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ABSTRACT

In some salamander species the retention of larval characteristics in sexually mature adults (paedomorphosis) is an alternative to metamorphosis. In many species paedomorphosis is facultative, thus offering a unique opportunity to test predictions on the evolution of life history variation. Here I expand upon a previous hypothesis ("paedomorph advantage") and present two alternative selection mechanisms ("best of a bad lot" and "dimorphic paedomorph" hypotheses) for the maintenance of facultative paedomorphosis. Each hypothesis makes specific predictions regarding the environmental conditions favoring paedomorphosis, the resulting larval growth patterns, and the fitness consequences to each morph. I evaluate each hypothesis by testing these predictions using published data. No study has conclusively determined the relative fitness of paedomorphs and metamorphs, which limits our understanding of the evolution of this polymorphism. Larval growth patterns suggest, however, that both the paedomorph advantage and the best of a bad lot hypotheses are viable alternatives for the evolutionary maintenance of facultative paedomorphosis in different species. Thus current data on facultative paedomorphosis support the premise that selection can favor the production of an environmentally induced polymorphism through more than one mechanism.

PLASTICITY in phenotypic response often provides a reproductive advantage over a genetically fixed response in organisms that exist in temporally or spatially varying environments. Higher fitness may result because environmentally induced phenotypes have a higher probability of conforming to prevailing environmental conditions than genetically fixed phenotypes. Phenotypic plasticity can be elicited by a variety of selection pressures and can be fundamentally important for evolutionary change; however, the ecological and evolutionary mechanisms that produce and maintain plasticity remain unclear (Schlichting, 1986; West-Eberhard, 1989; Wilbur, 1990; Thompson, 1991; Moran, 1992; Scheiner, 1993).

Phenotypic plasticity occurs when genotype by environment interactions give rise to either continuously or discretely varying phenotypes (Smith-Gill, 1983; Lloyd, 1984; Lively, 1986a; Stearns and Koella, 1986; West-Eberhard, 1989; Stearns, 1992; Scheiner, 1993). Continuous phenotypic plasticity occurs when a trait exhibits a wide distribution of phenotypes in response to different values of some environmental variable. Plants often alter their relative investment in reproduction or survivorship in a continuous manner, based on the type and frequency of selection acting upon them (Lloyd, 1984; Schlichting, 1986). Similarly, snails modify life history traits by investing more heavily

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in growth and survival when predation threat is greater (Crowl and Covich, 1990).

Discrete plasticity, in contrast, occurs when trait variation is limited to two or more alternatives rather than a continuous distribution. The best examples of discrete plasticity are often ones that involve the production of distinct morphs, whether they deal directly with reproduction (Eberhard, 1979; Dominey, 1980, 1981; Harrison, 1980; Gross, 1982, 1991; Roff, 1986; Crespi, 1988) or alternative life histories (Collins, 1981; Collins and Cheek, 1983; Semlitsch, 1985, 1987a; Lively, 1986b,c; Pfennig, 1990, 1992; Pfennig, Loeb, and Collins, 1991; Collins et al., 1993; Pfennig and Collins, 1993; Loeb et al., in press). Such discrete polymorphisms provide an excellent opportunity for understanding the evolutionary processes influencing phenotypic plasticity, because tactics (and their resultant fitness consequences) are easily separated into distinct morphs, and are likely produced as a direct result of selection (Caswell, 1983; Smith-Gill, 1983; see also Scheiner, 1993). By understanding how selection acts on alternative morphotypes, the evolutionary mechanisms maintaining phenotypic plasticity per se can be clarified.

Plasticity in life history strategies is a common theme within the Amphibia, affecting such traits as body size, growth rate, and even metamorphosis (Dent, 1968; Wilbur and Collins, 1973). Many amphibians exhibit obligate metamorphosis, in which individuals always transform from an aquatic larval stage to terrestrial or semiterrestrial adults, regardless of environmental conditions. The propensity to metamorphose, however, varies among and within some species, and with environmental conditions (Wilbur and Collins, 1973; Duellman and Trueb, 1986). Some salamander species exhibit paedomorphosis (Gould, 1977; Alberch et al., 1979; McKinney and McNamara, 1991), defined here as reproduction while in a larval or branchiate morphology, which is either obligate or facultative depending on the species. In obligate paedomorphs, such as the hellbender, *Cryptobranchus alleganiensis*, individuals never metamorphose, but remain within the aquatic habitat for their entire life (Duellman and Trueb, 1986). In contrast, in facultative paedomorphs such as *Notophthalmus viridescens dorsalis*, the broken-striped newt, and *Ambystoma talpoideum*, the mole salamander (Reilly, 1986, 1987; Harris, 1987; Semlitsch, 1987a), individuals either become paedomorphic and remain in the aquatic habitat, or metamorphose and enter the terrestrial environment (Duellman and Trueb, 1986). Individuals of these species are facultative because they can become metamorphs or paedomorphs depending on the ecological conditions experienced as larvae, rather than solely as a result of different genotypes. This environmentally induced dimorphism is one of the most extreme examples of phenotypic plasticity in the Amphibia.

The coexistence of two adult morphs in populations of facultatively paedomorphic species begs several questions, such as why natural selection maintains genes that confer plasticity rather than produce one or the other phenotype, and what ecological factors induce each phenotypic response. Selection should favor genes for plasticity, if environmental conditions are sufficiently spatially or temporally variable, because their bearers will be more likely to survive and reproduce in the prevailing habitat than individuals whose phenotypes are genetically fixed (see Semlitsch et al., 1990). Empirical support of selection for such plasticity, however, is limited. Thus understanding the maintenance of facultative paedomorphosis can provide insight into adaptive phenotypic responses and the evolution of phenotypic plasticity.

Experimental and observational studies on various salamander species have provided support for some of the prerequisites for the origin and maintenance of facultative paedomorphosis by natural selection: Conspecific populations vary in the frequency of paedomorphs in nature (Sprules, 1974a; Collins, 1981); individuals of the same population vary in production of paedomorphs when reared under different conditions (Snyder, 1956; Sprules, 1974b; Harris, 1987; Semlitsch, 1987a); and individuals of different populations vary in the production of paedomorphs when reared under similar conditions (Semlitsch and Gibbons, 1985; Semlitsch and Wilbur, 1989; Harris et al., 1990; Semlitsch et al., 1990). Thus, heritable phenotypic variation can be documented, at least in some species. Differential fitness, however, remains difficult to docu-

ment. For example, neither of the two studies that provide estimates of reproductive success conclusively show a fitness advantage for either morph (Rose and Armentrout, 1976; Semlitsch, 1985).

Here I attempt to clarify the evolution of facultative paedomorphosis and provide insight into the ecological and evolutionary situations in which this dimorphism should be maintained in natural populations. I present three hypotheses for the evolutionary maintenance of facultative paedomorphosis, discuss the unique predictions of each, and present data from the literature to test these predictions. Each hypothesis assumes that plasticity per se should be maintained in variable environments; that is, facultative paedomorphosis provides a selective advantage relative to morph determination based solely on genetic differences among individuals. Thus the three hypotheses address the conditions under which plasticity is maintained and the subsequent fitness consequences to each morph.

Predictions from these hypotheses are discussed in terms of larval growth patterns and adult fitness. Larval growth predictions assume that current body size relative to recent growth rate influences whether larvae metamorphose or become paedomorphic (Wilbur and Collins, 1973). These predictions also assume that larger larval size leads to increased fitness, which has been hypothesized and empirically demonstrated in a variety of amphibians (e.g., Martof, 1956; Turner, 1962; Wilbur and Collins, 1973; Clarke, 1974; Wilbur, 1980; Berven, 1981; Berven and Gill, 1983; D. G. Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Pfennig, Mabry, and Orange, 1991; Goater et al., 1993). Predictions are also made regarding the environmental conditions (both aquatic and terrestrial) that select for paedomorphosis under each hypothesis. Adult fitness predictions do not necessarily assume size-based fitness differences, although this is often the case in amphibians (Kaplan and Salthe, 1979; Wilbur, 1980). Adult fitness predictions assume that lifetime reproductive success (LRS), or some component of LRS, adequately estimates fitness differences between morphs. LRS provides a useful estimate of fitness when the underlying causes of natural variation are known or are being concurrently explored (Grafen, 1988; Reeve and Sherman, 1993).

TABLE 1

Predicted relative fitness differences between paedomorphic, metamorphic and larval strategies for each alternative selection mechanism of facultative paedomorphosis

	Paedomorph fitness relative to:	
Mechanism	Metamorph	Larvae[1]
Paedomorph advantage	higher	higher
Best of a bad lot	lower	higher
Dimorphic paedomorph	higher[2]	higher
	lower[3]	higher

[1] refers to individuals that delay the life history and maturation "decision"

[2] large paedomorphs

[3] small paedomorphs

ALTERNATIVE HYPOTHESES FOR THE MAINTENANCE OF FACULTATIVE PAEDOMORPHOSIS

Paedomorph Advantage Hypothesis

The paedomorph advantage hypothesis predicts that paedomorphs should have higher fitness, on average, than metamorphs (Table 1). This scenario was first envisioned by Wilbur and Collins (1973), who suggested that facultative paedomorphosis can result from both abiotic and biotic selective pressures. They argued that paedomorphosis should evolve when relatively permanent aquatic habitats are surrounded by harsh terrestrial conditions. Metamorphosis would be maintained within the population by selection during the occasional years of unfavorable aquatic conditions. The biotic hypothesis they proposed concentrates on demographic effects, specifically that facultative paedomorphosis depends on the density of the larval and paedomorph population. For example, larvae with an initial growth advantage should remain within the good growing conditions of the aquatic environment and eventually become paedomorphic. Slower growing larvae should metamorphose to escape the density-dependent effects of competition with larger larvae or paedomorphic adults (Fig. 1). Both proximate mechanisms suggested by Wilbur and Collins (1973) predict that paedomorphs should have higher fitness than metamorphs. Paedomorphosis has also been suggested as an advantageous alternative to metamorpho-

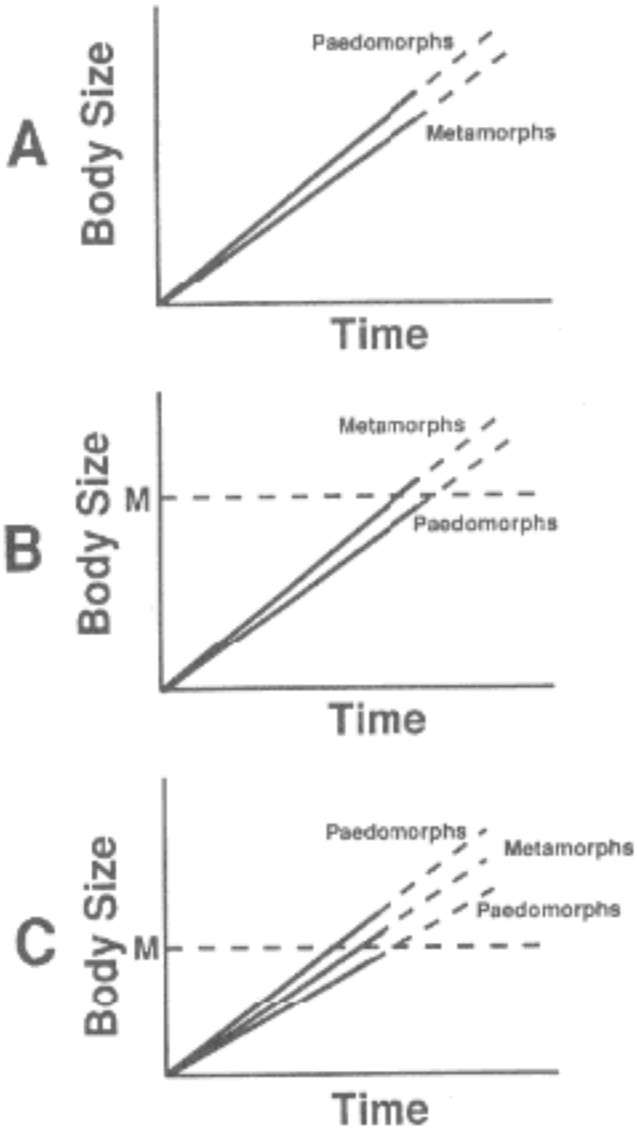

FIG. 1. PREDICTED LARVAL GROWTH PATTERNS FOR THREE ALTERNATIVE EVOLUTIONARY MECHANISMS OF FACULTATIVE PAEDOMORPHOSIS

A: Paedomorph advantage hypothesis, based on Wilbur and Collins's (1973) demographic model. B: Best of a bad lot hypothesis. C: Dimorphic paedomorph hypothesis. *M* represents the minimum body size necessary for metamorphosis, which is a prerequisite for hypotheses B and C. Dashed lines signify reproductive maturity.

sis when aquatic habitats are permanent, but free of competing/predatory fish (Brandon and Bremer, 1966; Sprules, 1974a; Collins et al., 1993).

The paedomorph advantage hypothesis would be supported if, relative to metamorphs, paedomorphs had greater LRS, or some advantage in a fitness component, such as survival, fecundity, age at first reproduction, seasonal breeding success, or growth rate. Further support includes the demonstration that larger larvae are more likely to become paedomorphic, while smaller larvae are more likely to metamorphose (Fig. 2). Paedomorphosis should also be more common under low densities, long growing seasons, high food levels, high temperatures, and low aquatic predation pressure (Table 2). Thus the aquatic environment is more suitable for growth than the terrestrial environment ("harsh" terrestrial conditions; Wilbur and Collins, 1973; Sprules, 1974a). Poor terrestrial conditions include low humidity, lack of cover, and/or high predation pressure.

Best of a Bad Lot Hypothesis

Alternatively, paedomorphosis may have evolved in some species because it provides a way to make the best of a bad lot (Dawkins, 1980; Dominey, 1984; Gross, 1984). Paedomorphic individuals may not have higher LRS than those individuals that metamorphose; rather, they may only have higher LRS than those that delay sexual maturation (Table 1). According to this hypothesis, in unfavorable habitats larvae that reach a minimum critical size for metamorphosis (Wilbur and Collins, 1973) do metamorphose; larvae that do not attain this size but can mature sexually become paedomorphic (Fig. 1B). Larvae that metamorphose should be larger than those that become paedomorphic, and larvae that become paedomorphic should be larger than individuals that remain as larvae and forgo both metamorphosis and maturation (Fig. 2). Paedomorphosis is maintained because the fitness advantages of paedomorphosis at an early age and small size outweigh the consequences of delaying reproduction to attain larger size and subsequent metamorphosis or metamorphosis at a small size. Thus, some individuals are "forced" into paedomorphosis through unfavorable aquatic conditions, because the alternatives confer lower fitness. Although paedomorphs have decreased fitness relative to metamorphs, the fitness benefits they do accrue are sufficient to maintain paedomorphs in the population. Delayed metamorphosis due to resource limitation is common in amphibians (e.g., Semlitsch and Caldwell, 1982; Travis, 1984), suggesting that some facultatively paedomorphic species may have gone one step

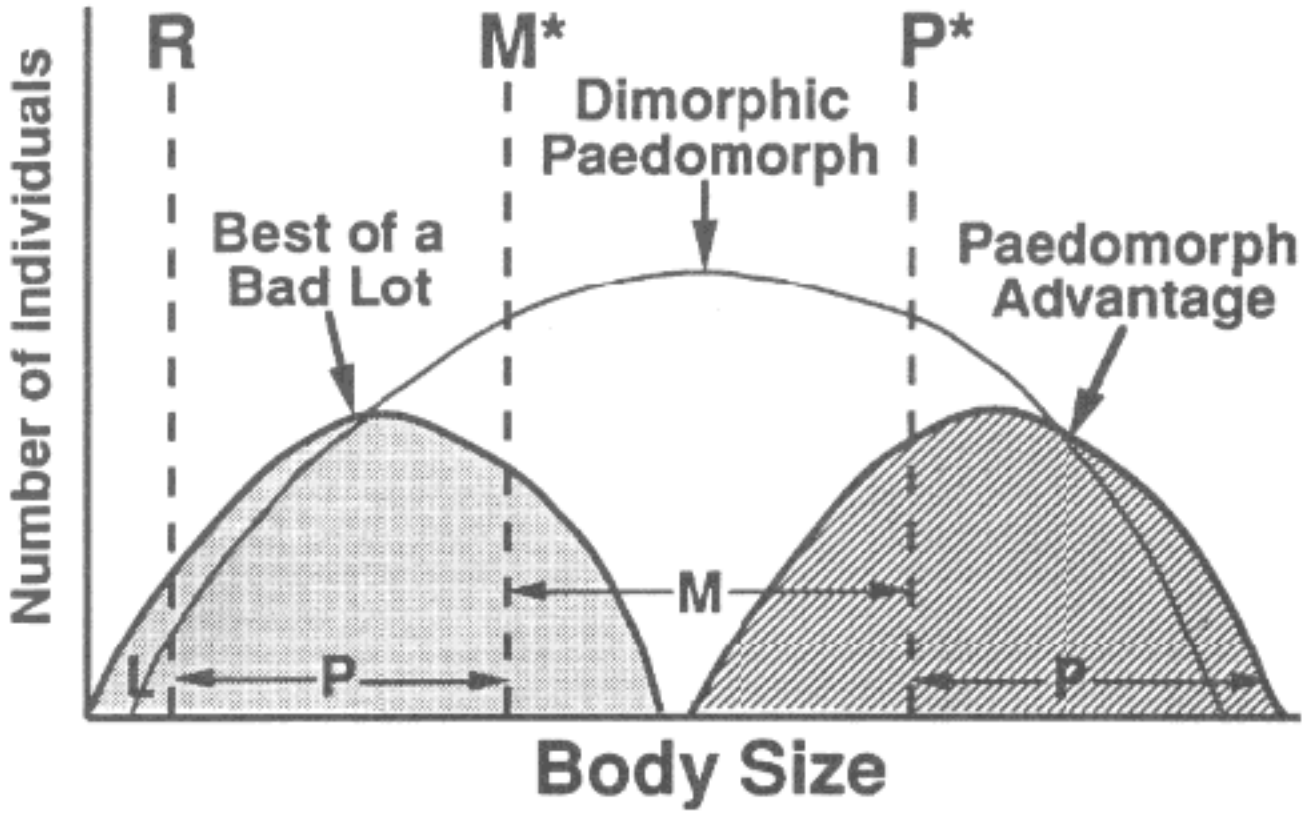

FIG. 2. PREDICTED LARVAL BODY SIZE DISTRIBUTIONS FOR EACH ALTERNATIVE HYPOTHESIS

Distributions are shown normalized, but could take a variety of shapes, including lognormal. R represents the minimum body size necessary for reproductive maturity. Larvae smaller than R remain as larvae (L). M^* represents the minimum body size necessary for metamorphosis. Larvae smaller than M^* but larger than R become paedomorphic (P) through the best of a bad lot mechanism. P^* represents the minimum body size necessary for paedomorphosis through the paedomorph advantage. Larvae larger than P^* become paedomorphic (P) through this mechanism. Larvae smaller than P^* but larger than M^* become metamorphic (M).

TABLE 2

Predicted environmental factors that select for paedomorphosis through each alternative mechanism

		Aquatic parameters					Terrestrial parameters		
Mechanism	Aquatic environment	Temp.	Density	Food	Predation	Growth season	Humidity	Cover	Predation
Paedomorph advantage	favorable[1]	high	low	high	low	long	low	sparse	high
Best of a bad lot	unfavorable[1]	low	high	low	high	short	suitable	suitable	low
Dimorphic paedomorph[2]	variable[1,3]	—	—	—	—	—	—	—	—

[1] relative to the terrestrial environment

[2] this hypothesis does not make predictions regarding the specific aquatic and terrestrial parameters selecting for paedomorphosis; see text

[3] depends on relative size of individual; see text

farther and eliminated metamorphosis under such conditions. Alternatively, in species in which paedomorphs may metamorphose later in life (e.g., *Ambystoma talpoideum*), delayed metamorphosis and maturity can both occur (Semlitsch, 1985).

The predictions of the best of a bad lot hypothesis are opposite to those predicted by the paedomorph advantage hypothesis. The best evidence would be decreased lifetime fitness (or some fitness component) in paedomorphs relative to metamorphs; additionally, paedomorphs should have higher fitness than same-aged individuals that remain as immature larvae through at least one subsequent breeding period. The best of a bad lot hypothesis can also be tested with larval growth data: Smaller larvae should become paedomorphic, while larger larvae should metamorphose (Fig. 2). This mechanism is likely to occur in unfavorable aquatic habitats, such as under high densities, short growing seasons, low food levels, low temperatures, and high aquatic predation pressure (Table 2). Under these conditions, the terrestrial environment is more suitable for growth than the aquatic environment, provided that the terrestrial environment has adequate humidity, cover, and/or few predators.

Dimorphic Paedomorph Hypothesis

Under certain conditions the opposing predictions of the paedomorph advantage and best of a bad lot hypotheses might both be met and produce two types of paedomorphs in the same population. Under the dimorphic paedomorph hypothesis, three size classes of larvae must co-occur. The largest larvae become paedomorphic because they outcompete smaller individuals; medium-sized larvae metamorphose to escape this competition; and the smallest larvae, which cannot reach the minimum size requirement for metamorphosis, also become paedomorphic, rather than delaying maturity (Fig. 1C, Fig. 2). Because the largest paedomorphs are predicted to have the highest fitness relative to same-aged individuals and metamorphs are predicted to have higher fitness than small paedomorphs, this hypothesis predicts similar mean lifetime reproductive success between paedomorphs and metamorphs in a population, depending on the relative abundance of the three modes. Mean fitness might be higher or lower for paedomorphs relative to metamorphs if there are unequal numbers of paedomorphs produced through the paedomorph advantage versus the best of a bad lot. LRS is thus predicted to be bimodal in paedomorphs, and the variance in LRS should be greater in paedomorphs relative to metamorphs (Table 1).

The dimorphic paedomorph hypothesis is best supported by demonstrating that same-aged paedomorphs exhibit a bimodal distribution of LRS. Mean LRS may not differ between metamorphs and paedomorphs, but the variance in fitness should be higher in paedomorphs. In addition, both morphs should have greater fitness than same-aged larvae that forgo the life history decision. This hypothesis could also be tested by following larval growth patterns. Note that the dimorphic paedomorph hypothesis makes no specific predictions about habitat types that produce this dimorphism because an individual's relative size within a common environment should influence the degree to which the habitat is favorable or unfavorable (Table 2). For example, larger larvae that become paedomorphic would experience a favorable habitat, because they can outcompete and possibly prey on smaller individuals. Smaller individuals that either become metamorphic or paedomorphic would experience an unfavorable habitat, in which larger larvae outcompete and prey on them, and same-sized conspecifics compete with them intensely. Therefore, predictions regarding relative growth success in the aquatic versus terrestrial habitat are not explicitly considered in this hypothesis.

All three hypotheses are robust whether paedomorphosis is permanent during an individual's ontogeny or is abandoned later in life. Fitness differences should also reveal the evolutionary consequences of reproduction through early metamorphosis versus delayed metamorphosis. This logic is supported by the observation that individuals of the paedomorphic species that will sometimes metamorphose seemingly do so in response to desiccation of the aquatic environment (*Ambystoma talpoideum*; Semlitsch, 1985; Semlitsch and Gibbons, 1985), rather than as a distinct alternative strategy. If a species is discovered to have an alternative strategy in which paedomorphs commonly metamorphose in permanently aquatic habitats that are still suitable for growth, then these hypotheses would need to be extended.

EMPIRICAL EVIDENCE FOR ALTERNATIVE EVOLUTIONARY MECHANISMS

Differential Fitness

Relative LRS must be assessed for each morph to test the above hypotheses. Few studies, however, have even estimated relative seasonal RS of paedomorphs and metamorphs. Paedomorphic tiger salamander (*Ambystoma tigrinum*) females produce larger clutch sizes than metamorphic females, on average (Rose and Armentrout, 1976). This difference is strongly influenced by the larger overall size of female paedomorphs in this study. The females sampled, however, were of unknown age, and correlations between age and body size are common in amphibians (e.g., Halliday and Verrell, 1988; Francillon-Vieillot et al., 1990; Bastien and Leclair, 1992). Paedomorphic females may have been larger than metamorphic females because they were older. Thus, it is unclear whether the observed reproductive success differences result from differential growth rates, clutch sizes, or survivorship. Assuming no age differences among morphs, these data support the paedomorph advantage hypothesis for this population of *A. tigrinum*.

First-year *Ambystoma talpoideum* metamorphs are longer in snout-vent length (SVL), but lower in body mass, than first-year paedomorphs (Semlitsch, 1985). In addition, first-year metamorphs produce more eggs than first-year paedomorphs, supporting the best of a bad lot hypothesis. Unfortunately, fecundity differences of later age classes of the two morphs are unknown. Because paedomorphs do not have to depend on favorable conditions in the terrestrial environment to migrate to breeding sites, they may compensate for their lower clutch size if they reproduce earlier in the season (Semlitsch, 1985). Offspring produced by early-breeding paedomorphic *A. talpoideum* have larger body sizes than hatchlings produced later in the year by metamorphs (Scott, 1993). Larger larval size could provide advantages in resource competition (Wilbur, 1980), or in escaping size-limited predators (Caldwell et al., 1980).

Age at maturity can strongly influence LRS. For example, paedomorphosis can confer a selective advantage through decreased age at reproduction in the red-spotted newt (*Notophthalmus viridescens viridescens*) when new or recently filled pools are colonized (Healy, 1974). In harsh coastal populations in which the terrestrial eft stage is rare or nonexistent, newts become reproductively mature in two years by remaining aquatic, possibly because recurrent droughts reduce competition by decreasing population density. In inland populations that typically produce terrestrial efts, sexual maturity is delayed for three to seven years. These data support the paedomorph advantage hypothesis, provided that individuals exhibit similar body sizes at first reproduction (Healy, 1974), because decreased age at maturity in paedomorphs would increase their LRS relative to individuals that metamorphose.

Besides differences in fecundity between female morphs, male morphs could also differ in mating success. The paedomorph advantage hypothesis would predict a mating advantage for male paedomorphs, possibly through increased body size (which may lead to greater success in male-male contests); in contrast, the best of a bad lot hypothesis would predict decreased mating success in male paedomorphs, if smaller body size decreases competitive ability. However, no study has thus far determined the relative mating success of male metamorphs and paedomorphs, or even explored the mating systems of facultatively paedomorphic species in general.

In addition to the lack of data on the reproductive success consequences of paedomorphosis, no information is available on the relative survivorship differences between morphs, though increased survival in paedomorphs has been consistently hypothesized throughout the literature (Brandon and Bremer, 1966; Wilbur and Collins, 1973; Sprules, 1974a). Survivorship has a dramatic effect on an organism's LRS, and can often be more important than variation in fecundity when predicting lifetime fitness (Hausfater et al., 1981; Howard, 1983). Thus an understanding of the fitness differences between paedomorphs and metamorphs will not be complete until both reproductive success and survivorship are studied closely.

Colonization and Larval Growth Patterns

Differential growth patterns between larvae that become paedomorphs rather than metamorphs can also be used to test these alterna-

tive hypotheses. For example, paedomorphosis in the newt *Notophthalmus viridescens dorsalis* is negatively correlated with adult density, at least after a drought (P. M. Harris and J. E. Fauth, unpub.). These data support the hypothesis of Healy (1974) that pond desiccation decreases adult density and thus competition, which increases growth rates and leads to a higher frequency of paedomorphosis. These data are consistent with the paedomorph advantage hypothesis, in that paedomorphs are more frequent under lower densities and larvae that become paedomorphic have higher growth rates; thus, paedomorphosis is selectively advantageous during the good growth conditions of pond recolorization.

In controlled density experiments on *Notophthalmus viridescens dorsalis*, low larval density resulted in faster growth and a higher incidence of paedomorphosis; high densities slowed growth rates and led to an increased frequency of metamorphosis (Harris, 1987). P. M. Harris and J. E. Fauth (unpub.) have also shown experimentally that only the fastest growing newt larvae become paedomorphic. Similarly, Semlitsch (1987a) examined the effects of larval density, food level, and pond drying regime on paedomorphosis in *Ambystoma talpoideum*. The frequency of paedomorphosis was greater in constant water-level and low-density ponds than in drying and high-density ponds. Food level had no effect. Although all three variables significantly affected body size (mean SVL) which, in turn, was positively correlated with the frequency of paedomorphosis, the effect of density and drying regime on percent of paedomorphic individuals remained significant after controlling for SVL. These data support the paedomorph advantage hypothesis that paedomorphosis is selectively advantageous in aquatic environments with favorable growth conditions.

Jackson and Semlitsch (1993) studied the effect of a fish predator (the bluegill, *Lepomis macrochirus*) on paedomorphosis in *Ambystoma talpoideum*. Fish had no effect on larval growth rate across treatments, although the proportion of paedomorphs was positively correlated with body size (SVL), and after controlling for SVL, the proportion of paedomorphs was lower in the presence of fish. However, because more individuals remained as larvae within fish treatments, rather than metamorphosing, this result is inconsistent with any of the alternative hypotheses presented here. Salamanders may have delayed maturity to increase larval growth rate, which would in turn reduce mortality from size-specific predation.

Jackson and Semlitsch's (1993) data may support the best of a bad lot hypothesis, because individuals that become paedomorphic may have decreased fitness relative to individuals that metamorphose (and thus decrease their mortality risk through precation), but higher than those that delay maturity for increased growth opportunities (and thus increase their size-specific fecundity). These fitness differences may occur because metamorphs and paedomorphs can both reproduce at one year of age (and metamorphs would be predicted to have increased survivorship to reproduction), but individuals that remain as larvae must wait until age two to reproduce (Semlitsch, 1985; Semlitsch et al., 1988; Jackson and Semlitsch, 1993). It is unclear, however, whether the fitness payoffs to each tactic are actually accrued this way; for example, if larvae that reproduced at age two were much larger than same-aged paedomorphs, then they might overcome any loss in fitness from delayed maturity.

Few other data currently support the best of a bad lot hypothesis, possibly because of the few species/habitat combinations that have been adequately studied. Sprules (1974b) manipulated food level and temperature regime for *Ambystoma gracile*, the northwestern salamander, and found that decreased food level and low temperatures reduced larval growth rates and increased the frequency of paedomorphosis, supporting the best of a bad lot hypothesis. Experiments testing for an interaction between the two variables were not performed, and unfortunately the body sizes of larvae that became paedomorphic versus metamorphic were not measured at similar times. In contrast, Licht (1992) found no effect of food level or growth rate on paedomorphosis in this species and thus no support for any of the current hypotheses.

There is indirect evidence that the best of a bad lot mechanism may be acting on high-elevation populations of *Ambystoma tigrinum*.

Correlations between decreased pond temperature and lower growth rates with paedomorphosis in montane *A. tigrinum* support the idea that larvae that become paedomorphic are smaller than those that metamorphose (Bizer, 1978), and mark-recapture data support this result (H. H. Whiteman, unpub.).

DISCUSSION

Facultative paedomorphosis has been an intriguing ecological and evolutionary phenomenon since it was first recognized (Duméril, 1870, 1872; see Hanken, 1989; H. M. Smith, 1989 for reviews). Although considerable research has focused on the proximate and genetic mechanisms influencing paedomorphosis, few data exist concerning its fitness consequences. Recent studies, however, make several points clear: (1) further study across species and populations is needed to understand the proximate mechanisms affecting paedomorphosis, (2) the paedomorph advantage hypothesis most likely explains the evolution of facultative paedomorphosis in some species and/or populations, and (3) alternative mechanisms may maintain paedomorphosis in other species and populations. The last two results suggest that selection may favor a similar life history strategy for different reasons, depending on the species or population (see Southwood, 1988). This conclusion is supported by evidence that facultative paedomorphosis has evolved independently several times (Shaffer, 1984) and may involve different physiological and developmental pathways in different species and in different populations of the same species (Harris et al., 1990). A similar phenomenon has been documented in sunfish (*Lepomis* sp.), in which polymorphic male mating strategies seem to be maintained through different mechanisms (Dominey, 1980, 1981; Gross, 1982).

Proximate Mechanisms

Current research has concentrated on proximate factors such as pond drying, larval density, and food level. Understanding other environmental variables should clarify which evolutionary mechanisms act on different species/populations; this is especially true for biotic factors such as predation and parasitism, which can result in frequency-dependent selection, influence larval growth patterns, or otherwise affect the fitness of each morph.

Predation can influence paedomorphosis directly and indirectly. Jackson and Semlitsch (1993) found that predation could influence paedomorphosis in *Ambystoma talpoideum* directly, mediated through chemical or visual cues. Because several different age/size classes co-occur in some paedomorphic salamanders (*Ambystoma gracile*: Eaglesor., 1976; *Ambystoma tigrinum*: Sexton and Bizer, 1978; Wissinger and Whiteman, 1992), individuals may be especially subject to direct threat of predation through cannibalism. Cannibalism by paedomorphs has been observed in *A. tigrinum* (Holomuzki and Collins, 1987; Collins et al., 1993; H. H. Whiteman and S. A. Wissinger, unpub.) and indirect evidence suggests the same is true in *A. gracile* (Taylor, 1983).

It is well documented that predatory interactions can affect amphibian competitive interactions (Wilbur, 1972; Morin, 1981, 1983a,b; Wilbur et al., 1983), and thus may influence paedomorphosis indirectly. Predators also influence amphibian populations by affecting activity levels (Figiel and Semlitsch, 1990), spatial patterns (Petranka, 1983; Taylor, 1983; Colley et al., 1989), and microhabitat use (Holomuzki, 1986; Semlitsch, 1987b; Stangel and Semlitsch, 1987; Kats et al., 1988; Sih et al., 1988; Peterson et al., 1992). These effects can indirectly reduce growth rates and/or survival (Semlitsch, 1987b, 1988; Figiel and Semlitsch, 1990), which can also influence paedomorphosis. Thus, there are a variety of ways in which predation can influence paedomorphosis, but only Jackson and Semlitsch (1993) have studied its effect.

Parasites can negatively affect a variety of life history traits, such as growth rate, fecundity, and age at maturity. In addition, changes in host dispersal, foraging strategies, and other behaviors may indirectly influence host life history (Minchella and Scott, 1991). In *Ambystoma tigrinum*, pathogens decrease the length of the larval period required for metamorphosis (Pfennig, Loeb, and Collins, 1991), suggesting that they might also influence paedomorphosis. The presence of pathogens can select against cannibalistic morphs of this species (Pfennig, Loeb, and Collins, 1991), again suggesting similar selection against paedomor-

phosis. The one study that has addressed this question, however, found no effect of pathogens on the frequency of paedomorphs (Collins et al., 1988).

Data are also needed on the relative intensity of parasitism on coexisting paedomorphs and metamorphs. For example, pathogenic bacteria and parasites enter amphibians through ingestion (Hoff and Hoff, 1984; Sprent, 1984), such as through cannibalism (Pfennig, Loeb, and Collins, 1991). Higher frequencies of cannibalism by paedomorphic relative to metamorphic individuals (*Ambystoma tigrinum*; H. H. Whiteman and S. A. Wissinger, unpub.) might increase the frequency of parasite infection in paedomorphs and reduce their fitness. No research, however, has focused on intermorph differences in parasite load or the resulting fitness consequences.

Frequency-Dependent Selection

The effect of frequency-dependent selection on paedomorphosis has not been adequately explored. Fitness may be frequency dependent in other polymorphisms (e.g., Gadgil, 1972; Hamilton, 1979; Gross and Charnov, 1980; Maynard Smith, 1982; Gross, 1991; Pfennig, 1992), and there are several situations in which fitness of paedomorphs and metamorphs would change with morph frequency. For example, paedomorph cannibalism on larvae can exhibit a frequency-dependent effect on metamorph fitness, because when paedomorphs are rare, metamorph offspring would exhibit high survival, but when paedomorphs are abundant, their survival would decrease. Predation (or perhaps parasitism) on adults could also have strong frequency-dependent fitness effects. If one morph is differentially preyed upon or parasitized relative to the other, then the fitness consequences of each will be affected by their relative frequency in the population. For example, when paedomorph prey are abundant, predators might increase their foraging rate on paedomorphs, and metamorphs would have the frequency-dependent advantage through increased survival. When the paedomorph population begins to decrease, the predator may switch to the metamorph population, leading to increased paedomorph fitness.

Similarly, the seasonal mating success of males of each morph might vary inversely with morph frequency. Such a "rare male effect" (Grant et al., 1974; Muggleton, 1979) occurs when females exhibit a negative frequency-dependent mating preference. A "sneaker male" strategy (Gross, 1982, 1991) by the competitively "inferior" morph could also occur. The relative breeding success of the "superior" morph might decrease as its frequency increased, because of increased competition with other superior morphs for mates; the sneaker morph success would subsequently increase, because of increased opportunities to obtain a mating. Conversely, when the superior morph was rare, sneaker morph success would decrease.

Thus there are several possible situations in which frequency-dependent selection can influence morph fitness. Of the possibilities outlined above, cannibalism may be most common, since it has been documented or suggested in paedomorphic populations (Taylor, 1983; Holomuzki and Collins, 1987; Collins et al., 1993; H. H. Whiteman and S. A. Wissinger, unpub.), and both morphs typically breed in the same ponds (Harris, 1987; Semlitsch, 1987a; Wissinger and Whiteman, 1992; Scott, 1993). No research, however, has concentrated on the effect of frequency-dependent selection on facultative paedomorphosis, nor have the potential mechanisms for such selection, such as breeding behavior and predator-prey/parasite-host interactions, been adequately studied.

Alternative Selection Mechanisms: Geographic Variation

The selective forces maintaining facultative paedomorphosis may vary considerably among species and populations. These differences are likely due to variation in the environmental conditions that different populations or species experience. For example, the paedomorph advantage hypothesis has been supported by several studies, which have focused on *Notophthalmus viridescens viridescens* (Healy, 1974), *Notophthalmus viridescens dorsalis* (Harris, 1987; P. M. Harris and J. E. Fauth, unpub.), and *Ambystoma talpoideum* (Semlitsch, 1987a). Other studies on *N. v. dorsalis* and *A. talpoideum* provide further insight into why the paedomorph

advantage hypothesis is the most plausible evolutionary mechanism for these species. Both species are found in similar habitats within the southeastern U. S. and often breed in the same ponds (Semlitsch and Pechmann, 1985). The warm climate provides a long growing season (>7 months; Semlitsch, 1985) and populations often exist in permanent ponds, which might be considered favorable habitats (Table 2) that would favor larger individuals becoming paedomorphic.

In other habitats, with shorter growing seasons (less favorable), the best of a bad lot hypothesis is predicted to be the more likely selection mechanism maintaining paedomorphosis. Such habitats include high-elevation ponds in which growing seasons are short, water temperatures are low, and the food supply may be decreased relative to lower-elevation ponds (see below). Limited evidence from such populations supports this interpretation (Sprules, 1974b; Bizer, 1978; H. H. Whiteman, unpub.).

Facultative paedomorphosis has been extensively studied in *Ambystoma talpoideum* (Semlitsch, 1985, 1987a; Semlitsch and Wilbur, 1988, 1989; Harris et al., 1990; Semlitsch et al., 1990) using both observational and rigorous experimental approaches. Research on a wider variety of species, especially the western populations of facultatively paedomorphic salamanders (*Ambystoma tigrinum, Ambystoma gracile*, and *Dicamptodon ensatus*, the Pacific giant salamander) that live in a variety of habitat types (e.g., high versus low elevation, arid versus humid) is crucial for evaluating the hypothesized alternative mechanisms maintaining facultative paedomorphosis.

Elevational Variation

Larval growth predictions of these hypotheses may help clarify the effect of temperature on the frequency of paedomorphosis in some populations of salamanders. For example, strong evidence for the influence of temperature on paedomorphosis was provided by Sprules (1974b), Bizer (1978), and Sexton and Bizer (1978). As previously described, Sprules (1974b) found significant increases in the frequency of paedomorphosis in *Ambystoma gracile* when temperature was decreased experimentally. By surveying 60 Colorado ponds, Sexton and Bizer (1978) found a negative correlation between thermal ranges of the ponds and the presence of older larvae and paedomorphs in *Ambystoma tigrinum*. Bizer (1978) complemented this study by obtaining field data on the growth rates of larval *A. tigrinum*. The data depict the typical amphibian pattern of decreasing growth rate with decreasing temperature, and led Bizer (1978) to the conclusion that low temperature inhibits metamorphosis through physiological mechanisms. In contrast to these three studies, Collins (1981) surveyed 98 habitats within east-central and southeast Arizona, and found no relationship between elevation and the occurrence of paedomorphic *A. tigrinum*. Because temperature covaries with elevation in this area, temperature could not be linked to paedomorphosis. Collins (1981) revealed that Sexton and Bizer's (1978) temperature pattern also correlates with pond permanence, that is, lower mean temperatures are characteristic of more permanent habitats. He suggested that temperature might influence paedomorphosis, but the causal link remains unclear. Collins's (1981) argument is consistent with the work of Snyder (1956), Eagleson (1976), Rose and Armentrout (1976), Sexton and Bizer (1978), Dzukic et al. (1990), and Allison (1991), all of whom reported paedomorphs of either *A. gracile, A. tigrinum*, the alpine newt *Triturus alpestris*, or the smooth newt *T. vulgaris* at a variety of elevations.

These data are intriguing, because it can be demonstrated that temperature influences paedomorphosis, yet consistent elevation/temperature trends cannot be demonstrated across populations. One explanation for this paradox could be that temperature does significantly affect paedomorphosis in these species, but that its effects occur through different mechanisms under different temperature regimes. For example, in permanently aquatic habitats at lower elevations, high temperatures lead to increased growth rates and increased paedomorphosis through the paedomorph advantage mechanism. In contrast, at higher elevations lower temperatures lead to decreased growth rates and increased paedomorphosis through the best of a bad lot mechanism. Thus, paedomorphosis may not be correlated with elevation or temperature, but the selection mechanism that maintains it is strongly influenced by

temperature. In support of the general predictions of this scenario, lower elevation populations of *Ambystoma tigrinum* often metamorphose or mature as paedomorphs within one year (Collins et al., 1988), while higher elevation populations may take several years to reach this stage (Sexton and Bizer, 1978; Wissinger and Whiteman, 1992). Genetic differences in larval growth traits across elevational and latitudinal gradients (*Rana sylvatica*: Berven, 1982; Berven and Gill, 1983; *A. tigrinum*: Allison, 1991) also provide support for the hypothesis that different selection mechanisms can maintain facultative paedomorphosis in different populations. To test this hypothesis, both fitness consequences of adults and the growth history and fate of larvae in the two habitat types need to be explored. Lower elevation habitats should support the predictions of the paedomorph advantage hypothesis, while higher elevations should support the best of a bad lot.

In addition, because increases in latitude correspond to increases in elevation (Ives and Barry, 1974), a general trend of increased paedomorphosis through the best of a bad lot mechanism with increasing latitude should be apparent when controlling for elevation and species. Paedomorphosis through the paedomorph advantage should decrease with latitude, eventually disappearing altogether when lower elevation populations begin to approximate conditions at lower latitudes and higher elevations. Large-scale latitudinal surveys of *Ambystoma tigrinum, Ambystoma gracile*, and *Dicamptodon ensatus* would provide appropriate tests of this prediction.

Dimorphic Paedomorph Hypothesis

Empirical support for the dimorphic paedomorph hypothesis is lacking, partially because it has not yet been adequately tested in the situations most likely to produce it. For example, the dimorphic paedomorph hypothesis is consistent with the premise that paedomorphosis could evolve through each component mechanism (paedomorph advantage, best of a bad lot) given appropriate environmental conditions. Year-to-year variation in the environment and resultant variance in larval body size could produce a complex situation in which in some years paedomorphs occur because of a paedomorph advantage mechanism and in others because of a best of a bad lot mechanism. For example, in populations in which it takes several years to reach sexual maturity or metamorphosis, several age-size classes of larvae may coexist in the same ponds. This often occurs in high-elevation populations of *Ambystoma tigrinum, Ambystoma gracile*, and *Dicamptodon ensatus*, in which growing seasons are short and larvae require two or more summers of development before either metamorphosing or becoming paedomorphic (Nussbaum and Clothier, 1973; Sprules, 1974a,b; Eagleson, 1976; Sexton and Bizer, 1978; Wissinger and Whiteman, 1992). These size-structured populations, depending on the relative population sizes of each age class, might allow some cohorts of larvae with few competing or predatory conspecifics to become large and thus paedomorphic through the paedomorph advantage mechanism. The age classes that follow this cohort, however, would be affected by the larger cohort's extreme size advantage and thus experience increased competition and possibly predation. These selective pressures might lead to metamorphosis and paedomorphosis through the best of a bad lot. Thus size-structured populations with long larval tenure are ideal study populations for testing these hypotheses.

Facultative Paedomorphosis and Complex Life Cycles

Several models explore the mechanisms by which amphibians metamorphose (or become paedomorphic). Wilbur and Collins (1973) suggested that initiation of metamorphosis is based on an individual's current size relative to its recent growth history as a larva, and thus takes into account the trade-off between future growth in the aquatic versus terrestrial environments. Werner (1986) proposed that the ratio of size-specific mortality rate to size-specific growth rate in both the aquatic and terrestrial phases of the life cycle predicts the optimal size at metamorphosis. Jackson and Semlitsch (1993) suggested that these models are not sufficient to explain facultative paedomorphosis in salamanders, because they fail to take into account reproductive trade-offs, such as size, age, and timing of first reproduction. Jackson and Semlitsch (1993) suggested

that the model developed by Gilliam (1982), which considered size-specific fecundity rate as well as growth and mortality, may be more useful for understanding the ecological factors influencing paedomorphosis in salamanders. These reproductive trade-offs have also been used for understanding environmentally induced polymorphisms in other organisms (e.g., Harrison, 1980; Lively, 1986a,c; Moran, 1992).

The three alternative hypotheses presented here incorporate both growth rate and reproductive trade-offs to predict conditions under which paedomorphosis is adaptive. Larval growth predictions are based on factors directly influencing larval growth; however, they incorporate age and size at first reproduction as important factors influencing paedomorphosis. Likewise, adult fitness predictions inherently include reproductive trade-offs when estimating LRS. These hypotheses should thus provide a clearer framework for understanding the ecological and evolutionary mechanisms maintaining facultative paedomorphosis in natural populations. A more general interpretation of these hypotheses may be useful for predicting amphibian metamorphosis per se, understanding the evolution of complex life cycles, and understanding the maintenance of similar environmentally induced polymorphisms.

CONCLUSIONS

Current data suggest that facultative paedomorphosis is selectively maintained through different mechanisms. These studies are not definitive, however, since fitness differences between the two morphs have not been adequately explored. Although a paedomorph advantage through early maturity has been shown in some newt populations (Healy, 1974), neither of the two studies that provide estimates of reproductive success conclusively show a fitness advantage for paedomorphs (Rose and Armentrout, 1976; Semlitsch, 1985). In addition, no research has estimated the survivorship and seasonal breeding success differences between morphs, which makes estimating the relative LRS between metamorphs and paedomorphs impossible. Data on larval growth patterns, however, support both the paedomorph advantage and the best of a bad lot hypothesis in different species. Thus, at least two of the three mechanisms described here are likely alternative explanations for the maintenance of paedomorphosis in different species. Although research concentrating on fitness consequences in a variety of species and populations is necessary before the selective mechanisms maintaining this polymorphism will be completely understood, these data show that alternative mechanisms are operating in natural populations.

The data presented here suggest that plasticity in one trait or suite of traits can be adaptive for different evolutionary reasons among organisms from the same population, species, or higher taxonomic level. This conclusion offers further support for the premise that phenotypic plasticity is fundamentally important for evolutionary change (Schlichting, 1986; West-Eberhard, 1989; Wilbur, 1990; Thompson, 1991; Scheiner, 1993), and suggests that research on other environmentally induced polymorphisms, such as wing dimorphisms in insects (Harrison, 1980; Roff, 1986), and amphibian trophic polymorphisms (Collins and Cheek, 1983; Pfennig, 1990, 1992; Pfennig, Loeb, and Collins, 1991; Collins et al., 1993; Pfennig and Collins, 1993; Loeb et al., in press) may produce further insight into the mechanisms producing and maintaining plasticity in natural populations.

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