

Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*

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Summary

Facultative paedomorphosis in salamanders occurs when larvae respond to varying environmental conditions by either metamorphosing into terrestrial metamorphic adults or retaining their larval morphology to become sexually mature paedomorphic adults. Several hypotheses have been proposed for the evolutionary maintenance of this environmentally induced dimorphism, but few data are available to assess them adequately. We studied a montane population of the tiger salamander, *Ambystoma tigrinum nebulosum*, and measured the adult growth rate and body condition across three growing seasons to assess the relative costs and benefits of each morph. Metamorphic adults grew more than paedomorphic adults in terms of snout–vent length across years and in weight within years. Dietary analyses and foraging experiments revealed some of the proximate factors that may underlie these differential growth patterns. Across all prey, metamorphs had significantly higher biomass and calories per stomach sample than paedomorphs. Metamorphic diets primarily consisted of the fairy shrimp *Branchinecta coloradensis*, whereas paedomorphic diets contained a variety of benthic and terrestrial invertebrates. Foraging experiments revealed that both morphs are more successful at capturing fairy shrimp relative to other prey types and both show high electivity toward this prey. However, fairy shrimp occurred only in non-permanent ponds and thus are inaccessible to paedomorphs, which can survive only in permanent ponds. Paedomorphs also experience higher levels of intraspecific competition with large larvae in permanent ponds than metamorphs do in non-permanent ponds. Thus, metamorphs obtain a growth advantage over paedomorphs by foraging in non-permanent ponds that contain fairy shrimp and have reduced intraspecific competition. These results suggest that paedomorphs should have decreased fitness relative to metamorphs, primarily because metamorphs can move into the best habitats for growth. The net fitness effect of morph-specific differences in dispersal depend on whether there are trade-offs with other life history traits. Nonetheless, because the relative benefit of metamorph dispersal will change with environmental conditions in permanent ponds and the surrounding habitat, the relative fitness payoff to each morph should track changes in the environment. Thus, facultative paedomorphosis may be maintained in part by variable, environmentally-specific fitness payoffs to each morph.

Keywords: facultative paedomorphosis; polymorphism; phenotypic plasticity; alternative evolutionary mechanisms; growth rate; dietary analyses; salamanders; *Ambystoma*

Introduction

Organisms often exhibit phenotypic plasticity when confronted with environmental change. Phenotypically plastic traits respond to a variety of selection pressures that are often associated

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with spatial and temporal heterogeneity (Bradshaw, 1965; Levins, 1968; Lloyd, 1984; Lively, 1986a; Schlichting, 1986; West-Eberhard, 1989; Wilbur, 1990; Thompson, 1991; Scheiner, 1993). However, the extent to which plasticity has evolved as an adaptation to environmental heterogeneity, and the evolutionary mechanisms maintaining plasticity in these populations, has only begun to be explored (Schlichting, 1986; West-Eberhard, 1989; Moran, 1992).

Perhaps the most dramatic examples of phenotypic plasticity are environmentally cued polymorphisms. Such polymorphisms are ideal models for studying the evolutionary mechanisms maintaining phenotypic plasticity, because each alternative has discrete fitness consequences and is likely produced as a direct result of selection (Caswell, 1983; Smith-Gill, 1983). Environmentally cued polymorphisms in animals include alternative male morphologies in insects and fish (Eberhard, 1979; Dominey, 1980, 1981; Gross 1982, 1991; Crespi, 1988), wing dimorphisms in insects (Harrison, 1980; Roff, 1986), trophic polymorphisms in amphibians (Collins and Cheek, 1983; Pfennig, 1990, 1992; Pfennig *et al.*, 1991; Collins *et al.*, 1993; Pfennig and Collins, 1993), shell dimorphisms in barnacles (Lively, 1986b,c) and facultative paedomorphosis in salamanders (Collins, 1981; Semlitsch, 1985, 1987; Harris, 1987; Collins *et al.*, 1993; Jackson and Semlitsch, 1993; Whiteman, 1994).

Paedomorphosis, the retention of juvenile characteristics in sexually mature adults (Gould, 1977; Albrech *et al.*, 1979; McKinney and McNamara, 1991) and defined here as reproduction while in a larval or branchiate morphology, appears to have arisen independently across a variety of salamander taxa (e.g. Shaffer, 1984). In some salamander species paedomorphosis is facultative in that the fate of a larva depends on a genotype–environment interaction. In these species, some larvae transform into terrestrial metamorphic adults, while other individuals retain larval characteristics such as gills, remain fully aquatic, and mature as paedomorphic adults (Semlitsch, 1985, 1987; Harris, 1987; Whiteman, 1994). Although experimental and observational studies on a variety of salamander species confirm that selection can act on facultative paedomorphosis (Snyder, 1956; Sprules, 1974a,b; Collins, 1981; Semlitsch and Gibbons, 1985; Harris, 1987; Semlitsch, 1987; Semlitsch and Wilbur, 1989; Harris *et al.*, 1990; Semlitsch *et al.*, 1990), the relative fitness of each morph is poorly documented. Furthermore, although several hypotheses have been proposed for the maintenance of this dimorphism (e.g. Brandon and Bremer, 1966; Wilbur and Collins, 1973; Sprules, 1974a; Werner, 1986; Collins *et al.*, 1993; Whiteman, 1994; Roff, in press), few data exist to test these hypotheses adequately.

One reason that the fitness consequences of facultative paedomorphosis are unknown is the difficulty in obtaining accurate estimates of lifetime reproductive success in any organism (e.g. Clutton-Brock, 1988; Grafen, 1988). However, characters such as body size, which are positively correlated with fitness components such as survivorship and fecundity in amphibians, can be used to estimate fitness differences between individuals (Kaplan and Salthe, 1979; Wilbur, 1980). Growth increases body size, so long-term differences in adult growth rate also reflect fitness differences between individuals. Likewise, changes in body condition (e.g. weight change within a growth season) can also be used as a fitness indicator, because increased body weight is likely correlated with increased survival and future increases in size-specific fecundity.

The purpose of this study is to use between-year growth rate and within-year weight change as fitness estimators for the facultatively paedomorphic tiger salamander, *Ambystoma tigrinum nebulosum*. Although between-year growth rate and within-year weight change are likely to be correlated with one another, and thus do not represent independent tests of the mechanisms maintaining paedomorphosis, they do provide both immediate (weight change) and longer term (growth rate) estimates of fitness. We also present dietary analyses to explore the mechanism by which differences in growth occur. In addition, we test the foraging behaviour of each morph to

understand how differences in foraging ability and prey electivity influence dietary and growth differences between morphs.

Materials and methods

Tiger salamanders (*A. tigrinum*) are found across North America and western subspecies are often facultatively paedomorphic (Behler and King, 1979; Collins, 1981). The subspecies *A. t. nebulosum* occurs in a variety of habitats from western Colorado and Utah to south-central New Mexico and central Arizona (Behler and King, 1979). The population that we studied is within The Nature Conservancy's Mexican Cut Nature Preserve, located at 3640 m within the Elk Mountains of western Colorado. Mexican Cut contains a complex of subalpine ponds that vary in hydroperiod and other abiotic and biotic variables (Wissinger and Whiteman, 1992). This site is ideal for studying salamander life history because there is within-site variation in habitat types, and because it is isolated from other ponds by several kilometres, minimizing the possibility of successful dispersal in or out of the watershed. Because of short growing seasons, low pond temperatures and variation in density-dependent effects, larval development takes from 14 months to 5 years (Sexton and Bizer, 1978; Wissinger and Whiteman, 1992; H.H. Whiteman and S.A. Wissinger, unpublished data). Thus, the salamander populations within these ponds are stage-structured (*sensu* Wilbur, 1984); permanent ponds often contain several age classes of larvae as well as paedomorphic and metamorphic adults, whereas non-permanent ponds contain hatchlings and metamorphic adults. Although the Mexican Cut population is unique in that it is protected for the sole purpose of ecological research, several other similar populations are found within subalpine areas of west-central Colorado; thus, we believe our study is representative of these populations.

Salamanders at Mexican Cut were captured during the summers of 1990–1992 by hand or using dip nets. Paedomorphs were captured in three of the five permanent ponds at Mexican Cut (the other ponds did not contain paedomorphs during this time period) and metamorphs were captured in all pond types. Individuals were identified visually to age class or morph (by size and presence or absence of larval characters such as gills and tailfin) and sex (by the presence (males) or absence (females) of large darkened papillae posterior to the cloaca), measured for snout–vent length (SVL; distance from the snout to the posterior end of the cloaca) and weight, individually marked with toe clips and scored visually for general condition. Repeated mark and recapture censuses over the 3 year period allowed calculation of growth rates.

Growth rate (SVL or weight) was calculated using animals captured at similar times during the 1990 and 1992 field seasons. Only data collected after the breeding season (late July–August) were used to minimize the effects of seasonal size variation and differences due to reproductive condition. Growth was not correlated with initial SVL for either metamorphs or paedomorphs (all $R^2 < 0.05$; all $p > 0.25$), nullifying an assumption of ANCOVA (Sokal and Rohlf, 1981). In addition, the weight of metamorphs was highly variable because of large stomach volumes in some individuals; exclusion of these data leads to prohibitively small sample sizes for between-year comparisons. Thus, we compared the mean change in SVL per year for each morph using a *t*-test.

Within-season weight change was calculated using individuals captured during the beginning (days 1–30) and end (day 45 +) of each field season (1990–1992). Only one morph–year combination showed a significant relationship between weight change within a season and initial SVL (1992 paedomorphs: $R^2 = 0.26$, $p = 0.03$); all other combinations were non-significant (all $R^2 < 0.13$; all $p > 0.20$), nullifying an assumption of ANCOVA (Sokal and Rohlf, 1981). Thus, we compared the mean change in weight for each morph using two-way ANOVA (morph and year

effects). Only males were used in this analysis, because of the high proportion of gravid females during the beginning of each field season and the variation in reproductive condition of females at the end of the season (H.H. Whiteman, unpublished data). Weight change data were square-root transformed before analysis to avoid heteroscedastic variances.

Dietary analyses

We obtained dietary data for each morph during July and August 1990 using a modified gastric-lavage technique (Zerba, 1989). Dietary differences were compared between metamorphs captured in both permanent and non-permanent ponds and paedomorphs in permanent ones. A previous paper contrasted metamorph diets between the two pond types (Whiteman *et al.*, 1994): we combined these data to provide an overall estimate of metamorph diet in this population. Samples were taken during the day, since diel sampling of stomach contents suggested that both morphs foraged primarily during this time (S.A. Wissinger, H.H. Whiteman, W.S. Brown and D. Weigle, in preparation).

Stomach contents were stored in 90% EtOH and later identified to genus based on specimens in quantitative benthos and plankton samples (S.A. Wissinger, W.S. Brown, K. Buhn, J. Jannot, J. McGrady and A. Bohonak, in preparation). Each prey item was measured using a Wild M8 dissecting microscope and biomass was estimated using taxon-specific regressions or taxon- and stage-specific size to biomass conversions. Conversions for each taxon were based on field-collected individuals that were measured, dried for 24 h at 60°C and then weighed to the nearest 0.01 mg on a Cahn C-31 electrobalance. The biomass values obtained from these regressions were then converted to calories using data summarized in Cummins and Wuycheck (1971). The distributions of numbers of prey items, biomass and calories between metamorphs and paedomorphs were non-normal with heteroscedastic variances. Thus, we used Mann-Whitney *U*-tests to compare the diets of the two morphs.

Foraging behaviour

Because both metamorphs and paedomorphs in this population feed in ponds during the summer (Whiteman *et al.*, 1994), we experimentally evaluated the foraging behaviour of each morph in an aquatic environment. Experiments were conducted in foraging chambers, consisting of a plastic box (approximately 49 × 27 × 13 cm) filled with filtered pond water, twigs, rocks and other pond debris. Five prey types were added to each chamber: caddisfly larvae (Limnephilidae and Phryganeidae), midge pupae (Chironomidae), mosquito larvae (Culicidae), adult copepods (Copepoda) and adult fairy shrimp (Anostraca). Both morphs normally encounter four of these prey types; however, fairy shrimp are typically limited to non-permanent ponds and thus are only accessible to metamorphs. Prey densities reflected natural densities and were held constant between experimental trials within days, but were allowed to differ slightly between days to mimic natural changes in prey abundance.

Two salamanders of each morph were captured, measured and starved for 24 h. A haphazardly chosen individual was then placed into a foraging chamber and observed for 30 min following the first attempted prey capture. We measured the frequency and success of attacks on each of the five prey types for each morph, and calculated electivity (Ivlev, 1961) based on capture attempts to reveal prey preference. Ivlev's electivity (*E*) ranges from -1 (complete avoidance) to +1 (complete preference) with 0 representing attempted captures which are dependent only on prey density. After testing, salamanders were released at the site of capture; individuals were used only once. We tested for differences in foraging success between morphs using *t*-tests, but used

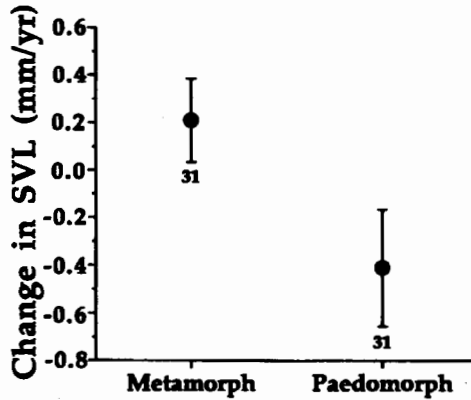


Figure 1. Mean SVL growth rate (± 1 SE) of metamorphic and paedomorphic tiger salamanders between the 1990 and 1992 field seasons ($t = 2.06$, $p = 0.02$, $n = 62$). Sample sizes are presented near each mean.

goodness of fit tests when sample sizes were low or variances did not meet assumptions of normality even after transformation. Mann–Whitney U -tests were used to test for differences in mean electivity because variances did not meet assumptions of normality.

Results

Growth rate

Metamorphs had a significantly greater mean yearly growth rate than paedomorphs (Fig. 1). In fact, paedomorphs exhibited negative growth rates, whereas metamorphs exhibited positive growth. SVL loss appeared to be associated with slight changes in tissue structure and robustness of the body cavity that accompanied weight loss. Initial body size did not differ significantly between morphs (initial SVL, $p > 0.07$). Thus, differences in growth rate were not due to size differences

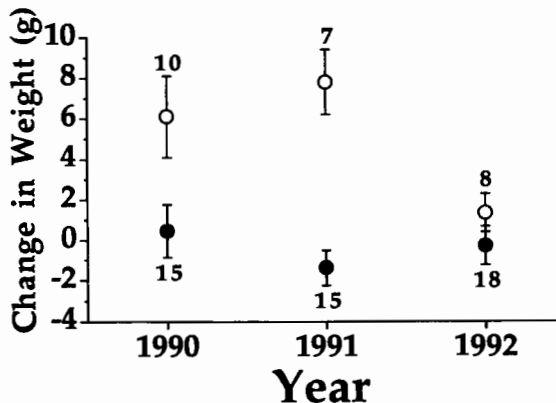


Figure 2. Mean seasonal weight change (± 1 SE) for metamorphic and paedomorphic male tiger salamanders during the 1990–1992 growth years. Filled circles represent paedomorphs and open circles represent metamorphs. See Table 1 for statistical analyses. Sample sizes are presented near each mean.

Table 1. Two-way ANOVA for seasonal weight change between morphs and years

Source	df	Mean square	F	p
Morph	1	14.19	24.68	<0.0001
Year	2	1.06	1.84	0.17
Morph × year	2	1.67	2.90	0.06
Residual	67	0.58		

Analysis was performed on square-root transformed data to stabilize heteroscedastic variances. Assuming a significant interaction, within-season weight change differed significantly between morphs in 1991, but not 1990 or 1992 (Scheffe's *S*, $\alpha = 0.05$).

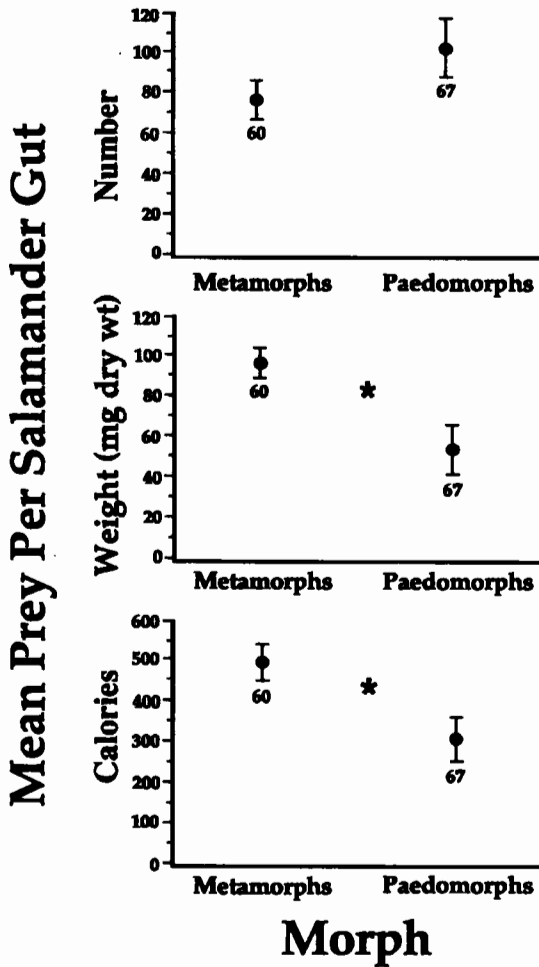


Figure 3. Mean prey per gut in metamorphs and paedomorphs in terms of number, weight, and calories. Number: $U = 1620$, $p = 0.059$; biomass: $U = 1521$, $p = 0.018$; calories: $U = 1564$, $p = 0.031$. Sample sizes are presented near each mean; asterisks represent $p < 0.05$.

between morphs in this sample. Sex-specific differences in SVL growth were not evident within a morph (metamorphs, $t = 0.36$, $p = 0.72$, $n = 31$; paedomorphs, $t = 0.41$, $p = 0.69$, $n = 31$); thus, sexes were combined for analysis.

Within-season weight change

Metamorphic males increased in weight during the summer whereas paedomorphic males either decreased or showed little change in weight (Fig. 2). Differences were more pronounced in 1990 and 1991 than in 1992; thus, there is a morph \times year interaction ($p = 0.06$; Table 1). Initial body size did not differ significantly between morphs, years or the morph \times year interaction (all $p > 0.13$), so these results were not due to size differences between groups.

Diet

Metamorph stomach samples contained significantly greater total biomass and total calories per individual gut relative to that of paedomorphs (Fig. 3). The total number of prey per individual was not significantly different between the two morphs (Fig. 3). Metamorphs and paedomorphs also differed in the prey taxa that comprised their diet. Metamorph stomach contents consisted primarily of fairy shrimp (*Branchinecta coloradensis*, a large zooplankton), in terms of number of prey, biomass and caloric content, while paedomorph gut samples never contained these prey (Fig. 4). Paedomorph guts contained significantly more benthic invertebrates in terms of number, biomass and calories, and significantly more zooplankton (other than fairy shrimp) in terms of number, than metamorph guts did (Fig. 4). Neither dietary analysis (totals per individual or distribution of taxa) was affected by body size differences between morphs (ANOVA; all $p > 0.28$).

Foraging behaviour

Paedomorphs had higher capture success (number of captures/number of attempts) than metamorphs for three out of four prey types (Table 2). Paedomorphs had significantly higher capture success than metamorphs for mosquito larvae, copepods and fairy shrimp, but were only marginally more successful at harvesting midge pupae ($p = 0.08$). Because of few attempted captures, caddisflies were excluded from this analysis. Across prey types, paedomorphs had significantly greater mean capture success than metamorphs (Table 2).

Electivity values were highest for both morphs feeding on fairy shrimp ($E = 0.83$ for metamorphs and 0.71 for paedomorphs; Fig. 5). There were significant differences between morphs in mean electivity for copepods and mosquito larvae, but not for fairy shrimp or midge pupae. Paedomorphs attempted to capture copepods as a function of prey density but actively avoided consumption of mosquito larvae. In contrast, metamorphs avoided copepods and attempted to capture mosquito larvae in proportion to density (Fig. 5).

Discussion

The evolution of facultative paedomorphosis in salamanders has been debated for years (e.g. Duméril, 1870, 1872; Wilbur and Collins, 1973; Werner, 1986; Smith, 1989; Whiteman, 1994), yet few studies have attempted to estimate the relative fitness of each morph. In this study, we addressed the relative costs and benefits of paedomorphosis using between-year growth rate and within-year weight change as fitness estimators.

Growth differences

Metamorphs grew more between years (Fig. 1) and gained more weight within years (Fig. 2, Table 1) than paedomorphs, which actually decreased in length during our study. These differences

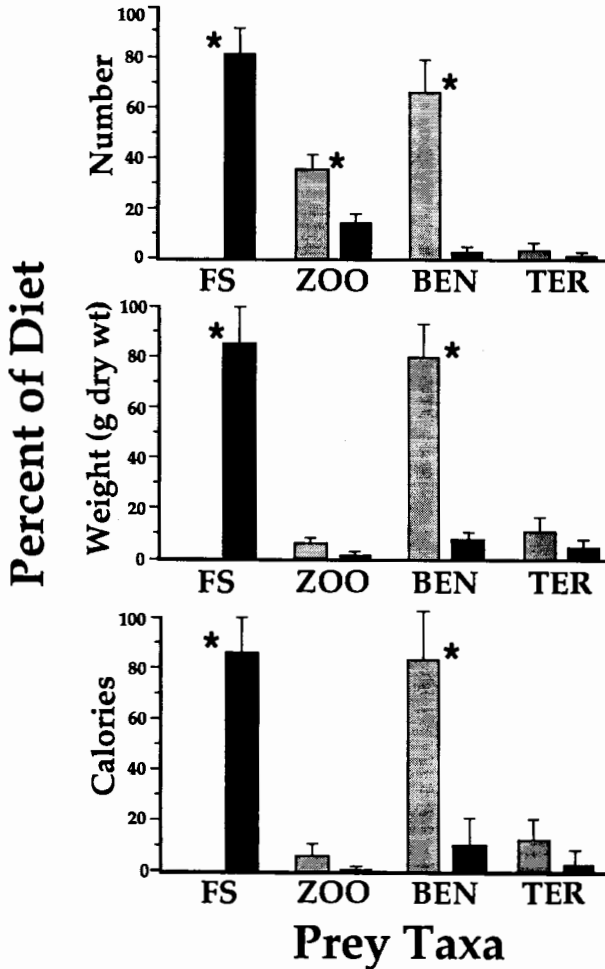


Figure 4. Percent composition of metamorph and pedomorph diets in terms of number, weight and calories ($\bar{x} \pm 1$ SE). FS, fairy shrimp; ZOO, other zooplankton; BEN, benthic invertebrates; TER, terrestrial insects; light bars represent pedomorphs, dark bars signify metamorphs. Comparisons between morphs for each taxonomic grouping were made with Mann-Whitney *U*-tests. Asterisks represent $p < 0.05$.

should lead to a fitness advantage for metamorphs, because body size in amphibians is often positively correlated with survival, fecundity and male mating success (e.g. Kaplan and Salthe, 1979; Wilbur, 1980; Arak, 1983). In this population, larger body size is correlated with increased survivorship and male mating success in both morphs (H.H. Whiteman, J.J. Gutrich and R.S. Moorman, submitted; H.H. Whiteman, submitted).

Proximate mechanisms for growth differences

Several proximate mechanisms appear to underlie differences in the growth rates between morphs in this population. Metamorph stomach samples had increased prey biomass and higher caloric content than pedomorph samples did (Fig. 3); metamorphs feed primarily on fairy shrimp,

Table 2. Capture success of metamorphic and paedomorphic tiger salamanders for four different aquatic prey types

Prey type	Mean % capture ^a		Overall % capture ^b		Test	<i>p</i>	<i>n</i>	
	P	M	P	M			P	M
Mosquito larvae	–	–	76.2(16/21)	50.0(11/22)	$\chi^2 = 5.85$	0.016	14	18
Midge pupae	–	–	69.2(18/26)	42.4(39/92)	$\chi^2 = 3.15$	0.076	14	18
Copepods	69.4 ± 3.5	26.0 ± 3.6	–	–	$t = 9.55$	<0.001	15	14
Fairy shrimp	84.8 ± 3.5	58.9 ± 3.7	–	–	$t = 4.97$	<0.001	11	15
Overall	72.8 ± 2.8	40.6 ± 2.9	–	–	$t = 7.76$	<0.001	14	18

P, paedomorph; M, metamorph.

^a $\bar{x} \pm 1$ SE.

^b When insufficient samples were present for mean comparisons, % capture was calculated across all trials. Numbers in parentheses represent the number of captures/number of attacks.

whereas paedomorphs feed primarily on benthic and terrestrial invertebrates (Fig. 4). Thus, metamorphs that forage in ponds have a dietary advantage over paedomorphs. The foraging experiment revealed that paedomorphs are consistently better than metamorphs at capturing a variety of different prey types. This result was expected because paedomorphs are better adapted for aquatic foraging (Lauder and Shaffer, 1986). Both morphs showed a strong positive electivity for fairy shrimp, and either negative or zero electivity for the other prey types tested. Both morphs also exhibited a high capture success on this species (Table 2). Fairy shrimp have a higher caloric content per individual than all other prey types tested, except caddisflies, which were not a

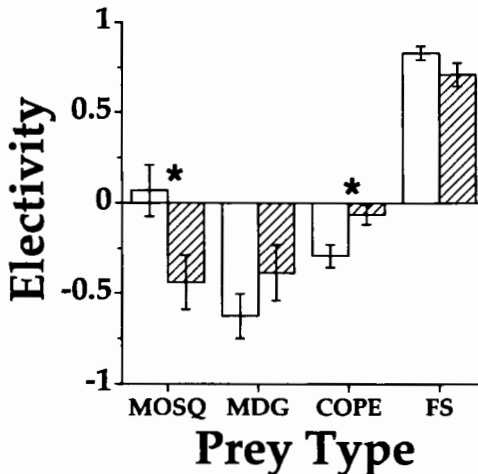


Figure 5. Mean electivity (± 1 SE) of metamorphic and paedomorphic tiger salamanders during the foraging experiment. Prey types include mosquito larvae (MOSQ), midge pupae (MDG), copepods (COPE) and fairy shrimp (FS). Open bars represent metamorphs and hatched bars represent paedomorphs. MOSQ: $U = 65$, $p = 0.021$; MDG: $U = 99$, $p = 0.31$; COPE: $U = 64$, $p = 0.019$; FS: $U = 67$, $p = 0.18$. Sample sizes are in Table 2; asterisks denote significant differences between morphs.

preferred prey (H.S. Mun and H.H. Whiteman, unpublished data). Fairy shrimp are thus extremely energetically profitable, both in terms of capture success and caloric content.

Under natural conditions, paedomorphs do not have the opportunity to capture fairy shrimp because these prey are found only in non-permanent ponds (Dodson, 1970; Sprules, 1972; Whiteman *et al.*, 1994). In contrast, metamorphs that forage in ponds during summer usually congregate in non-permanent ones (Whiteman *et al.*, 1994). Thus, although paedomorphs are more successful at foraging in the aquatic environment than metamorphs, metamorphs are at an advantage because the most profitable prey are only present in non-permanent ponds. Our dietary analyses support this idea: fairy shrimp make up the highest proportion, on average, of the typical metamorph's stomach contents, in terms of number, biomass and caloric content (Fig. 4).

Metamorphic adults in this population can forage in permanent ponds, non-permanent ponds and the terrestrial environment (Whiteman *et al.*, 1994). Metamorphs that enter the terrestrial environment and do not forage in ponds were included in yearly SVL growth estimates, but were not measured for within-season weight change. Although we do not know the extent to which these individuals fed on land, our yearly growth data suggest that even if prey densities in the terrestrial habitat were poor, metamorphs grew faster than paedomorphs. In addition, many metamorphs fed in ponds in some years, but not in others (H.H. Whiteman, unpublished data); thus, the benefits of aquatic foraging are not limited to a subset of the metamorph population.

Metamorphs may also experience weak intraspecific competition in non-permanent ponds because large larvae and paedomorphs are absent. In contrast, large larvae and paedomorphs are present in permanent ponds, often at high densities (Wissinger and Whiteman, 1992; Whiteman *et al.*, 1994). The negative growth exhibited by paedomorphs in this study suggests that competition for food was particularly strong during these years, and the presence of a large larval cohort which has overlapped in diet with paedomorphs since 1990 supports this view (Wissinger and Whiteman, 1992; S.A. Wissinger, H.H. Whiteman and W.S. Brown, unpublished data). Metamorphs that are found in permanent ponds, in contrast, are more likely to be in ones with the lowest densities of conspecific competitors (Whiteman *et al.*, 1994). Thus, growth rate differences between metamorphs and paedomorphs are likely affected by differences in both prey availability and intensity of competition. Under these conditions, metamorphs are at an advantage because they can potentially move to the most productive habitats, whether they are non-permanent ponds with fairy shrimp, permanent ponds with weak intraspecific competition or the terrestrial environment.

Maintenance of facultative paedomorphosis

Our results reveal a potential life history trade-off between the two morphs, the magnitude of which should vary with environmental conditions. Paedomorphs are constrained to permanent ponds and are bound by the environmental conditions (e.g. competitor and prey densities) which they experience there. In contrast, metamorphs have the ability to enter habitats which are optimal for growth, survival and reproduction, and leave those which are suboptimal (i.e. permanent ponds). Metamorphs exhibited increased growth relative to paedomorphs, and growth differences were directly attributable to habitat use of the two morphotypes.

It is unclear whether the dispersal ability of metamorphs is a trade-off with some other fitness component (e.g. decreased survival) as has been suggested in the literature (Brandon and Bremer, 1966; Wilbur and Collins, 1973; Sprules, 1974a; Roff, in press). However, the relative advantage of metamorph movement ability is predicted to change under different environmental conditions (i.e. reduced competition in permanent ponds), with subsequent changes in the relative fitness accrued by each morph. Thus, facultative paedomorphosis might be maintained in part by variation in fitness payoffs under different environmental conditions (see Roff, in press). Further

study of this and similar populations, across a range of environmental conditions, should provide insight into this hypothesis.

These data also suggest that paedomorphosis might be maintained as a secondary strategy when metamorphosis is not reproductively advantageous. For example, assuming that decreased growth in paedomorphic relative to metamorphic adults is representative of the overall fitness differences between morphs, these data are consistent with the 'best of a bad lot' hypothesis for the maintenance of facultative paedomorphosis (Whiteman, 1994). The best of a bad lot hypothesis suggests that permanent ponds which are not conducive to growth (e.g. because of strong competition), lead to decreased fitness for paedomorphs relative to metamorphs, but paedomorphs are maintained because smaller larvae do better by becoming paedomorphic rather than metamorphosing. That is, the fitness benefits of becoming paedomorphic at an early age and small size outweigh the consequences of foregoing another reproductive season to attain larger size and subsequent metamorphosis or metamorphosing at the current small size. A more detailed analysis is necessary to confirm this possibility, by documenting larval growth of individuals becoming each morph and analysing life history traits more directly associated with fitness, such as survivorship, fecundity and age at maturity (Whiteman, 1994).

The data presented here suggest that relative fitness between the morphs can be strongly influenced by environmental conditions, and that facultative paedomorphosis may be maintained in part due to trade-offs which change in magnitude under different environmental conditions. Wing dimorphism in insects is also thought to be maintained through similar trade-offs (Roff and Fairbairn, 1993; Roff, 1994). A complete understanding of relative morph fitness is necessary to adequately assess such trade-offs, yet documenting morph-specific fitness under field conditions remains difficult in both of these polymorphisms (Whiteman, 1994; Roff, in press). Future research on facultative paedomorphosis, wing dimorphism in insects and other environmentally based polymorphisms (e.g. trophic polymorphisms in amphibians; Collins and Cheek, 1983; Pfennig, 1990, 1992; Pfennig and Collins, 1993), should provide further insight into the evolutionary maintenance of polymorphic phenotypes.

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