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Condition-dependent expression of trophic polyphenism: effects of individual size and competitive ability

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ABSTRACT

Understanding the adaptive significance of alternative phenotypes may require knowing how the internal state of an organism affects the relationship between phenotypic variation and fitness across selective environments. Here, we explore how individual state interacts with environmental variation to affect expression of a trophic polyphenism in larval amphibians. Following the consumption of fairy shrimp, typical omnivorous plains spadefoot toad tadpoles (*Spea bombifrons*) may express an alternative 'carnivore' phenotype. The carnivore phenotype confers rapid growth and development, but these benefits come at the expense of condition at metamorphosis. Larval habitats vary in longevity, food availability and tadpole morph frequency, each of which potentially affects the relationship between tadpole state (e.g. size) and morph fitness. Hence, we predicted that phenotype expression should depend on both tadpole size and larval environment. We found that small tadpoles were more likely to develop into carnivores than large tadpoles when each was raised in isolation. When tadpoles were raised in pairs, however, relatively smaller tadpoles were less likely to express the carnivore phenotype than larger tadpoles. We present results to support the hypothesis that these contrasting effects of absolute and relative size on carnivore morph expression stem from the effects of tadpole size on the ability to consume fairy shrimp. We conclude that competition for shrimp imposed by larger tadpoles may often inhibit relatively smaller tadpoles from expressing the carnivore phenotype. Thus, we find support for our prediction that morph expression in *Spea* depends on both an individual's internal state and larval environment. Our understanding of the adaptive significance and, ultimately, the evolution of this and other state-dependent responses may be enhanced by considering how interactions among individuals affect the relationships among fitness, internal state and phenotype expression across different selective environments.

Keywords: adaptive plasticity, alternative phenotypes, amphibian, development, *Spea*, state-dependent strategy, tadpole.

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INTRODUCTION

Many organisms exhibit condition- or state-dependent responses to the environment, where phenotype expression is influenced by an individual's current internal state or condition. Such responses are favoured by natural selection when an organism's absolute or relative state affects the fitness conferred by alternative morphological or behavioural phenotypes. (Parker, 1982, 1984). For example, males of many species adopt alternative reproductive phenotypes based on their ability to compete for mates, which is determined in part by relative size. Relatively large, competitive males generally engage in territorial behaviours, whereas smaller, less competitive males often employ satellite or 'sneaking' mating behaviours (for a review, see Gross, 1996). The role of relative size in this example illustrates how the relationship between individual state and the fitness conferred by each phenotype can vary across environments; the same individual may be relatively small and uncompetitive in one environment and relatively large and competitive in another. Consequently, the same individual might express different alternative phenotypes depending on the prevailing environmental conditions. Such environmental effects can complicate evaluation of the adaptive significance of state-dependent responses and, perhaps more importantly, affect the evolution of the responses themselves.

In particular, the fitness of alternative phenotypes (alternative tactics within mixed or conditional strategies *sensu* Maynard Smith, 1982) can be affected by the density or frequency of individuals expressing the same phenotype in a given environment (Wilson, 1989). In the case of intrasexual competition outlined above, the density of males and females and the ratio of territorial to satellite males could affect the relative fitness of both mating tactics. Moreover, the distribution of male size in the population may influence the size at which individuals could effectively compete for matings, which determines the threshold size at which males should switch mating tactics (see Gross, 1996). Although the roles of such frequency- and density-dependent interactions in shaping state-dependent behaviours has been examined (for a review, see Gross, 1996), how these factors affect the expression and evolution of state-dependent morphological phenotypes is less well known (but see Maret and Collins, 1994).

Here, we describe a series of experiments in which we first determine if larval phenotype expression in tadpoles of the plains spadefoot toad, *Spea bombifrons*, is state-dependent, and then determine if the relationship between individual state and phenotype expression changes across larval environments. Adaptive phenotypic plasticity is common in spadefoot toad larvae (e.g. Newman, 1989, 1994, 1998; for a review, see Newman, 1992); development rate changes in response to changes in water level (Denver *et al.*, 1998) and food availability (Morey and Reznick, 2000). Moreover, plasticity in development rate is state-dependent, being affected by tadpole size or recent growth history (Morey and Reznick, 2000). Under some environmental conditions, *S. bombifrons* larvae may express an alternative trophic phenotype that conveys accelerated growth and development rates.

Typical, omnivorous tadpoles of *S. bombifrons* may develop an alternative, carnivore phenotype after consuming anostracan fairy shrimp (*Thamnocephalus* sp. and *Streptocephalus* sp.). Carnivores have modified oral and digestive morphologies that enable them to feed effectively and almost exclusively on shrimp and other tadpoles (Pomeroy, 1981). This polyphenism is maintained as an adaptation to spatial and temporal variation in pond longevity and relative food source availability (Pfennig, 1990, 1992a). Carnivores are favoured in highly ephemeral pools because that is where shrimp are most abundant

(Pfennig, 1990) and where a carnivore's rapid growth and development increases the likelihood that metamorphosis will be achieved before the pond dries (Pfennig, 1990, 1992a). Longer-lasting pools favour omnivores because these slowly developing tadpoles invest substantially in fat reserves, which increases post-metamorphic resistance to starvation (Pfennig, 1992a). Within ponds, competition for food imposes negative frequency-dependent selection that favours the rarer larval morph (Pfennig, 1992a). Variation in longevity, food availability and tadpole density dramatically affects the among-pond equilibrium morph frequency and morph fitness (Pfennig, 1992a). Regardless of the cause of the apparent trade-off in carnivore development rate and condition at metamorphosis (e.g. mutually exclusive investment in fat reserves versus growth and development; nutrient limitation resulting from a meat-based diet), tadpole size could dramatically alter the cost–benefit ratio of morph expression in a given environment. Hence, tadpole size could affect the likelihood that an individual will develop into a carnivore.

In two steps, we tested the hypothesis that the expression of larval morph is affected by a tadpole's absolute size and its larval environment (as defined by relative tadpole size and food abundance). We first sought to determine if development of the carnivore phenotype is state-dependent. Specifically, we predicted that the propensity to express the carnivore phenotype would be inversely related to a tadpole's absolute size because the likelihood of achieving the minimum size necessary for metamorphosis decreases with tadpole size (Hensley, 1993; Morey and Reznick, 2000). Hence, the benefits of rapid growth and development outweigh the costs of low condition at metamorphosis associated with the carnivore phenotype (Pfennig, 1992a) for small omnivores and, consequently, they should have a lower threshold for induction of the carnivore tactic than large tadpoles. Second, we sought to determine if any observed size-dependent phenotype expression could be modified by environmental variation. Specifically, we predicted that the social environment would change the relationship between size and propensity to express the carnivore phenotype because interactions among tadpoles would alter the costs and benefits associated with expressing each larval morph.

Our results indicate that the threshold for induction of the carnivore phenotype depends on an omnivore's absolute size. However, the likelihood that an omnivore will develop the carnivore phenotype is affected by an individual's ability to compete for shrimp in a given environment, which is a function of both an omnivore's relative size and shrimp abundance. In particular, although small tadpoles have a greater probability of expressing the carnivore phenotype when alone, they have a reduced probability of developing into carnivores in the presence of larger tadpoles. Consideration of density- or frequency-dependent interactions among individuals, and how these interactions vary in space or time, may help elucidate the adaptive significance and evolution of state-dependent phenotype expression.

METHODS

Experimental animals

We conducted four experiments. In Experiments 1 and 2, we tested the hypothesis that development of the carnivore phenotype was related to the absolute mass of a tadpole by using natural variation in tadpole mass and by manipulating diet to affect tadpole mass. In Experiment 3, we tested the hypothesis that the propensity to develop the carnivore phenotype is related to the size of a tadpole relative to that of its competitors. Finally, in

Experiment 4, we determined if the effects of relative size on carnivore development might be related to size-mediated prey handling times.

For all experiments, amplacent pairs of *S. bombifrons* were collected from breeding aggregations near Rodeo, NM (31°50′N, 109°03′W) (see Pfennig and Frankino, 1997, for methods). Eggs were aerated until shortly after hatching (day of hatching is always identified as day 0), at which time tadpoles were transferred by sibship to mass-rearing containers. All experiments were conducted at 27 ± 1°C on an 18 : 6 light : dark cycle at the Southwestern Research Station near Portal, AZ. *Spea* tadpoles naturally express high variation in size throughout ontogeny (Pfennig *et al.*, 1991; Pfennig, 1992a; Newman, 1994, 1998). We were therefore able to use tadpoles of the same developmental stage (Gosner stage; Gosner, 1960) but different sizes in our experiments. Hence, observed differences among tadpole groups were due to effects of tadpole size or experimental treatments and were not confounded by differences in developmental stage. Although the tadpoles may have differed in size among treatments in various experiments (see below), the tadpoles were always of the same Gosner stage (Gosner, 1960) when entered into experiments. Tadpoles were identified as omnivores or carnivores using the criteria of Pfennig (1989, 1992b); assignments were never ambiguous and were conducted blindly with respect to sibship or treatment.

Experiment 1: effects of natural variation in absolute mass on carnivore production

On day 6, several hundred tadpoles were haphazardly collected from each of six clutches and passed through a sieve with 6 mm diameter holes to create two size classes of tadpoles from each clutch. Eight tadpoles were haphazardly selected from each group and weighed individually to the nearest 0.01 mg before being placed alone in a 500 ml cup filled with 350 ml dechlorinated water. All tadpoles were fed approximately 2 mg rabbit chow and approximately 50 fairy shrimp daily. Pulverized rabbit chow closely approximates in form and in nutrition the organic detritus on which spadefoot tadpoles feed in natural ponds (Pfennig *et al.*, 1991). On day 12, each tadpole was categorized as an omnivore or carnivore. The prediction that tadpole size affects the propensity of developing the carnivore phenotype was tested by comparing the frequency of carnivores between size classes with a *G*-test.

Experiment 2: effects of experimentally induced variation in absolute mass on carnivore production

In Experiment 1, the variation in mass among tadpoles presumably arose from both genetic factors and differences in competitive ability while tadpoles were in the mass-rearing tanks. To avoid the possibility of any confounding effects of competition on generating the distribution of tadpole size or other factors that might influence carnivore expression, we manipulated the diet of individuals to produce a range of tadpole sizes independent of competitive ability. Using these tadpoles, we again tested the hypothesis that the propensity to develop the carnivore phenotype is related to tadpole size. We also fed these tadpoles different amounts of shrimp to determine if tadpole size interacts with shrimp level to affect the probability of developing the carnivore phenotype.

Consumption of live shrimp induces the carnivore phenotype in some individuals, but consumption of dried shrimp does not (D.W. Pfennig, unpublished data); nor does consumption of rabbit chow (Pfennig, 1992b). To produce a range of tadpole sizes, we raised isolated tadpoles on high, medium or low amounts of rabbit chow. To raise tadpoles under high and low carnivore-inducing environments, we manipulated the ratio of live shrimp (cue) to dry shrimp (non-cue) in live-shrimp mass equivalents (1 mg dry shrimp = 18.5 mg live shrimp). By manipulating the ratio of live-to-dry shrimp, we manipulated the cue for induction of the carnivore phenotype while maintaining a constant caloric and nutritional contribution to the diet from shrimp. This experiment was conducted in two parts, 2A and 2B.

Experiment 2A was a 2 × 2 factorial design, in which the factors were cue level (live : dry shrimp ratio) and background food (non-shrimp food). Forty tadpoles were haphazardly taken from each of six clutches of *S. bombifrons* on day 0, isolated in individual 500 ml cups filled with 350 ml dechlorinated water, and divided equally among the following four treatments. Rabbit chow was provided at one of two levels, high (approximately 5 $\text{mg} \cdot \text{day}^{-1}$) or medium (approximately 2.5 $\text{mg} \cdot \text{day}^{-1}$) and the live : dry shrimp ratio was also provided at one of two levels (high live, 75% live : 25% dry shrimp mass; low live, 25% live : 75% dry shrimp mass). Cups were placed randomly on a single shelving unit. On day 3, the tadpoles were weighed individually to the nearest 0.01 mg and the treatments were applied, after which the tadpoles were weighed and provisioned with treatment rations every 2 days. On day 8, the tadpoles were categorized as to morph and the experiment was terminated. Six days after Experiment 2A was initiated, 20 tadpoles were haphazardly collected on day 0 from each of three new *S. bombifrons* clutches and used in Experiment 2B. These tadpoles were divided equally between the same two shrimp levels as in Experiment 2A and rabbit chow was provided at a single low level (approximately 1.75 $\text{mg} \cdot \text{day}^{-1}$). All other methods were the same for Experiments 2A and 2B.

Based on our results from Experiment 1 (see Results), we predicted that the number of carnivores would decrease as tadpole size increased (i.e. across shrimp treatments, the number of carnivores would be greatest in the low chow level and decrease as chow level increased). Across live shrimp levels (within chow treatments), tadpoles fed on the high live shrimp ration would experience higher levels of cue, and thus were predicted to have a greater propensity to become carnivores than individuals fed the low live shrimp ration.

Experiment 3: effects of relative mass and competition on carnivore production

We conducted the following experiment to test the hypothesis that an individual's size relative to that of its competitors affected carnivore induction or expression. Tadpoles from eight sibships were raised in a large wading pool and fed rabbit chow *ad libitum*. Six days after hatching, 200 tadpoles were haphazardly chosen and placed individually into cups. Mass (to the nearest 0.01 mg) and developmental stage (Gosner, 1960) were recorded for all individuals. Tadpoles were then selected in pairs such that the difference in mass between pair members ranged from very small (~0.02 mg) to very large (~0.6 mg). Furthermore, these dyads were constructed from along the continuum of tadpole sizes such that a tadpole of a given mass would be the relatively large tadpole in one dyad and the relatively small tadpole in another dyad. Moreover, the difference in mass between dyad members was replicated across the range of sizes in our sample. In this way, we constructed 80 replicate dyads from across the range of natural variation in tadpole mass. Dyads were raised in 4.5 litre (8 × 13 × 30 cm) tanks filled with 3 litres of dechlorinated water. Each tank received 20 small (total length < 10 mm) live fairy shrimp daily and 0.05 g of rabbit chow every 3 days. Both diets were restricted, as all shrimp and chow had disappeared from each tank before the tadpoles were scheduled to be fed again. Moreover, these food levels generate competition among tadpoles for shrimp and chow (Pfennig and Murphy, 2000).

Six days after construction of the dyads, the tadpoles were categorized as to morph as in Experiment 1 and, 4 days later, they were killed by immersion in methane sulphonate (MS-222) and preserved in 70% ethanol to allow dissection and measurement of the width of the orbitohyoideus (OH) muscle. This muscle is the primary abductor of the buccal cavity (Satel and Wassersug, 1981), and the residual value of OH on snout–vent length (SVL) is the single best morphological character that discriminates between the larval morphs and it describes the extent to which an individual expresses the omnivore (small residual value) or carnivore (large residual value) phenotype (Pfennig, 1992b).

Experiment 4: tadpole size and shrimp handling time

We conducted an experiment to determine if differences in propensity to develop the carnivore phenotype between dyad members (Experiment 3; see Results) could be due to effects of size on an individual's ability to compete for shrimp. To measure the competitive ability of different morphs and different sized tadpoles, we compared the size-specific shrimp handling times for each morph.

Forty tadpoles of each morph ranging in mass from approximately 0.05 to 1.0 g were collected from a single pond, placed in individual cups and provided with approximately 10 equally sized live shrimp. We measured individual handling times for each tadpole by recording the time (to the nearest 0.5 s) between when the tadpole captured a shrimp and when the tadpole ceased mastication. We calculated a mean handling time for each tadpole based on how long it took to eat four different shrimp. We analysed mean handling times by analysis of covariance, with tadpole morph as a main effect and mass as a covariate.

RESULTS

Experiment 1: effects of natural variation in absolute mass on carnivore production

One tadpole in the small size class died and was eliminated from the analysis. Tadpoles in the small size class were significantly smaller than those in the large size class (mean mass = 0.04 ± 0.01 and 0.09 ± 0.02 mg, respectively; $F_{1,93} = 155.51$, $P = 0.0001$). Small tadpoles were over three times more likely to develop the carnivore phenotype than large tadpoles (likelihood ratio, $\chi^2 = 9.299$, $P = 0.003$; Fig. 1). Because tadpoles larger than those included in this study can express the carnivore phenotype (Pomeroy, 1981; Pfennig, 1989; Frankino, 2000), the tadpoles in the large size class described here were physiologically capable of developing into carnivores. Our results therefore suggest a size-dependent sensitivity to shrimp consumption resulting in a greater propensity of small tadpoles expressing the carnivore phenotype.

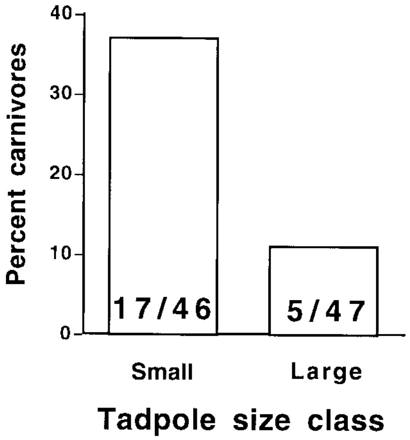
Experiment 2: effects of natural variation in absolute mass on carnivore production

Tadpoles in the three different chow treatments diverged in mass over the course of Experiments 2A and 2B, with those in the high chow treatment becoming the most massive and those in the low chow treatment becoming the least massive (Fig. 2, Table 1). In contrast to these effects of chow level, the two levels of live shrimp (high and low) did not have a significant effect on tadpole mass (Fig. 2, Table 1). Thus, manipulating chow level successfully altered tadpole mass, whereas manipulating the live : dry shrimp ratio varied exposure to the cue that induces carnivores (live shrimp) while maintaining a constant caloric and nutritional intake from shrimp.

In Experiment 2A, tadpoles fed on medium levels of chow were significantly more likely to develop into carnivores than those on a high chow diet (log-likelihood ratio, $P = 0.052$). However, there was no effect of shrimp on the propensity to develop the carnivore phenotype (log-likelihood ratio, $P = 0.386$). In Experiment 2B, tadpoles fed on high levels of live shrimp were significantly more likely to develop into carnivores than those fed on low levels of live shrimp ($G = 6.067$, $P = 0.014$). Pooling the data from the two experiments revealed significant effects of chow level on the propensity to develop the carnivore phenotype (log-likelihood ratio, $P = 0.002$) and a chow by live shrimp level interaction (log-likelihood ratio, $P = 0.039$; Fig. 3). Thus, these data provide a causal link between tadpole size and propensity to develop into carnivores: tadpoles that were the smallest (those fed low chow and high levels of live shrimp) were the most likely to become carnivores (Fig. 3).

Experiment 3: effects of relative mass and competition on carnivore production

In tanks in which carnivores were produced, relatively small individuals were five times *less* likely to develop the carnivore phenotype than relatively large tadpoles (likelihood ratio, $\chi^2 = 17.693$, $P = 0.001$; Fig. 4), in contrast to the effects of absolute tadpole size in Experiments 1 and 2. We believe that the relatively small tadpoles produced fewer carnivores in Experiment 3 because of factors other than small absolute size (e.g. resulting from stunted growth) for two reasons. First, tadpoles far smaller than those included in Experiment 3



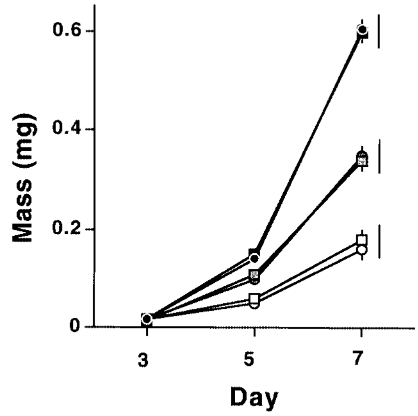


Fig. 1. (Left) Percentage of tadpoles from different size classes that developed into carnivores when raised in isolation. Different size classes were constructed using naturally occurring variation in tadpole mass.

Fig. 2. (Right) Mean masses of tadpoles raised under different ratios of rabbit chow to live and dry shrimp. Squares and circles indicate high and low live-shrimp treatments, respectively. Black symbols indicate high chow levels, grey symbols medium chow levels and white symbols low chow levels. Bars next to the symbols indicate means that are not significantly different from one another.

Table 1. Analysis of variance of the effect of chow and live : dry shrimp ratio on tadpole mass

Effect	d.f.	*F*	*P*
Chow	2	159.97	0.0001
Live : dry shrimp	1	0.42	0.5173
Chow × live : dry shrimp	2	0.09	0.9148
Error	251		
	$r^2 = 0.563$		

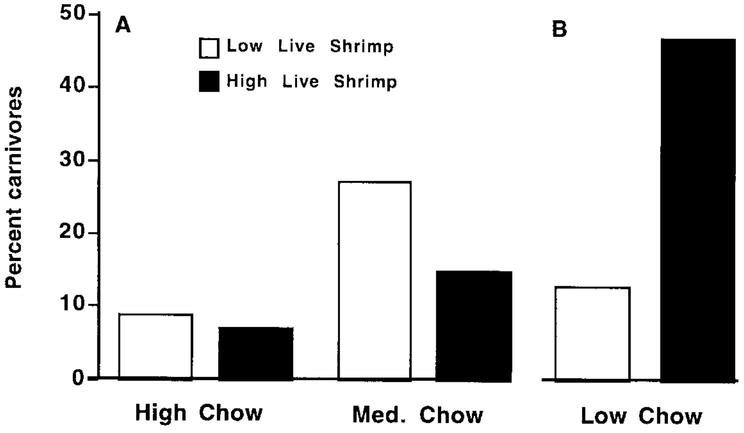


Fig. 3. Percentage of tadpoles in different diet treatments that developed into carnivores when raised in isolation. (A) Experiment 2A, (B) Experiment 2B.

can express the carnivore phenotype in the field and laboratory (Pomeroy, 1981; Pfennig, 1989, 1990; Frankino, 2000). Second, the size distribution of the relatively small tadpoles in Experiment 3 contained the distribution of tadpole sizes in Experiments 1 and 2, and the mean size of the relatively small tadpoles in Experiment 3 (mean mass = 0.13 ± 0.007 mg) significantly exceeded the mean size of the small absolute size class in Experiments 1 and 2 (mean mass = 0.03 ± 0.002 mg; test for differences between means in these two groups, $F_{1,344} = 358.96$, $P = 0.0001$). Hence, the relatively small tadpoles in Experiment 3 were large enough to express the carnivore phenotype because smaller tadpoles develop the carnivore phenotype in other environments. This suggests that interactions with the relatively large tadpole affect carnivore expression in the relatively small tadpole.

We tested for the effects of tadpole mass and the disparity in mass between dyad members on the extent to which the carnivore phenotype developed by performing multivariate regression of residual OH values versus the initial mass of the larger tadpole and the difference in mass between tadpoles. Multivariate regression revealed that different models should be used to describe residual OH values for relatively large versus small tadpoles (Wilks' $\lambda = 0.904$, $P = 0.02$). To identify which variables were associated with residual OH size in the relatively large and small tadpoles, we performed stepwise multiple regression on residual OH value separately on the tadpole relative size classes. For the relatively small tadpoles, stepwise multiple regression indicated that neither initial size nor the difference in size between dyad pairs affected residual OH value. For the relatively large tadpoles, stepwise multiple regression revealed that, although the residual OH value of the relatively larger tadpole was not related to the initial mass of the tadpole, the residual OH value increased with the difference in size of dyad members ($F_{2,77} = 7.03$; $P = 0.001$, $r = 0.16$; Fig. 5). We then performed multivariate analysis using the reduced models generated by the multiple regression to confirm that the reduced models differed between the relatively large and relatively small tadpoles. This reduced model explained the variation in residual OH value differently for the relatively large and small tadpoles (Wilks' $\lambda = 0.841$, $P = 0.001$). These results indicate that the greater the difference in mass between dyad members, the more extreme the development of the carnivore phenotype in the relatively large tadpole (Fig. 5).

Experiment 4: tadpole size and shrimp handling time

Mean time to consume a shrimp was affected by tadpole size, and the relationship between size and handling time differed between morphs (Table 2). Carnivores were able to process shrimp much more rapidly than omnivores at all sizes, but the difference in shrimp handling time between morphs declined as tadpole size increased (Fig. 6).

DISCUSSION

State-dependent responses can be complex because the fitness conferred by alternative tactics may have frequency- or density-dependent components that vary across environments, thereby producing variation in the relationships among individual state, phenotype

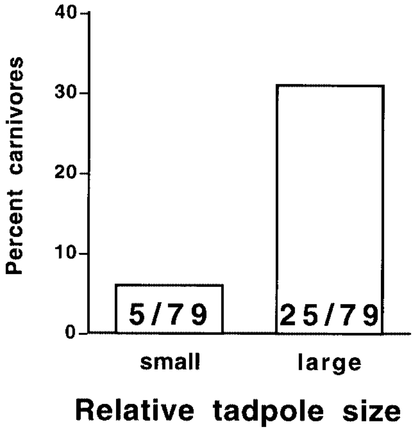


Fig. 4. (Left) Percentage of tadpoles in different size classes that developed into carnivores when raised in pairs.

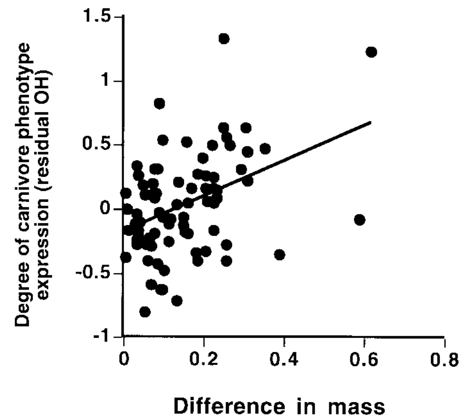


Fig. 5. (Right) Extent to which the carnivore phenotype was expressed in the relatively large tadpoles as a function of the difference in initial mass between dyad members in Experiment 3. The regression line is from a stepwise multiple regression which removed the effect of tadpole mass (residual OH = −0.04 − 0.09 (large tadpole mass) + 0.37 (difference in mass between dyads)).

Table 2. Analysis of covariance of the effect of tadpole mass and morph on shrimp handling time

Effect	d.f.	*F*	*P*
Morph	1	158.86	0.0001
Tadpole mass	1	102.97	0.0001
Morph × mass	1	75.85	0.0001
Error	76		
	$r^2 = 0.82$		

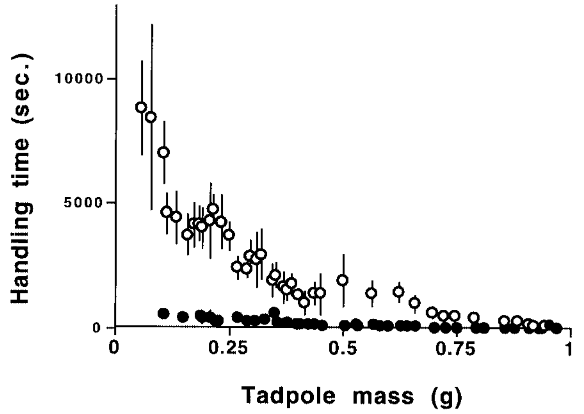


Fig. 6. Mean time to consume fairy shrimp for omnivores (○) and carnivores (●) of different sizes. Points are individual tadpole means ± 1 standard error.

expression and fitness. We anticipated that carnivore morph production in spadefoot tadpoles would be state-dependent because the costs and benefits associated with the carnivore tactic vary with metamorph size and larval environment (Pfennig, 1989, 1992a) and because tadpoles change larval phenotype in response to the competitive environment (Pfennig, 1992a; Pfennig and Murphy, 2000). The observed effects of absolute size, relative size and food availability on carnivore expression point to a complex state-dependent switch in this system.

When raised alone, small tadpoles were more likely to develop into carnivores than large tadpoles (Figs 1, 3). When raised in pairs, however, the relatively larger tadpole was more likely to develop into a carnivore (Fig. 4) and the extent to which the carnivore phenotype was expressed increased as the size disparity between dyad members increased (Fig. 5). The different relationships between tadpole size and induction of the carnivore phenotype for isolated tadpoles and those raised in pairs suggest that the state-dependent response to shrimp is affected by size-mediated interactions among tadpoles.

We hypothesize that these effects of the social environment on morph expression result from changes in the costs and benefits associated with the carnivore phenotype in different competitive environments. In non-competitive environments (i.e. those with low tadpole densities or high shrimp densities), small tadpoles can benefit greatly by becoming a carnivore. By developing into a carnivore, a small tadpole's shrimp handling time decreases dramatically (Fig. 6) and its growth and development rates accelerate (Pfennig, 1992a), thereby increasing the probability that the tadpole will metamorphose before the pond dries. Hence, the cost of low condition at metamorphosis associated with the carnivore phenotype (Pfennig, 1992a) is outweighed by the benefits of successful metamorphosis for small omnivores. This suggests that the carnivore phenotype may represent an 'optimistic' growth and development strategy (Arendt and Wilson, 1997) for small individuals. By contrast, larger omnivores need not pay this cost of developing the carnivore phenotype because they already process shrimp rapidly (Fig. 6) and are generally closer to achieving the minimum size necessary for metamorphosis. Hence, larger tadpoles should often retain the omnivore phenotype.

In contrast, the benefits of developing into a carnivore probably outweigh the costs for tadpoles of all sizes in competitive environments (i.e. those with high tadpole or low shrimp densities). However, their low handling times could enable larger tadpoles to monopolize the limited shrimp resource (Fig. 6). Competition imposed by larger tadpoles may make the carnivore tactic unprofitable for smaller tadpoles and, consequently, relatively small tadpoles retain the omnivore phenotype in competitive environments.

Interactions among tadpoles may affect morph expression in several, non-exclusive ways. For example, larger tadpoles may decrease carnivore morph expression in smaller tadpoles through exploitative competition for shrimp. Because larger tadpoles are more efficient shrimp foragers (Fig. 6), they may consume most of the shrimp and effectively eliminate the smaller tadpoles' exposure to the cue for carnivore induction. This scenario appears plausible, given that tadpoles of *S. bombifrons* competitively exclude *S. multiplicata* from consuming shrimp, producing an asymmetry in carnivore production when tadpoles of these species co-occur (Pfennig and Murphy, 2000, submitted). Moreover, size-mediated competitive exclusion could explain the positive relationship between the size difference of dyad members and the extent to which the carnivore phenotype is expressed in the relatively large tadpole (Fig. 5); as the disparity in size between competitors increases, so does the asymmetry in the proportion of shrimp consumed by the tadpoles.

In addition to exploitative competition, larger tadpoles may inhibit carnivore production in smaller tadpoles through interference competition. Carnivores may produce water-borne chemicals that inhibit development of the carnivore phenotype in smaller tadpoles. Such inhibition would benefit both individuals: the larger tadpole benefits through reduced competition for shrimp and the smaller tadpole benefits by not developing a phenotype that is competitively inferior in that environment. Such chemical cues reduce *S. bombifrons* carnivore expression in the presence of kin (Pfennig and Frankino, 1997) and chemical cues similarly affect expression of alternative phenotypes in other amphibians (e.g. McCollum and Van Buskirk, 1996; for a review, see Anholt and Werner, 1999), even in a size-dependent manner (Eklov, 2000).

Individual tadpoles could use cues to assess their relative size and then respond to fairy shrimp abundance based on where the individual falls in the local distribution of tadpole sizes. In some salamanders, the likelihood of developing a superficially similar, alternative larval cannibal phenotype increases with larval density (Collins and Cheek, 1983), the relative size of the focal larva and the variance in larval size within a population (Maret and Collins, 1994). Presumably, relatively larger salamander larvae develop into cannibals under these conditions because the relatively smaller individuals represent abundant and vulnerable prey (Maret and Collins, 1994). A similar pattern may hold in spadefoot tadpoles because the smaller individuals represent potential prey for larger carnivores (Pomeroy, 1981; Pfennig, 1989). Thus, relative size assessment could also play a role in carnivore induction in spadefoot tadpoles. Individuals that perceive themselves to be relatively small may have a lower likelihood of developing the carnivore phenotype because they will be inferior competitors for shrimp, whereas relatively large individuals may be more likely to develop into carnivores because they could consume smaller congenerics in addition to shrimp.

Many environmental factors potentially influence the relationship between individual state and the fitness conferred by alternative phenotypes. Hence, to optimize fitness, individuals must first assess their absolute state and the relative fitness that will be conferred by phenotypes potentially expressed in a particular environment. Because the fitness of a phenotype may have a density- or frequency-dependent component, the environment an individual must assess may include the phenotypes expressed by other individuals. In spadefoot toad tadpoles, detritus and shrimp availability, tadpole density and morph frequency all affect the fitness conferred by each tactic (Pfennig, 1992a). Our results suggest that these factors should interact to affect the size at which individual tadpoles develop the carnivore phenotype in a given pond. Consideration of such interactions could also elucidate the processes that shape how state-dependent switches function and evolve other systems.

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