

POLYPHENISM IN SPADEFOOT TOAD TADPOLES AS A LOCALLY ADJUSTED EVOLUTIONARILY STABLE STRATEGY

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Abstract.—I examined the evolutionary factors maintaining two environmentally induced morphs in ponds of variable duration. Larvae of New Mexico spadefoot toads (*Scaphiopus multiplicatus*) often occur in the same pond as a large, rapidly developing carnivorous morph and as a smaller, more slowly developing omnivorous morph. Previous studies revealed that carnivores can be induced by feeding tadpoles live fairy shrimp and that morph determination is reversible. Field and laboratory experiments indicated that the ability of an individual to become a carnivore or an omnivore is maintained evolutionarily as a response to variability in pond longevity and food abundance. Carnivores survived better in highly ephemeral artificial ponds, because they developed faster. Omnivores survived better in longer-duration artificial ponds, because their larger fat reserves enhanced postmetamorphic survival. The two morphs also occupy different trophic niches. Experimental manipulations of morph frequency in ponds of intermediate duration revealed that increased competition for food among individuals of the more common morph made the rarer form more successful. Morph frequency within each pond was stabilized at an equilibrium by frequency-dependent morph reversal, which reflected frequency-dependent natural selection on size at metamorphosis: larger metamorphs had higher survival, and individuals reared at a frequency above the pond's equilibrium frequency were smaller at metamorphosis than were individuals of that morph reared at a frequency below the pond's equilibrium. Because neighboring ponds often differed in pond longevity and food abundance, each pond possessed a unique equilibrium morph frequency. This implies that morph determination in *Scaphiopus* is a locally adjusted evolutionarily stable strategy (ESS).

Key words.—Adaptation, assessment, competition, evolutionarily stable strategy (ESS), frequency-dependent selection, polyphenism, *Scaphiopus multiplicatus*.

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Many populations contain multiple, functionally distinctive morphs. One classical argument for the evolutionary maintenance of such morphs is that natural selection favors diversity in heterogeneous environments (Levene, 1953; Levins, 1968). A seeming paradox arises, however, when alternative morphs cooccur. If all individuals experience similar environmental patch types, then what prevents fixation of the phenotype best adapted to the highest quality patch type? One possibility is that competition within patch types lessens the disparity in their quality (Fretwell and Lucas, 1970; Parker, 1970; Fretwell, 1972). Selection then favors a morph more when it is rare than when it is common (Milinski and Parker, 1991), and alternative morphs may persist as component tactics of an evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973).

If frequency-dependent morphs represent phenotypically plastic alternatives (polyphenism; Stearns, 1989) as opposed to genetically fixed forms, then their relative proportions may be finely tuned to highly local conditions (West-Eberhard, 1989). Although the relative proportions of genetically fixed morphs may attain a global equilibrium, populations in different patches may be far from a local equilibrium, for two reasons. First, gene flow counters any tendency for separate populations to attain different equilibria (Wright, 1969; Dobzhansky, 1970). Second, local environments (hence local equilibria) change frequently (Van Valen, 1973). However, phenotypically plastic alternatives may closely approximate local equilibria even in temporally fluctuating environments. Such "environmentally determined ESSs" (Parker, 1984) have been largely unexplored (but see Charnov, 1982; Lively, 1986).

Here, I employ both experimental and game theoretic approaches to examine the maintenance of alternative morphs in New

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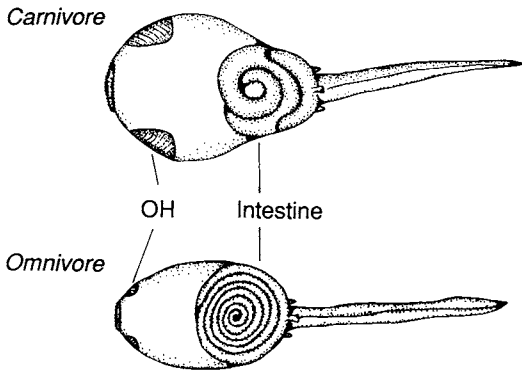


FIG. 1. Ventral view of a carnivore and an omnivore (both eight days old). Carnivores have a distinctive diamond-shaped silhouette, which is caused primarily by enlargement of the orbitohyoideus muscle (OH), the primary buccal floor depressor muscle. The omnivore's OH is much smaller, making this morph's body outline oval-shaped. The two morphs differ structurally in several other respects, including the relative length of the intestine.

Mexico spadefoot toads (*Scaphiopus multiplicatus*). Larvae of this species occur in ephemeral ponds as two morphologically distinctive, environmentally induced phenotypes: a large, rapidly developing carnivore morph and a smaller, more slowly developing omnivore morph (Fig. 1; Pomeroy, 1981; Pfennig, 1990a, 1992). Carnivores eat anostracan shrimp, whereas omnivores eat detritus primarily (Pomeroy, 1981). Both morphs typically inhabit the same pond (Bragg, 1965; Pomeroy, 1981; Pfennig, 1990a). Carnivores arise facultatively through the ingestion of shrimp (Pomeroy, 1981; Pfennig, 1990a, 1992), and tadpoles can change back to the alternative morphology if their diet is switched (Pomeroy, 1981; Pfennig, 1992). This developmental switch is summarized in Figure 2.

Given that *S. multiplicatus* breeds exclusively in ephemeral ponds (Bragg, 1965; pers. obs.), and that carnivores develop faster than omnivores, why do populations not consist only of carnivores? One possibility is that carnivores incur a cost not borne by omnivores. Carnivores develop rapidly at the expense of accumulating significant lipid reserves (Pomeroy, 1981; this study), the metamorph's primary mode of energy storage (Fitzpatrick, 1976; Seymour, 1973). If survival tradeoffs exist, natural selection may favor alternative morphs in *Scaphio-*

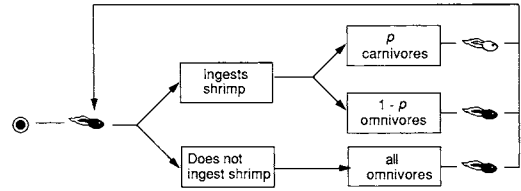


FIG. 2. Schematic of the developmental "switch" that triggers carnivores. At hatching all animals have an omnivore morphology. If these animals ingest macroscopic animal food, most notably fairy shrimp, a reversible switch is triggered resulting in a fraction p of the animals developing into carnivores. The remainder develop into omnivores. The carnivores must continue to consume large animal prey or they assume the omnivore morphology; likewise omnivores have the possibility of becoming a carnivore through a large portion of larval ontogeny. See discussion for further details. Based on data in Pomeroy (1981) and Pfennig (1990a, 1992).

pus as a response to variability in pond duration. Tadpoles can assess pond longevity indirectly because shrimp abundance, the cue that triggers the faster-developing carnivore, correlates with pond ephemerality (Pfennig, 1990a). Thus ephemeral ponds should contain all carnivores, because carnivores develop faster. More permanent ponds, by contrast, should contain all omnivores, because their greater lipid reserves enhance postmetamorphic survival.

In intermediate duration ponds morph frequency may reflect the availability of different prey items to which the two morphs are differentially specialized. Ponds harboring high densities of shrimp might contain a high frequency of carnivores, because the carnivore's buccal morphology is specialized for consuming shrimp (Wassersug and Hoff, 1979; Satel and Wassersug, 1981). By contrast, ponds harboring few shrimp but a rich supply of organic detritus might contain more omnivores, because the omnivore's buccal morphology is specialized for consuming microscopic food (Wassersug and Hoff, 1979; Satel and Wassersug, 1981). If either food item became limiting, competition for food would be more severe among individuals of the same morph. Frequency-dependent selection might then maintain the two morphs in a pond at an equilibrium morph frequency. If so, omnivory and carnivory may be component tactics of an environmentally determined ESS. Because ponds differ in food level each

might possess a characteristic equilibrium morph frequency.

This study experimentally addresses two questions regarding the evolutionary maintenance of alternative morphs in *Scaphiopus*. First, do pond duration and food availability affect morph fitness differentially? Second, does selection maintain polyphenism in *Scaphiopus* as an environmentally determined ESS, with different ponds possessing different equilibrium morph frequencies? I examined the effects of pond longevity by manipulating pond duration and assessing its effects on morph fitness. I examined the effects of food abundance indirectly by producing different morph frequencies within enclosed sections within each of five ponds. I then evaluated the effects of this manipulation on (1) morph determination and (2) morph fitness. Finally, I use a game theory model to predict the equilibrium morph frequency for a given pond.

METHODS

General Procedures

I conducted field surveys and experiments near Portal, AZ, USA (32°N, 109°W) in natural ponds and in artificially deepened earthen stock tanks. The latter typically occurred in areas that probably held water temporarily before human intervention (Hedrickson and Minckley, 1985). Locations and descriptions of ponds are in Pfennig (1990a, 1990b) and in Pfennig et al. (1991b). I also used plastic wading pools (1.83 m diameter by 0.38 m deep with vertical sides and a flat bottom) that I arranged in a rectangular array 2.5 km northeast of Portal. For experiments in these artificial ponds, pool sizes, tadpole densities, and food levels fell within the range of values for natural *Scaphiopus* breeding ponds (Pfennig et al., 1991b). The uncovered pools experienced a natural photoperiod and diurnal temperature fluctuations (25–33°C at 5 cm below water surface).

I classified each animal as a carnivore or an omnivore according to the relative width (i.e., the distance perpendicular to the muscle fibers) of the m. orbitohyoideus (OH), the primary buccal floor depressor muscle (Fig. 1). The ratio of this muscle's width to

snout-to-vent length (SVL) is strongly bimodal with most carnivores and omnivores occurring in separate modes of the distribution (Pomeroy, 1981; Pfennig, 1992). The OH is visible through the tadpole's skin and can be examined without harming the animal.

Are the Two Morphs Adaptations for Different Pond Drying Conditions?

Carnivores and omnivores differ in mean age at metamorphosis (Pomeroy, 1981; this study). To determine if this could explain the evolutionary maintenance of both morphs, I evaluated over a three year period (1986–1988) spatial and temporal variability in pond duration for 37 natural ponds. I then bracketed this variability in 12 artificial ponds designed to mimic long-duration and short-duration ponds and examined if pond duration affected morph survival differentially. In this experiment I examined the effects of drying regime on each morph's survival (premetamorphic and postmetamorphic survival combined) up to about 2 months postmetamorphosis. The rationale for examining survival up to this age was that juvenile mortality in *Scaphiopus* is greatest immediately after metamorphosis. As few as 1% of all spadefoots survive to the sixth week of postmetamorphosis (Creusere and Whitford, 1976). Death results from incomplete development, insufficient nutrition, predation, disease, and desiccation. I postulated that the first two factors in particular may affect carnivore and omnivore survival *differentially*. Incomplete development may be important because omnivores metamorphose in short-duration ponds at a small body size. Nutrition should also be important given the disparity between morphs at metamorphosis in relative fat body size (Pomeroy, 1981; this study).

I collected 216 omnivores and 216 carnivores at Gosner (1960) developmental stage 36 from a single pond. I randomly assigned 36 individuals of each morph to a separate artificial pond that was filled 2 cm deep with pond substrate and 30 cm deep with well water. I added live shrimp according to their density in the tadpoles' natal pond (as determined by repeated samples with a plankton net). In the six long-

duration pools (three for each morph), water was lost to evaporation. In the six short-duration pools (three for each morph), water was lost to evaporation and by my removing water such that the pool would dry at the same time (2 weeks) as an ephemeral, natural pond that I had previously followed. The response variable was the proportion of individuals of each morph surviving each drying regime up to about two months post-metamorphosis. I followed postmetamorphic survival of all surviving metamorphs by placing each toadlet in a separate cup containing moistened vermiculite and arranging the cups in an environmental chamber (26°C, 14:10 hr day:night photoperiod). I approximated natural levels of nutrition by feeding each toadlet two small crickets every other day. This quantity and type of food mimicked that found in the stomachs of field-caught toadlets (Pfennig, pers. obs.). I decided a priori to end the experiment and compare the effects of pond longevity on each morph's survival when 50% of the toadlets—i.e., 50% of the survivors from the artificial ponds—had died, probably because of starvation.

Is Morph Determination Frequency-Dependent?

I hypothesized that morph frequency would also be affected by food abundance within a pond, because carnivores and omnivores occupy different trophic niches (Pomeroy, 1981). One way to examine if food affects morph frequency is to determine if morph success is frequency-dependent. I manipulated morph frequency within five natural ponds that differed in their initial proportion of carnivores and followed morph frequency with time. I started the manipulation four days after *S. multiplicatus* had bred in each pond. Using fences of fiberglass mesh, I divided each (roughly circular) pond into six equal-sized sections (triangular-shaped with the apex at the pond's center; 10–80 m by 4–12 m on the shore end). One area of the pond was left open. The fence's mesh size (1 mm) retained tadpoles and larger invertebrates (such as shrimp). I stapled the fence to wooden posts and pressed the fence base into the pond's bottom mud. Through repeated netting, I removed all tadpoles within the fenced ar-

reas, counted them, noted their morphotype, and placed them into an open area of the pond.

I returned tadpoles at random to the partitioned sections according to the following scheme: two sections contained an excess of omnivores (compared to the original pond-wide frequency, the exact frequency varied from pond to pond), two an excess of carnivores, and two "control" sections contained tadpoles at the original pond-wide morph frequency. The starting density of tadpoles in each section matched the original pond-wide tadpole density (both morphs considered together). An assistant, who did not know the starting morph frequency in any section, sampled morph frequency and shrimp density in each section every three to five days until all tadpoles metamorphosed. Censuses consisted of placing a drop box at five locations in each section and removing from within the box all tadpoles and shrimp (see Pfennig, 1990b). For each section, I followed morph frequency with time and compared initial and final morph frequency. In one pond, the experiment ended after three censuses when a flash flood destroyed the partitions.

I repeated the above experiment in 16 artificial ponds. I filled the bottoms of each pool 2 cm deep with well-mixed substrate from a dry pond bed and then filled the pools 30 cm deep with well water. Nine pairs of *S. multiplicatus* adults were collected in amplexus and allowed to oviposit in the pools. Shrimp hatched from diapausing eggs in the soil just as if their pond had filled from rain. After most anuran eggs had hatched, I redistributed the tadpoles such that all clutches were equally represented among the 200 tadpoles in each pool. I did not add water, shrimp, or nutrients from then on. After four days I calculated the mean percentage of carnivores across the 16 artificial ponds (= 42% carnivores). I manipulated morph frequencies by randomly distributing 200 tadpoles in each pool such that four received 200 (100%) omnivores, four received 200 (100%) carnivores, four received 133 (67%) omnivores and 67 (33%) carnivores, and four received 67 (33%) omnivores and 133 (67%) carnivores. As controls, I left four pools at the initial, average morph frequency (42% carnivores). As be-

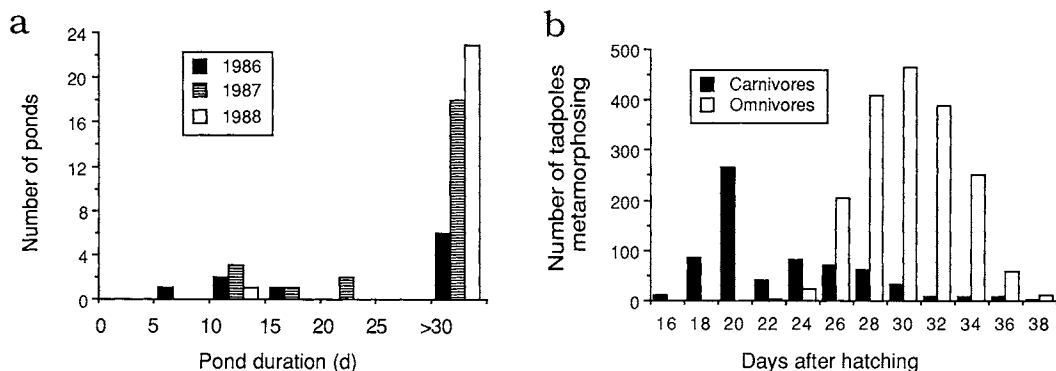


FIG. 3. a. Frequency distributions of breeding pond longevities over a three year period. At least some tadpoles failed to metamorphose in ponds that dried within 30 days. b. Frequency distributions of metamorphic ages for a cohort of tadpoles emerging from a single pond.

fore, the response variable was percent carnivores in each treatment, which was measured 6 and 17 days after egg hatching.

Is Morph Fitness Frequency-Dependent?

Two mechanisms may produce frequency-dependent morph frequencies: frequency-dependent mortality and frequency-dependent morph reversal. In the laboratory *S. multiplicatus* can switch morphs when their diet is changed to that of the alternative morph's (Pomeroy, 1981; Pfennig, 1992). Thus a frequency-dependent response in a partitioned pond may be due to differential reversion, not to differential mortality, and the actual *fitness* of a tadpole may not necessarily be frequency-dependent.

To distinguish between the above two mechanisms, I surrounded two partitioned ponds from the previous experiment with a 20 cm high fence of aluminum flashing, which enabled me to capture all metamorphs. I then compared premetamorphic survival in the manipulated sections with that in the control sections. If the frequency-dependent response were due to differential premetamorphic mortality, the manipulated sections should have produced fewer metamorphs than the control sections. Frequency-dependent selection can also affect morph determination by acting on an individual's *postmetamorphic* fitness. To test this I examined a factor that correlates positively with *postmetamorphic* fitness: size

at metamorphosis (Martof, 1956; Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Pfennig et al., 1991b). I compared mean size of individuals of each morph emerging from sections when each morph was overrepresented (i.e., initially present at a frequency above the starting overall pond-wide morph frequency) versus mean size of individuals of each morph emerging from sections when each morph was underrepresented (i.e., initially present at a frequency below the starting overall pond-wide morph frequency). If each pond's equilibrium morph frequency were stabilized by frequency-dependent selection, I anticipated that overrepresented individuals of each morph would be smaller at metamorphosis than individuals of that morph emerging from sections in which they were underrepresented.

RESULTS

Are the Two Morphs Adaptations for Different Pond Drying Conditions?

Breeding pond durations varied both spatially and temporally (Fig. 3a). I operationally defined a pond lasting more than 30 d as a long-duration pond, because most tadpoles metamorphosed within this time (Fig. 3b). Six of 24 ponds (25%) dried within 30 d in 1987, whereas only 1 (4%) of these same ponds dried within 30 d in 1988 (Fig. 3a). Overall, pond durations did not correlate significantly across these two years (Spearman correlation coefficient = 0.36, $P = 0.083$, $N = 24$ ponds).

Because they develop faster carnivores should be less likely to desiccate (Fig. 3b). However, many anuran larvae hasten developmental rate facultatively in the face of pond drying (e.g., Sokol, 1984; Wilbur, 1987; Newman, 1988, 1989; Crump, 1989), and omnivores might metamorphose earlier were their pond to dry. To resolve this issue for *Scaphiopus* I reared animals in artificial ponds that contained water for variable lengths of time.

Pond duration did not affect *premetamorphic* survival of the two morphs differentially, because omnivores accelerate metamorphosis if their pond dries. In long-duration pools 22 ± 9% of the omnivores and 25 ± 12% of the carnivores metamorphosed. In short-duration pools 16 ± 4% of the omnivores and 20 ± 9% of the carnivores metamorphosed. Pond duration did, however, affect *postmetamorphic* survival of the two morphs differentially. Carnivores had significantly greater survival than omnivores in short-duration pools; the opposite held in long-duration pools (Fig. 4). The physiological basis for the survival differences between carnivores and omnivores in long-duration pools may be the former's significantly smaller abdominal fat body ($P < 0.001$, two-tailed Mann Whitney *U*-test). In sum, the two morphs are adapted to different pond drying conditions with rapid-drying conditions favoring carnivores and slow-drying conditions favoring omnivores.

Is Morph Determination Frequency-Dependent?

If morph determination were inversely frequency-dependent, the rarer morph should have increased in frequency in manipulated sections of partitioned ponds, while morph frequency in control sections should have remained constant. The initial and final frequency of carnivores in manipulated sections of ponds differed significantly. Regardless of which morph the manipulated section contained in excess, morph frequency changed in an inverse frequency-dependent fashion (Fig. 5; Table 1). By contrast, the initial and final frequency of carnivores in control sections did not differ significantly (Table 1). Similar patterns were observed in artificial ponds (Fig. 6).

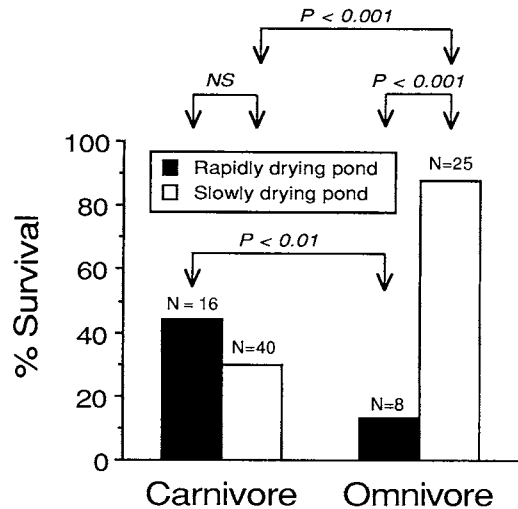


FIG. 4. Postmetamorphic survival for each morph when reared in wading pools designed to mimic ponds of different duration. Sample sizes are above each bar. *P* determined using a two-tailed Mann Whitney *U*-test.

Is Morph Fitness Frequency-Dependent?

Inverse frequency dependence may have arisen through differential mortality or through morph reversion. If differential mortality were responsible for the observed trend, then manipulated sections should have produced significantly fewer metamorphs than control sections. In pond 17, the control and manipulated sections did not differ significantly in number of metamorphs produced (mean number of metamorphs in control sections = 423 ± 33 animals; mean number of metamorphs in manipulated sections = 494 ± 35; $P = 0.275$, two-tailed *t*-test). These data, together with data showing that artificial ponds initially containing all carnivores or all omnivores later contained both morphs (Fig. 6), strongly imply that morph reversion and not differential tadpole mortality produced the frequency-dependent response.

Is there evidence that selection favors frequency-dependent morph reversal? In enclosed sections of ponds initially containing the same number of tadpoles, the overrepresented morph (i.e., the morph initially present at a frequency above the starting pond-wide morph frequency) was significantly smaller at metamorphosis than was the same morph when underrepresented (i.e., when

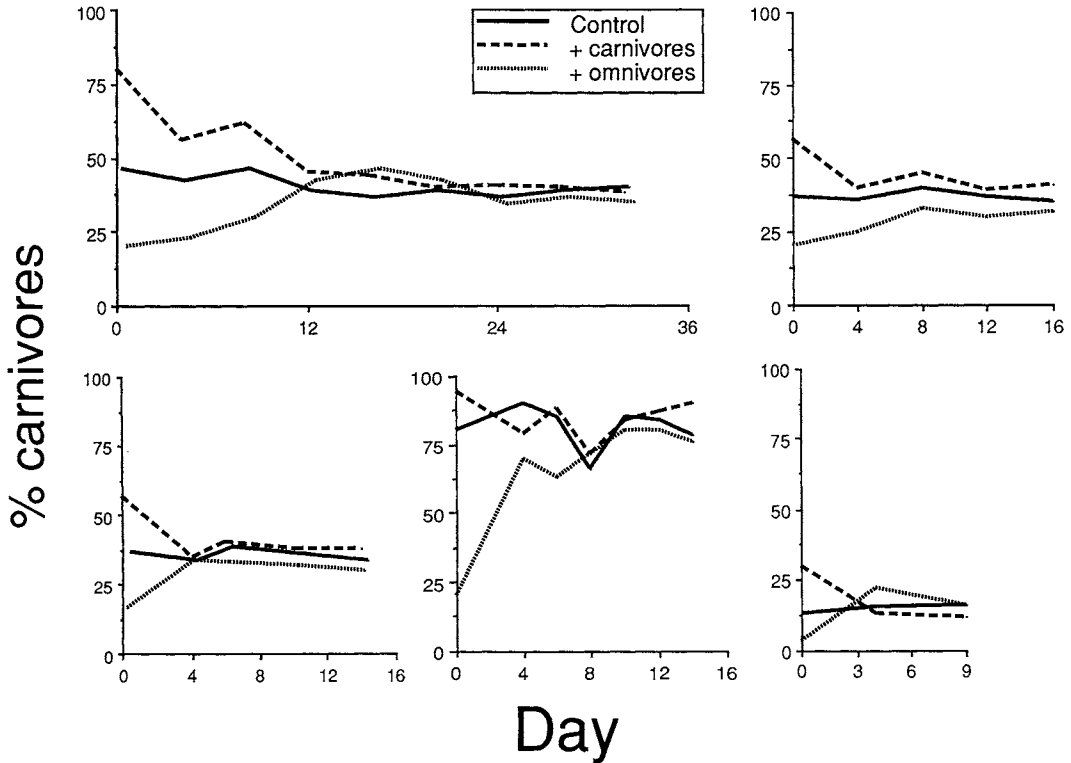


FIG. 5. Morph frequency (% carnivores), as a function of time, for ponds in which morph composition was manipulated differentially in enclosed areas of ponds. Data are mean percent carnivores from two replicates within each pond. For all graphs—solid line: control sections (i.e., sections in which morph frequency was left at the original pond-wide value); dashed line: excess carnivores; dotted line: excess omnivores.

initially present at a frequency below the starting pond-wide morph frequency; Fig. 7). Smaller metamorphs have lower survival as adults (Pfennig et al., 1991b). Food availability significantly affects metamorphic size in *Scaphiopus* (Pfennig et al., 1991b). Thus greater intramorph competition for food in manipulated sections likely created significant size differences; e.g., carnivores compete for shrimp as evidenced by the more rapid decline in shrimp abundance in sections containing higher frequencies of carnivores (Fig. 8). Thus frequency-dependent natural selection stabilized morph frequency in each pond through the fitness effects of differential size at metamorphosis.

DISCUSSION

This study examined two questions regarding the evolutionary maintenance of alternative morphs in *Scaphiopus*. First, do

pond duration and food availability affect morph fitness differentially? Second, does selection maintain polyphenism in *Scaphiopus* as an environmentally determined ESS, with different ponds possessing different

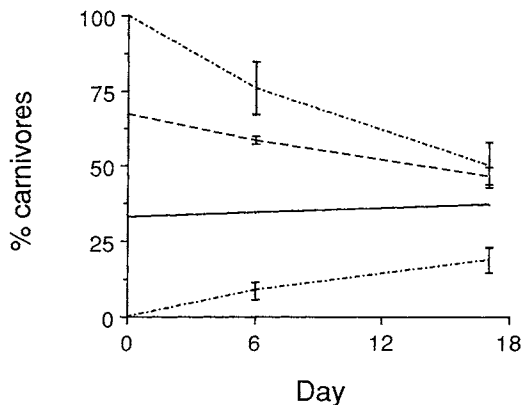


FIG. 6. Mean ± 1 SEM morph frequency as a function of time for 16 wading pools, of which 4 were set at each of four different initial morph frequencies.

TABLE 1. Comparison of initial and final frequency of carnivores in sections of different ponds. Data below are the mean percent carnivores from two sections (e.g., there were two excess carnivore sections in each pond). P was determined using a two-tailed, one-sample t -test where the null hypothesis was that the difference (initial - final carnivore frequency) = 0.

Pond	Section type	Mean % carnivores			P
		Initial	Final (± 1 SD)	Diff ($i - f$)	
17-1987	Excess carnivore	80	38 (6)	42	0.037
17-1988	Excess carnivore	57	40 (1)	17	
25	Excess carnivore	57	41 (2)	16	
19	Excess carnivore	30	13 (2)	17	
4	Excess carnivore	94	90 (3)	4	
	Mean			19.2	
17-1987	Excess omnivore	20	35 (1)	-15	0.049
17-1988	Excess omnivore	18	31 (3)	-13	
25	Excess omnivore	17	33 (1)	-16	
19	Excess omnivore	2	17 (4)	-15	
4	Excess omnivore	20	76 (2)	-56	
	Mean			-23.0	
17-1987	Control	46	40 (1)	6	0.423
17-1988	Control	39	40 (1)	-1	
25	Control	37	34 (2)	3	
19	Control	13	16 (3)	-3	
4	Control	80	78 (3)	2	
	Mean			1.4	

equilibrium morph frequencies? I discuss the evidence bearing on each question in turn and present a game theory model of *Scaphiopus* morph determination.

Pond longevity favors carnivores and omnivores differentially. In rapidly drying ponds, omnivores were poorly developed,

and died soon after metamorphosis; carnivores metamorphosed at a much larger size and survived better (Fig. 4). Given this advantage and the fact that a breeding pond may be short-lived (Fig. 3a), why are all *S. multiplicatus* tadpoles not carnivores? One possibility is that omnivores do better than carnivores if the pond is long-lived (Fig. 4).

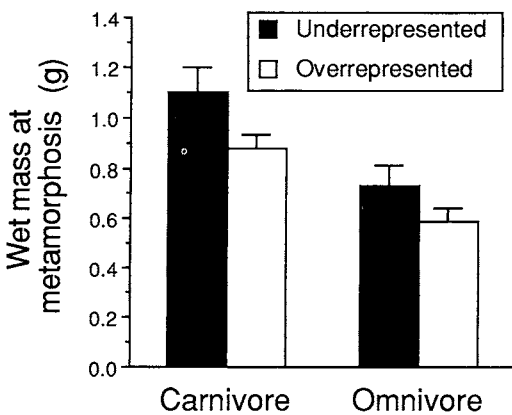


FIG. 7. Comparison of wet mass at metamorphosis of each morph when overrepresented and when underrepresented in different regions of a partitioned pond. Bars are means; vertical lines indicate ± 1 SEM. For both morphs, the differences in size in the two rearing regimes was significantly different ($P < 0.01$, two-tailed t -tests).

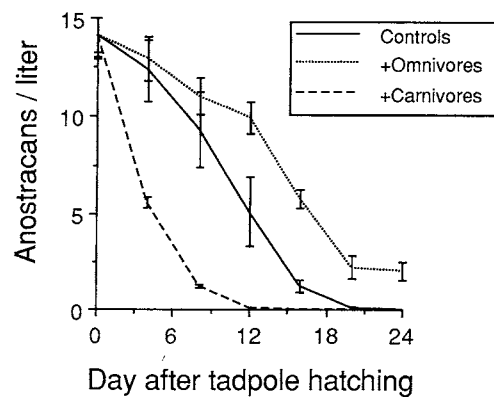


FIG. 8. Fairy shrimp (anostracans) abundance with time in pond 17 when tadpole morph frequencies were manipulated. Percent carnivores in each treatment: +Carnivores = 80% carnivores; +Omnivores = 20% carnivores; Controls = 46% carnivores, the initial pond-wide morph frequency. Values are means; vertical lines indicate ± 1 SEM.

Omnivores from longer-duration ponds had higher survival during the postmetamorphic period presumably because their larger abdominal fat body enhanced juvenile survival. Thus ephemeral pond conditions should favor carnivores, whereas more permanent pond conditions should favor omnivores.

Food availability also affected morph success. Carnivores and omnivores specialize on shrimp and detritus, respectively (Pomeroy, 1981). If either morph becomes food-limited, then the rarer morph should do better because of enhanced competition among individuals of the more common morph. Experimental manipulations of pond-wide morph frequency revealed that morph determination was inversely frequency-dependent (Fig. 5; Table 1). Competition among individuals of the same morph for food likely drove this response as indicated by two lines of evidence. First, individuals that were reared in sections of ponds above the initial overall morph frequency metamorphosed at a smaller size than did individuals of the same morph reared below this frequency (Fig. 7); food availability strongly influences size at metamorphosis (Pfennig et al., 1991*b*). Second, shrimp density declined most rapidly in sections of partitioned ponds containing excess carnivores (Fig. 8). Thus each morph's success depended partly on food availability, which depended in turn on each morph's frequency in the pond.

The pond-partitioning experiment indicated that competition for food maintains both morphs in a frequency-dependent state. Did frequency-dependent *selection* stabilize morph frequency within a pond? Both differential tadpole mortality and morph reversion could produce a frequency-dependent response. The evidence seems to point to the latter, since artificial ponds initially containing all carnivores or all omnivores later contained both morphs (Fig. 6). Frequency-dependent tactic choice may reflect frequency-dependent selection *indirectly*, however. Individuals reared above the original pond wide morph frequency were smaller at metamorphosis than were others of the same morph reared below the original pond wide morph frequency (Fig. 7). This strongly implies that the rarer morph was

favoured by frequency-dependent natural selection, because size at metamorphosis correlates positively with adult fitness (Martof, 1956; Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Pfennig et al., 1991*b*).

Enhanced competition for food apparently caused members of the more common morph to switch to the alternative morphology. In changing morphology, a tadpole may experience a decrement in growth for two nonmutually exclusive reasons. First, a tadpole passes through an intermediate morph that may be a relatively inefficient predator. Second, changing morphology likely consumes energy that otherwise could be spent on growth and development. Thus individuals undergoing reversion should have reduced fitness compared to individuals not required to revert.

Interestingly, the use of shrimp ingestion as an environmental signal to trigger the carnivore morphology is apparently adaptive for at least two reasons. First, carnivores are more efficient shrimp predators than omnivores (Pomeroy, 1981). Second, carnivores have greater survivorship in rapidly drying ponds, and shrimp density correlates negatively with pond longevity (Pfennig, 1990*a*). Thus tadpoles can assess pond longevity indirectly by evaluating shrimp density.

Selection may favor a specific, genetically specified developmental response to food abundance such as "if x shrimp are ingested over time t , then become a carnivore with probability p and an omnivore with probability $1 - p$ " (Fig. 2). The parameter p is apparently intrinsic to the individual and is not simply contingent on the environment (i.e., determined by how many prey are ingested; unpubl. data). This is because each morph's success depends in part on its frequency in the pond, and morph frequency may be difficult for a tadpole to assess.

Heritable variation in the threshold number of shrimp needed to trigger the carnivore morphology might occur across populations that differ significantly in factors affecting morph success. For example, in *S. bombifrons* carnivores are rare in more mesic parts of the animal's range. A reduced tendency to become a carnivore is expected in regions where ponds are long-lived, because such conditions favor omnivores.

Heritable variation in morph determination may even exist within populations of *S. multiplicatus* (Pomeroy, 1981). Such variation occurs in other polyphenic amphibians (e.g., paedomorphic and metamorphic salamanders: Harris et al., 1990; cannibalistic and noncannibalistic tiger salamanders: Pfennig et al., 1991a).

Polyphenic *Scaphiopus* tadpoles apparently assess shrimp density continuously, changing morphology if conditions so dictate (Pfennig, 1992). This is evident from the rapid, intragenerational convergence of morph frequency on a pond-wide, equilibrium value when morph frequency is perturbed (Fig. 5). A developmental rule that brings a population to an equilibrium may be an evolutionarily stable strategy (ESS; Maynard Smith, 1982).

Morph Determination as an ESS

Morph determination in polyphenic *Scaphiopus* maybe an environmentally determined mixed ESS as suggested by three lines of evidence. First, morph determination is *environmentally determined*: tadpoles develop into carnivores only if they ingest shrimp (Pomeroy, 1981; Pfennig, 1990a). Second, polyphenism is a *mixed strategy*: individual tadpoles can change morphology (Pomeroy, 1981; Pfennig, 1992). Third, morph determination is inversely frequency-dependent to a *stable equilibrium* in each pond (Fig. 5). In this section, I present a game theory model of *Scaphiopus* morph determination that summarizes the parameters determining the equilibrium morph frequency within a pond. I then outline some predictions derived from the model and discuss the model's broader implications for understanding the evolutionary maintenance of polyphenism.

I assume that each morph competes more with itself (for food) than with members of the alternative morph, which seems reasonable given the results of the pond partitioning experiment (Fig. 7). What factors determine the equilibrium proportion of carnivores within a pond? Let S be the total energy available in a pond from shrimp, D be the total energy available in a pond from detritus, N be the total number of tadpoles in a pond, α and β be, respectively, the carnivore and omnivore conversion constant

(i.e., the morph-specific fraction of available energy per individual that can be extracted before the pond dries). The population consists of two strategists: the wild-type strategist becomes a carnivore with probability p_p and an omnivore with probability $1 - p_p$. A mutant strategist becomes a carnivore with probability p_m and an omnivore with probability $1 - p_m$. Let η be the proportion of individuals in the population pursuing the mutant strategy, and $1 - \eta$ be the proportion pursuing the wild-type strategy. I assume fitness is inversely frequency-dependent such that the expected fitness of a mutant strategist in a population of wild-type strategists is

$$W_m(p_m, p_p) = p_m \left(\frac{\alpha S}{[\eta p_m + (1 - \eta)p_p]N} \right) + (1 - p_m) \left(\frac{\beta D}{[1 - \eta p_m - (1 - \eta)p_p]N} \right) \quad (1)$$

What is the unique evolutionarily stable value of p_p , which, when adopted by a population, cannot be invaded by a mutant strategist with a different value, p_m ? For p_p to be evolutionarily stable $W(p_p, p_p) > W(p_m, p_p)$ for all $p_m \neq p_p$. If W is a differentiable function, this is satisfied if

$$\left[\frac{\partial W(p_m, p_p)}{\partial p_m} \right]_{p_m=p_p=p^*} = 0 \quad (2)$$

where p^* is the evolutionarily stable probability of becoming a carnivore (Maynard Smith, 1982; p. 197). Solving for p^* in Equation 1 yields

$$p^* = \frac{\alpha S}{\alpha S + \beta D} \quad (3)$$

Thus the equilibrium frequency of carnivores within a pond depends on four parameters: the total energy available in the pond from shrimp (S) and detritus (D), and both the carnivore-specific (α) and omnivore-specific (β) fraction of available energy per individual that can be obtained before the pond dries. Pond ephemerality affects morph fitness through the latter two terms (i.e., $\alpha \gg \beta$, because the carnivore's shrimp

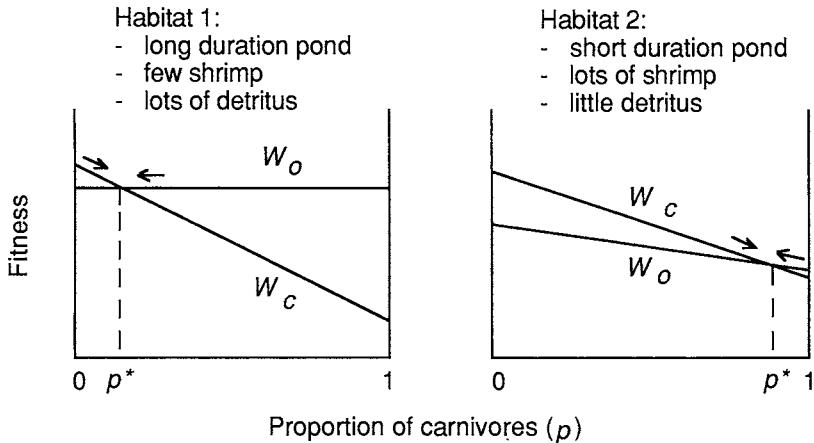


FIG. 9. Graphical representation of the hypothesized link between carnivore frequency (p) and the fitness of carnivores (W_c) and omnivores (W_o) in ponds of different duration. The equilibrium intrapond carnivore frequency (p^*) is where $W_c(p) = W_o(p)$. See text for details.

diet is more nutritious than the omnivore's detritus diet). Note that the equilibrium morph frequency is density-independent; i.e., N factors out.

The graphical results of this model (Fig. 9) reveal how neighboring ponds may possess different equilibrium morph frequencies. In long-duration ponds omnivores are expected to exceed carnivores in fitness for most values of carnivore frequency: long duration ponds contain few shrimp (Pfennig, 1990a) and competition among carnivores for the few shrimp present would be severe. Omnivores are not as food-limited, because pond duration does not affect detritus level. Risk of desiccation should be low for both morphs in long duration ponds. Thus the ESS morph frequency in a long-duration pond should be a low frequency of carnivores. In short-duration ponds, by contrast, carnivores are expected to exceed omnivores in fitness for most values of carnivore frequency, because omnivores should be more likely to desiccate. Unless the pond is highly ephemeral, however, not all tadpoles should become carnivores: release from competition for shrimp should stabilize morph frequency at a low frequency of omnivores. Thus the ESS morph frequency in a short-duration pond would be a high percentage of carnivores. The chief difference between morph fitness in long-duration and short-duration ponds is that in the latter a frequency-independent factor—pond

longevity—attains greater importance in determining omnivore survival.

This model can be applied to other polyphenisms. Trophic polyphenism occurs in caterpillars (Greene, 1989), cichlid fish (Meyer, 1987), and tiger salamander larvae (Collins and Cheek, 1983), among other species. The cues that trigger morph determination in each system are potentially "limiting" to individuals of each morph, and morph determination may be inversely frequency-dependent. The model need not be restricted to trophic polyphenism, however. It can be applied to any polyphenism in which individuals compete with others of the same morph more than with members of the alternative morph. For example, the terms for shrimp and detritus energy level can be replaced by the food content or mate availability in predator-infested and predator-free patches to examine the evolutionary dynamics of predator-induced polyphenism (e.g., see Lively, 1986).

Thus this study indicates how alternative developmental tactics are maintained evolutionarily within a single population. Frequency-dependent selection can favor diversification of a single population into multiple, functionally diverse morphs. If these frequency-dependent alternatives are environmentally determined, the relative proportions of these morphs may be maintained in an evolutionarily stable state that is highly variable depending on local con-

ditions. Such environmentally determined ESSs may be generally important for rapidly stabilizing polyphenism and for achieving highly local adaptation in heterogeneous environments.

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