The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole

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Summary. This study investigated the proximate basis of bimodally-distributed, environmentally-induced variation that occurs in natural populations of spade-foot toad tadpoles (*Scaphiopus multiplicatus*). Most individuals in most populations occur as a small, slowly-developing omnivore morph. In some of these same populations, a varying number of individuals occur as a large, rapidly-developing carnivore morph (Pfennig 1989). Censuses of 37 different natural ponds revealed that the frequency of the faster-developing carnivore morph correlated significantly positively with fairy shrimp density (their chief prey) and pond drying rate. By simultaneously varying two diet components and pond drying regime in artificial pools I found that only fairy shrimp density significantly affected the proportion of carnivores. Separate experiments established that the extent to which tadpoles developed the carnivore morphology correlated with shrimp density, and that morph determination depended on the ingestion of shrimp, not simply their presence. If a critical number of shrimp were ingested, the tadpole developed into a carnivore; if not, the tadpole developed by default into an omnivore. Thus a single cue – shrimp ingestion – triggers alternative ontogenetic trajectories. Using shrimp density to induce morph differentiation enables tadpoles to respond to their environment adaptively as shrimp are most abundant in highly ephemeral ponds, where the faster developing carnivores are favored.

Key words: Causes of polyphenism – Adaptive plasticity – Trophic polymorphism – Developmental strategies – Phenotypic plasticity

A fundamental issue in the study of phenotypic plasticity is resolving the extent to which the plastic response is due to selection and the extent to which it is due to

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nonadaptive processes. Phenotypic plasticity often occurs among organisms in variable environments (Shapiro 1976), which suggests to some that it provides an optimal response to environmental heterogeneity (Bradshaw 1965; Levins 1968; Lloyd 1984; Lively 1986a). This conclusion is reinforced by classical population genetic models, which show that alternative forms are favored in spatially varying environments (Levene 1953). However, not all plasticity need be adaptive. Any developmental system that is not buffered against changes in the environment to which critical chemical reactions in development are sensitive will be phenotypically plastic (Stearns 1982). To understand the evolutionary significance of phenotypic plasticity, one must discern the extent to which plasticity has evolved as an adaptation and the extent to which it is an unavoidable side effect of environmental heterogeneity.

Among the most striking examples of presumably adaptive phenotypic plasticity are all-or-nothing responses, which are induced by an environmentally-mediated developmental switch (polyphenism; *sensu* Mayr 1963). Levins (1968) suggested that natural selection should favor such developmental switches in "a fine-grained environment where the range of the environment exceeds the tolerance of the individual phenotype." Environmentally-induced developmental switches have been found in bryozoans (Harvell 1984), *Daphnia* (Grant and Bayly 1981), gastropods (Crowl and Covich 1990), barnacles (Lively 1986b), locusts (Kennedy 1956) caterpillars (Bernays 1986; Greene 1989) and various other insects (reviewed in Roff 1986), fish (Kornfield and Taylor 1983; Meyer 1987), salamanders (Collins and Cheek 1983), and anurans (Pfennig 1989).

Theoretical studies of developmental switches have indicated that one environmental cue may affect the development of two different morphs. Lively (1986a) recently used a game theoretic model to illustrate that in a two patch system, diphenism may persist even though the cue for one type of patch is poor, if the cue for the other type of patch leads to the "correct" developmental choice greater than 50% of the time. The

other morph develops by default if the cue is not detected. An example of this sort of dimorphism may occur in certain populations of spadefoot toad tadpoles.

In this study, I examined the mechanism and possible functional significance of a major developmental polymorphism in spadefoot toads. Tadpoles of three species of spadefoot toads (*Scaphiopus bombifrons, S. intermontanus,* and *S. multiplicatus*) are phenotypically variable in their behavior, development, and morphology. Depending upon the pond, a varying percentage of tadpoles are larger, assume a distinctive broad-headed morphology, and develop more rapidly. These larger tadpoles, the carnivore morph, are atypical among anuran larvae in that (early in ontogeny) the major proportion of their diet consists of live, macroscopic animal food (primarily shrimp and other tadpoles; Pomeroy 1981). The alternative morph, omnivores, feed on detritus and algae (Pomeroy 1981). Carnivores develop more rapidly than omnivores, achieving metamorphosis in as little time as 12 d as opposed to 19 d for omnivores (Pfennig 1989). These developmental rate differences may be critical: the temporary rain pools (often in deserts) in which *Scaphiopus* breed may last only a few days (Pfennig et al. 1990).

I studied morph determination in southern spadefoot toad tadpoles (*S. multiplicatus*). Morph determination in this species appears to be environmentally induced. Pomeroy (1981) showed that carnivore frequency in the laboratory correlated positively with the presence of shrimp. His study did not resolve, however, whether shrimp is the only factor that can trigger morph determination and, if so, whether by actual ingestion or simply by the presence of shrimp. Moreover, the functional significance, if any, of this response was uncertain.

This study asks three questions. First, what ecological factors correlate with the frequency of carnivores in natural ponds? Second, what factors actually trigger morph differentiation and how? Third, is the mechanism engendering plasticity in this system adaptive?

Materials and methods

Study area

I studied *S. multiplicatus* in playas and artificially deepened earthen stock tanks near Portal, Arizona, USA for three field seasons (June–August 1986–1988; Fig. 1). The habitat was semidesert grassland or Chihuahuan desertscrub (1000–1800 m elevation). The ponds were dry much of the year, filling after thunderstorms from June to August. Many breeding ponds dried and refilled multiple times. In addition to tadpoles, the ponds supported protozoans, rotifers, cladocerans, clam shrimp (Conchostraca), tadpole shrimp (Notostraca), and fairy shrimp (Anostraca).

Ecological correlates of morph frequency

To identify the ecological correlates of morph frequency I censused 37 different ponds for three summers (1986–1988). After *Scaphiopus* bred in a pond I began sampling tadpoles three days after initial hatching. I randomly sampled 5–10 locations within each pond by tossing into the water a 0.5-m × 0.5-m × 0.7-m drop box with an open top and bottom (see Pfennig et al. 1990). I used
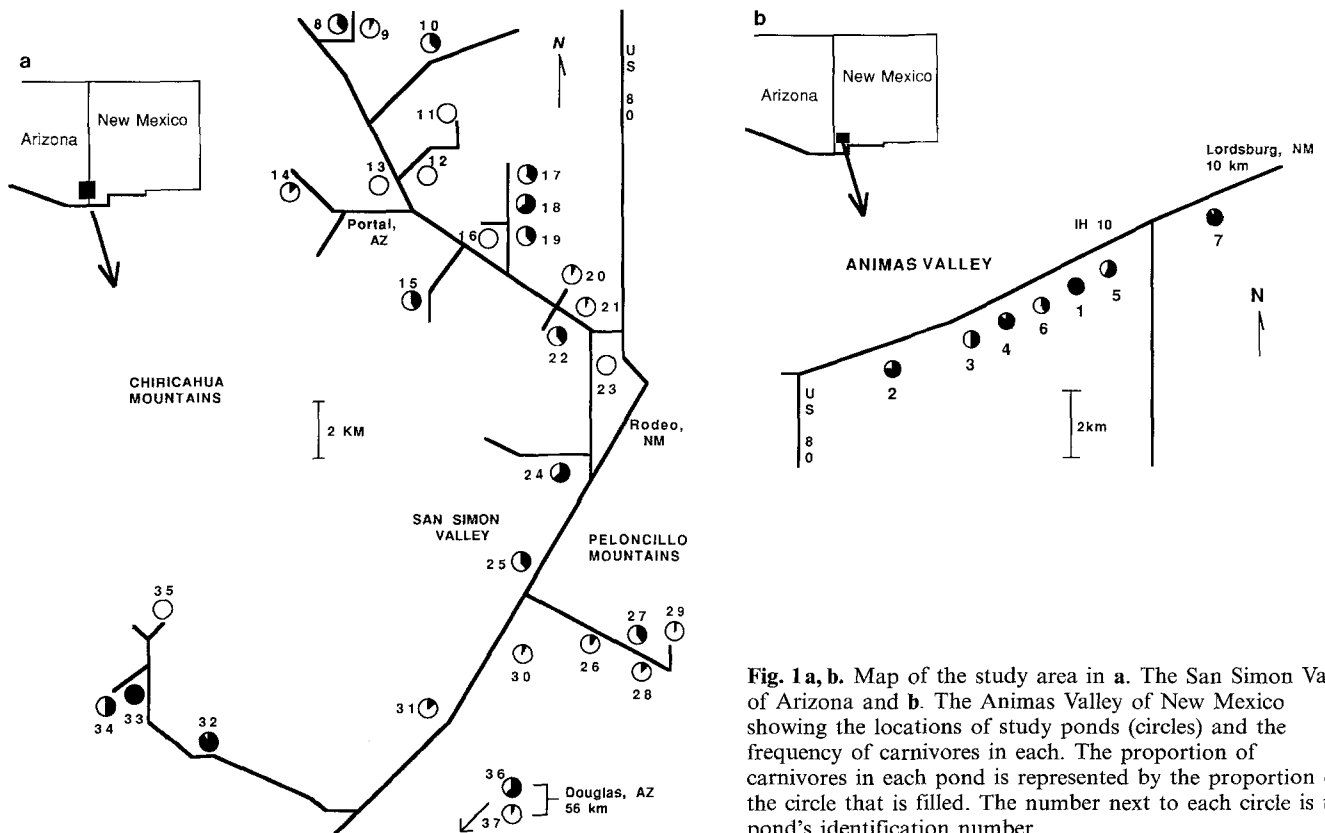
Fig. 1a, b. Map of the study area in a. The San Simon Valley of Arizona and b. The Animas Valley of New Mexico showing the locations of study ponds (circles) and the frequency of carnivores in each. The proportion of carnivores in each pond is represented by the proportion of the circle that is filled. The number next to each circle is the pond's identification number

a small net to sweep out all tadpoles. I categorized each animal as a carnivore or as an omnivore by visually characterizing the relative size of its orbitohyoideus (OH) and by examining its color and keratinized beak morphology (see below). I censused most ponds twice or more. My estimates of morph frequencies were within 1–4% of the actual pond-wide value as determined by removing all tadpoles from one large and one small pond and counting and morphologically scoring all tadpoles. I also examined the relationship between a cue triggering the two morphs (shrimp) and a presumed selective factor differentially affecting morph survival (pond duration). At five censusing locations in 19 breeding ponds I poured one liter of water through a plankton net (80-μm mesh) to remove zooplankton. I averaged the numbers of shrimp in each of 5 one-ml subsamples. I measured pond permanence by placing a pole in the center of each pond and noting water level changes over a 16 day interval (8–25 August 1988).

Two polymorphic species occurred in the study area (*S. bombifrons* and *S. multiplicatus*). As one species may be more likely than the other to produce carnivores (Simovich 1985) I had to ensure that any differences were not attributable to a bias among ponds in species composition. As tadpoles of the two species are indistinguishable morphologically (Altig 1970), I ascertained which anuran species bred in each pond by visiting the pond on the sole night that toads bred at that site. Since rains filled ponds asynchronously, I could concentrate on one or two ponds per evening. I noted the species affiliation of all breeding adults (usually 10–50 in each pond) using the morphological scoring criteria set forth in Simovich (1985). For parental species, there is 100% congruence between these morphological criteria and the toad's species affiliation as measured by four diagnostic marker loci (Simovich and Sassaman 1986). For hybrid adults, as many as one-third of all individuals may be scored incorrectly (Simovich 1985). I did not consider this a significant problem since hybrids are rare (Simovich 1985). A sample of tadpoles were scored using electrophoresis (Simovich and Sassaman 1986) to confirm my species designations. If one species were significantly more likely than the other to produce carnivores, then the frequency of carnivores should differ according to the number of species present (one or two).

What factors induce morph transformation?

Carnivore frequency in the field correlated with shrimp density and pond duration (see Results). Carnivores develop faster than omnivores (Pfennig 1989), and enhanced pond drying rate hastens development to metamorphosis in a number of anurans (Sokol 1984; Newman 1987, 1988; Crump 1989). Morph frequencies also may be related to the nutritional quality of the pond's bottom mud, on which the tadpoles feed. Bragg (1965) and Burton (1972) speculated that remains of desiccated tadpoles may facilitate development since tadpoles develop faster in pools that dry repeatedly. Enrichment of pond substrate by desiccated conspecifics may enhance development differentially since an omnivore's gut is approximately five times as long as that of the carnivore (Pomeroy 1981), perhaps allowing omnivores to assimilate low nutritive material more efficiently.

I experimentally varied substrate nutritional quality, shrimp density, and drying regime and examined their effects on the expression of the carnivore morphology in a $2 \times 2 \times 2$ factorial design in three randomized blocks. Shrimp density consisted of two levels: high (12 fairy shrimp per tadpole per feeding) and low (1 shrimp per tadpole per feeding). These values encompassed the range of shrimp supply to demand ratios sampled in 37 different ponds (Pfennig et al. 1990). Pond drying regime consisted of a constant water-level condition to simulate more permanent ponds and a drying treatment to simulate ephemeral pools. In the constant water-level treatment I added well water every 1–2 days as needed. In the high pond drying regime I allowed water to evaporate from each pond such that the ponds dried within 2 weeks, the longevity of the shortest duration breeding ponds in nature from which at

least some tadpoles metamorphosed (Pfennig et al. 1990). I occasionally intervened in the drying process by removing water. Many ecological factors change as a pond dries (e.g., density of conspecifics, temperature, and salt concentration increases); all these effects were subsumed under pond drying regime. Substrate quality consisted of a high (80 g per pool) and a low (5 g per pool) supplement of Purina™ catfish chow (37% protein). Catfish chow was used to mimic the rich organic detritus that accumulates in some ephemeral ponds. It is essentially impossible to estimate the range of available organic detritus in natural ponds. Some ponds are essentially barren of detritus. Others contain a rich substrate of decomposing matter, which is replenished as subsequent rains wash material into the pond. My intention was to approximate roughly this variation by allowing some tadpoles organic detritus *ad libitum* and others a very restrictive quantity. The chow should have been available to the animals immediately as evidenced by the disparity in growth between animals on high chow levels and those on low chow levels (Pfennig et al. 1990).

As experimental units I used 24 new, plastic pools (1.83 m diameter by 0.38 m deep with vertical sides and a flat bottom), which were within the lower size range of natural *Scaphiopus* breeding ponds (Pfennig 1989). I arranged the pools in a rectangular array 2.5 km northeast of Portal, AZ, USA (~1500 m elevation). I randomly assigned each pool a position in three spatial blocks within the array (three replicates, each containing eight treatments). On 26–28 June 1988 I filled each pool 30 cm deep with water from a subterranean well along with 2 cm of sand from the margin of a nearby dry pond. I mixed the water thoroughly among ponds. I left the pools uncovered exposing them to natural photoperiod and temperatures. All pools were eventually colonized by odonate predators, a significant source of mortality in natural ponds (Pomeroy 1981). Dipteran larvae were not detected. Colonization by odonates did not introduce systematic bias in the experiment since odonates colonized all pools in roughly equal numbers (5 to 7 per pool) and there were no significant block effects on mortality.

On 29 June 1988 I collected amplexed pairs of adult *S. multiplicatus* from two nearby "source" ponds. Only *S. multiplicatus* and *S. couchii* bred at the source ponds. I placed one amplexed pair into each pool. On 1 July 1988, after most eggs had hatched, I removed the adults and redistributed the larvae such that 14 clutches were equally represented among 196 tadpoles in each pool (14 tadpoles from each of 14 different clutches). The resulting density of 0.25 tadpoles/liter conformed to tadpole densities in natural ponds (Pfennig et al. 1990). I randomly assigned eight treatment combinations within each of three blocks (replicates). Chow was added once (on 28 June); fairy shrimp were replenished every two days starting on 1 July. I obtained fairy shrimp from the source ponds so that shrimp and tadpoles were synchronized in development. I stopped adding shrimp after one week to simulate the sharp decline in shrimp density seen in natural ponds (Loring et al. 1988; Pfennig et al. 1990).

On 14 July, when the tadpoles were 14 days old, and before any had metamorphosed, an assistant, who was unaware of which pools represented which treatments, removed from each pool ten randomly chosen animals of Gosner (1960) developmental stages 32–34. At this point in the experiment, mortality was random with respect to treatment (Pfennig 1989). I killed the animals ($n = 240$ animals total) in tricaine methanesulfonate and scored each animal's morphology as described below. The value representing the proportion of carnivores in each pool was arcsine-square root transformed to meet the assumptions of analysis of variance (Sokal and Rohlf 1981). An analysis of block (replicate) main effects and two-way interaction effects revealed no significant differences among blocks. I therefore pooled with the error term the blocks sums of squares and degrees of freedom and treated blocks as replicates (Cochran and Cox 1957). I analyzed the data with a three-way fixed-effects analysis of variance. Scheffé's F-test was used to compare treatment means.
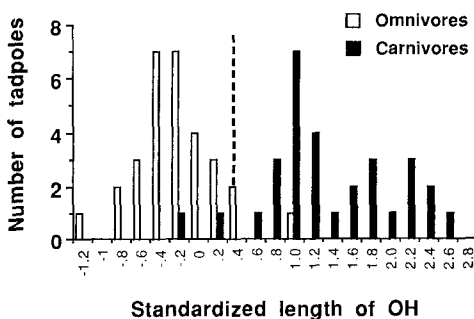
In a separate experiment, I investigated whether increasing shrimp density influenced carnivore morphology, as well as carnivore frequency. I reared 80 hatchlings from a single sibship in

individual 250-ml cups, exposing them to a natural photoperiod and temperatures fluctuating diurnally from 24–30° C. I randomly assigned animals to one of four groups (20 animals each). I fed each animal in the first group one live shrimp per feeding; the second group, two shrimp; the third group, four shrimp; and the fourth group, eight shrimp. Shrimp were matched for size by straining them through a net of fixed mesh size. I fed the animals twice daily. I also fed all animals Carolina Biological Supply™ tadpole chow *ad libitum*. As each animal reached developmental stage 34 I recorded its snout-vent length (SVL) and OH.

Finally, I investigated whether the actual ingestion as opposed to simply the presence of shrimp elicited morph transformation. I partially submerged inside 60, 250-ml plastic cups a smaller cup, the bottom of which consisted of 1 mm mesh net. I randomly assigned 30 tadpoles from a single sibship to each group. For animals in group one, I placed inside the inner cup 8–10 live fairy shrimp daily. Tadpoles in group two were fed 8–10 live fairy shrimp daily; the inner cup held only water. Thus, tadpoles in group one were exposed to shrimp but were unable to eat them. Tadpoles in group two were able to eat shrimp. I also fed all tadpoles chow *ad libitum*. Tadpoles were exposed to a natural photoperiod and their water was maintained at a constant 29° C. As each animal reached developmental stage 36 I recorded its SVL and OH.

Morph assignment

I classified each animal as a carnivore or an omnivore according to two criteria. These criteria were based on morphological characteristics previously shown to correlate highly with overall bimodality in morphology (Pfennig 1989). First, I examined under a microscope each animal's keratinized mouthparts. Carnivores possess a keratinized beak, in contrast to the omnivore's smooth mouthplates (Orton 1954). Second, I measured the length (i.e., the distance perpendicular to the muscle fibers) of the m. orbitohyoideus (OH), the primary buccal floor depressor muscle. I noted the extent to which each animal expressed the carnivore morphology by regressing OH on SVL (to control for body size). Standardized OH refers to the standardized residuals of these regressions. In wild-caught animals, standardized OH lengths of animals of the same cohort were bimodal, carnivores having positive values and omnivores negative values (Fig. 2). The midpoint between the two modes of the residual frequency distribution of wild caught animals from one of the source ponds was 0.45. My operational definition of a carnivore was any animal that had a beak *and* a standardized OH length of 0.45 or greater.

Results

Field surveys

Initial maximum depths of breeding ponds ranged from 5–200 cm ($\bar{x} \pm$ s.e.m. $= 46 \pm 8.2$ cm) and surface area to volume ratios ranged from 1.3–55 ($\bar{x} = 11.5 \pm 1.9$). Rotifers (*Platyias* sp.), cladocerans (*Daphnia* and *Moina* sp.), clam shrimp (*Eulimnadia texana* [Conchostraca]), tadpole shrimp (*Triops longicaudatus* [Notostraca]), fairy shrimp (*Streptocephalus texanus* and *Thamnocephalus platyurus* [Anostraca]), and, occasionally, mosquito larvae (*Aedes* sp.) were the dominant zooplankters (shrimp/liter: range 0–12.6, $\bar{x} = 4.4 \pm 0.7$). Durations of breeding ponds varied in the three years of the study from five days to several months, depending upon whether they were replenished by subsequent rain.

The 37 ponds sampled contained from 0–100% carnivores ($\bar{x} = 36.8 \pm 31.7\%$; Fig. 1). Carnivore frequency correlated significantly positively with shrimp density ($r = +0.702$, $n = 16$, $P < 0.01$) and two measures of pond longevity: water lost per day ($r = +0.468$, $n = 19$, $P < 0.05$) and the ratio of pond surface area to volume ($r = +0.409$, $n = 36$, $P < 0.01$). Thus, carnivores were most abundant in shallow, rapidly evaporating ponds that contained abundant shrimp. Carnivore frequency did not correlate significantly with conspecific density ($r = -0.338$, $n = 28$, $P > 0.05$). Whether the pond was a pure or mixed species pond did not significantly affect the frequency of carnivores. Carnivore frequency in the 21 ponds in which I detected at least one breeding adult *S. bombifrons* or *S. bombifrons* × *S. multiplicatus* hybrid was not significantly greater than that in the 16 ponds that contained only *S. multiplicatus* ($42.7 \pm 6.5\%$ vs. $27.0 \pm 8.3\%$, respectively; $P = 0.140$, two-tailed t-test). Thus, differences among ponds in morph frequency were likely not due to differences among ponds in species composition.

As indicated in Fig. 3 ponds that had higher densities of shrimp (and hence higher frequencies of carnivores) dried faster: shrimp density correlated significantly posi-

Fig. 2. Frequency distribution of m. orbitohyoideus regressed on snout-to-vent length for 60, 14 day-old wild-caught animals (30 carnivores and 30 omnivores) from a single pond. Animals were scored according to the criteria described in Pfennig (1989). The vertical dashed line indicates the midpoint between the two modes of the frequency distribution. This value, 0.45, served as the cutoff value for use in the operational definition of carnivores and omnivores
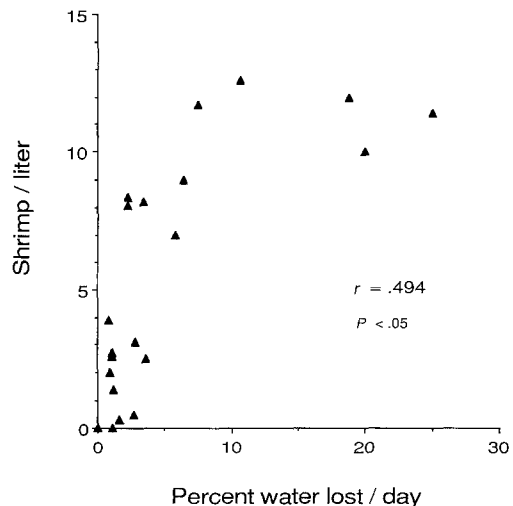

Fig. 3. Shrimp density as a function of pond ephemerality

tively with pond water loss rate (rSHRIMP DENSITY, HOH LOST / DAY = 0.494, n = 19, P < 0.05).

What factors induce morph transformation?

In the artificial pool experiment, of 240 animals sampled (10 from each of 24 artificial pools), 14 were carnivores. As shown in Table 1, carnivore frequency was affected by shrimp density but not by substrate nutritional quality or pond drying. The most carnivores (13%, 4 out of 30) occurred in the high substrate quality, high shrimp, high drying regime treatment and in the low substrate quality, high shrimp, low drying treatment. By contrast, three groups produced no carnivores: low substrate quality, low shrimp, high drying; high substrate quality, low shrimp, high drying; and high substrate quality, low shrimp, low drying.

Variation in orbitohyoidean muscle development was directly related to the density of shrimp to which the tadpoles were exposed in the laboratory. Figure 4 illustrates that the most extreme carnivores (i.e., the tadpoles with the largest orbitohyoideus muscle) were those reared on highest densities of shrimp (rSHRIMP DENSITY, TADPOLE OH = 0.701, n = 80, P < 0.001). Finally, as shown in Fig. 5, tadpoles fed shrimp had significantly greater OH development than did tadpoles ex-

Table 1. Summary of a three-way analysis of variance of proportion of 14 day-old tadpoles that transformed into carnivores in artificial ponds (data were arcsine-square root transformed before analysis). Means $\pm$ 1 s.e.m. of the untransformed data are shown below the ANOVA table. Common superscripts indicate that values differ significant (P < 0.05)

Source of variation	$d.f.$	MS	F	P
Substrate nutritional quality (A)	1	0.055	2.582	0.1277
Shrimp density (B)	1	0.375	17.715	0.0007
Drying regime (C)	1	0.001	0.04	0.8447
A × B	1	0.01	0.495	0.4917
A × C	1	0.026	1.214	0.2868
B × C	1	0.01	0.495	0.4917
A × B × C	1	0.001	0.04	0.8447
Residual	16	0.021		

| Sub-state quality	Shrimp density	Drying regime	# pools with a carnivore*	% carnivores (mean, s.e.m.)	OH × SLV** (mean, s.e.m.)
Low	Low	High	0	0, 0	−0.97, 0.37[a, b]
High	High	High	2	13.3, 3.3	0.57, 0.19[a]
Low	Low	Low	1	3.3, 3.3	−0.14, 0.22
High	High	Low	1	6.7, 6.7	0.31, 0.14[b]
Low	High	High	3	10.0, 0	−0.24, 0.21
High	Low	High	0	0, 0	0.27, 0.14
Low	High	Low	3	13.3, 3.3	−0.04, 0.14
High	Low	Low	0	0, 0	0.25, 0.02

* number of pools (out of 3/treatment) producing at least one carnivore
** mean residual of regression of OH on SVL (to control for body size)
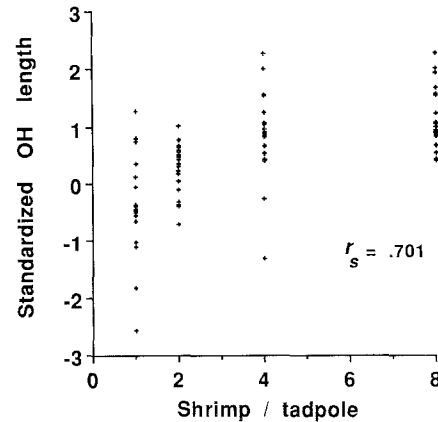
Fig. 4. Effect of shrimp density on the development of 4 day-old tadpoles reared in individual cups. Each point represents the standardized length of the OH muscle for one tadpole (N = 20 tadpoles in each group)
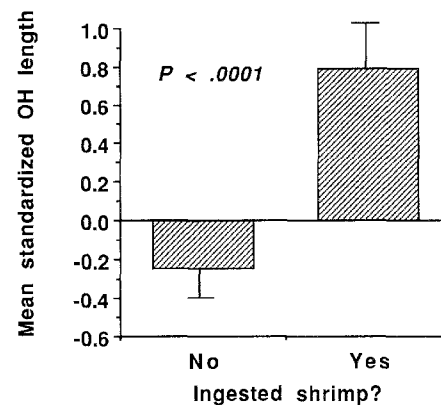
Fig. 5. Effect on OH development of exposure to shrimp (but not ingestion) versus actual ingestion. Vertical lines indicate 1 s.e.m.

posed to, but not fed, shrimp (P < 0.0001; two-tailed t-test; t = −5.45, $d.f.$ = 58).

Discussion

If a *S. multiplicatus* tadpole ingests some critical number of shrimp, it may become a carnivore; otherwise, it becomes an omnivore by default. These findings raise two questions. First, how does shrimp ingestion produce such pronounced effects on tadpole morphology, development, and behavior? Second, what does the mechanism of morph determination reveal about the potential adaptiveness of plasticity in this system? I address these two questions in turn.

Possible physiological basis of morph determination

The ingestion of shrimp, not simply their presence, triggers morph transformation. Variation in morphology in this species thus represents a trophic polyphenism. Interestingly, at least one other anuran tadpole (Cei 1969) and a cichlid fish (Meyer 1987) express dimorphism in oral features that may also be induced by macroscopic animal prey.

The use of food as a cue to induce polyphenism may be especially common. On the evolutionary level, prey encountered early in ontogeny may influence an animal's phenotype if alternative phenotypes are differentially effective at utilizing different prey. On the proximate level, the ingestion of different food types may induce morph transformation through the intake of chemical cues or material with different processing requirements. In the simplest sense, trophic polyphenism occurs when variation among conspecifics in diet texture causes differential growth of masticatory muscles. For example, anuran tadpoles reared on lettuce develop more massive hyoidean muscles than those fed softer food (Pomeroy 1981). Similar effects are seen in mammals (Moore 1965) and even in insects (Bernays 1986). The ingestion of different food types also may cause major morphological change. Minor phenotypic variation that results from variation in diet early in ontogeny may be enhanced through development to produce major modification. This is the analog to genetically-specified variation, which, though initially minor, may be amplified through ontogeny (e.g., see Hanken 1983). An alternative mechanism whereby food may produce qualitative changes in morphology is through the release of a hormone or a morphogen (or modification of target tissue responsiveness). All that is necessary for this type of change to occur is for the target cell or tissue to have a discrete threshold or binary switch (Raff and Kaufman 1983). Diversification of a taxa into separate trophic niches is often accompanied by an complex array of adaptations.

How might shrimp ingestion produce such varied effects on tadpole developmental rate, morphology, and behavior? Morph transformation from an omnivore to a carnivore may be caused by the premature exposure to significant levels of thyroid hormone (TH), the primary endocrine trigger of metamorphosis (White and Nicoll 1981). *Scaphiopus multiplicatus* omnivores treated with exogenous thyroxine mimic carnivores in every respect except in their smaller size and precocious limb bud development (Pomeroy 1981). Also, young carnivores fed chow and TH retain carnivore-like OH musculature whereas those fed chow alone do not (Promeroy 1981). A second possible mechanism involves differential nutrition. The heightened growth of carnivores may reflect the greater nutritional value of their diet (shrimp and conspecifics). However, this explanation does not address satisfactorily the development of specialized structures in carnivores, such as the keratinized beak and the reduced gut. Finally, a third possibility includes mechanical effects. An increase in orbitohyoidean muscle fiber mass with work is not surprising. Analogous effects of diet on growth of masticatory muscles occur in mammals (Moore 1965). *Scaphiopus multiplicatus* tadpoles that are reared on lettuce develop larger OH muscles than those reared on softer trout chow (Pomeroy 1981). Other morph-specific differences, such as the carnivore's keratinized beak, may similarly involve differential production of keratin in areas that receive repeated stimulation. In sum, the combination of carnivore-like oral morphology together with shortened guts may occur through distinct, though correlated, developmental processes. It seems unlikely that nutritional or mechanical processes alone can produce the concerted developmental change underlying morph differentiation. The physiological basis of morph determination remains virtually unexplored.

Adaptive significance of the mechanism of morph determination

Polyphenism is often triggered by a single cue. The cue that elicits alternative ontogenies may be the presence of predators, as in *Daphnia* (Grant and Bayly 1981), rotifers (Gilbert and Stemberger 1984), bryozoans (Harvell 1984), and barnacles (Lively 1986b); food as in caterpillars (Bernays 1986; Greene 1989), locusts (Kennedy 1956), and fish (Meyer 1987); temperature, as in butterflies (Janzen 1984); high conspecific density, as in salamanders (Collins and Cheek 1983); or unstable environments, as in salamanders (Semlitsch 1987).

In *Scaphiopus*, using shrimp density to trigger morph determination enables tadpoles to produce the phenotype with the higher expected mean fitness for the given pond conditions. Because shrimp are most abundant in the most ephemeral pools, the probability is greatest that a tadpole will become a carnivore in a highly ephemeral pool (Fig. 3). Desiccation is the chief cause of mortality in desert *Scaphiopus* tadpoles (Newman 1987). In one year alone, 4 of 41 breeding ponds (10%) in my study area dried up before *any* tadpoles metamorphosed. Carnivores develop faster than omnivores (Pomeroy 1981; Pfennig 1989). Even though they have sufficient plasticity to decrease facultatively the length of their larval period, omnivores still have significantly lower postmetamorphic survivorship than carnivores in highly ephemeral ponds (Pfennig 1989). As a result, carnivores are favored in highly ephemeral pools since only they metamorphose at a reasonable size before the pond dries (Pfennig 1989). Thus, the use of shrimp density to induce morph differentiation enables tadpoles to respond to their environment adaptively.

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