phenotypic plasticity or of selective mortality. This is a general problem with experiments of this nature and while there is strong evidence for phenotypic plasticity in many amphibian species (Relyea, 2004; Laurila et al., 2006; Van Buskirk, 2001), the potential role of selective mortality in shaping tadpole populations is often overlooked in laboratory experiments and yet is vital for understanding the evolution of plasticity and the ecology of amphibian populations. Most importantly in the context of this study, however, the different phenotypes expressed by tadpoles reared under high and low levels of competition translated into differences in the phenotypes of the corresponding froglets.

Froglets reared in a high competition environment as larvae had relatively shorter femurs than those reared under a low level of competition two and four weeks post-metamorphosis, as previously reported by Relyea & Hoverman (2003). Although it is possible that this difference is due to long-term effects of some other factor associated with competition, this result supports the prediction that investing in the body at the expense of the tail as a tadpole results in fewer resources being allocated to the developing hind limbs of the froglet. This also contradicts previous studies that have demonstrated that longer larval periods, as observed in the high competition treatment, generally result in the development of froglets with relatively long hind limbs, and conversely that rapid development, e.g. in response to pond drying, results in the development of relatively short hind limbs (Gomez-

Mestre & Buchholz, 2006; Ficetola & de Bernardi, 2006). A potential reason for this difference is that the correlation between larval duration and hind limb length has arisen in systems where the growth rate of tadpoles is not compromised, as demonstrated by their larger size at metamorphosis. Under high levels of competition, however, both the growth and developmental rates of tadpoles are delayed and it is likely that the prolonged larval development is a result of energetic constraints rather than an adaptive mechanism to increase the fitness of the juvenile phenotype. If pond-drying results in an increase in competition, due to the same number of individuals in a decreasing volume of water, then it is possible that it is food availability that influences hind limb length rather than developmental rate *per se*. However, studies have also found a positive correlation between the length of the larval period and hind limb length in tadpoles reared under different temperatures and *ad lib* food conditions, casting doubt on the validity of this hypothesis (e.g. Blouin & Brown, 2000; Relyea, 2001).

The length of the constituent parts of the hind limb is an important aspect of the biomechanics of both swimming and jumping in frogs (Tejedo et al., 2000) and it was expected that individuals with short femurs would experience reduced locomotory ability (Phillips et al., 2006). We found no significant difference in the swimming or jumping ability of froglets reared under high or low levels of competition as larvae, however. Evidence suggests that locomotor performance is not repeatable across metamorphosis in amphibians and thus we should not expect high-performance tadpoles to retain that performance as a froglet (Watkins, 1997), but one might expect to find a difference between individuals of differing phenotypes within a life-history stage. The fact that we did not suggest either that the observed difference in relative femur length was not big enough to have a detectable effect on performance ability or that our methods for detecting such differences did not offer high enough resolution. If the former is true and investing in a larger body at the expense of the tail in the larval environment has little impact on juvenile performance (whilst increasing body size at metamorphosis, and therefore increasing juvenile fitness), this could explain how this trade-off persists despite its association with reduced swimming ability in the larval stage of the life cycle.

The size difference between individuals from the two treatment groups also persisted through metamorphosis, suggesting that reduced growth rates during the larval period, indicated by smaller size and longer larval period, cannot be compensated for during, or shortly after, metamorphosis. By four weeks post-metamorphosis, however, there was no difference in the mass of froglets from different treatment groups, and by eight weeks there was no detectable difference in morphology either. These results suggest either that compensatory growth was occurring in the high competition population or that selective mortality was influencing the average phenotype of one or both treatment groups, but our data do not allow us to distinguish between the two as potential mechanisms underlying the observed results.

The results presented here suggest that the effects of selection on the larval phenotype are not fully compensated for via metamorphosis and that froglets may continue to express traits associated with the larval phenotype for some time after metamorphosis. The finding that tadpoles with shallow tails and thin tail muscles develop into froglets with shorter femurs lends support to the prediction that resources obtained from the reabsorption of the tail may be allocated to the development of structures in close proximity, i.e. to hind limb development. Thus, while life cycles with discrete life history stages may have evolved as responses to selection for developmental independence of different stages of the life cycle (Moran, 1994), our results suggest that the larval environment still has a significant impact on juvenile fitness.

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