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# Evolution of polyphenism: the role of density and relative body size in morph determination

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## ABSTRACT

**Questions:** Why and how do relative body size and density influence the expression of polyphenism?

**Background:** Facultative paedomorphosis in salamanders is a polyphenism. There are two alternative adult phenotypes: paedomorph (remains in the aquatic environment and matures within the larval form) and metamorph (transforms and matures in the terrestrial environment).

**Mathematical methods:** Evolutionary game model; evolutionary stability and convergence stability analysis justified by population genetics.

**Key assumptions:** The fitness of each morph is determined by density, relative body size, and the frequencies of phenotypes. Individual body size is environmentally determined. Each strategy is given by the probability of becoming paedomorphic as a function of body size.

**Conclusions:** Large animals become paedomorphic when density is low, small animals become paedomorphic when density is high, and the frequency of paedomorphosis is minimized when density is intermediate. These results are consistent with current empirical studies, and make testable predictions for future research on this and other polyphenisms.

*Keywords*: conditional strategy, evolutionary game model, facultative paedomorphosis, phenotypic plasticity, polymorphism, polyphenism.

## INTRODUCTION

Environmentally induced polymorphisms (polyphenisms) occur when discrete phenotypes are differentially expressed as a result of a genotype × environment interaction (West-Eberhard, 1986, 2003; Scheiner, 1993). These polymorphisms are ideal for understanding the evolution of phenotypic variation, because the trait of interest has a direct environmental component, each alternative is easily separated as a distinct morph, and the alternatives are likely produced as a direct result of selection (Caswell, 1983; Smith-Gill, 1983). Understanding the

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maintenance of alternative phenotypes thus provides a model system for clarifying the role of the environment in the evolution of phenotypic variation (West-Eberhard, 1986, 2003).

One common mechanism for the maintenance of polyphenisms is frequency dependence (Gross, 1996; Roff, 1996; West-Eberhard, 2003). Such a situation is readily modelled using evolutionary game theory, which assumes that the fitness of each strategy is dependent on the frequencies of the other strategies (Maynard-Smith, 1982). Indeed, many studies focusing on polymorphisms have assumed that each phenotype is a genetically determined strategy and developed game-theoretical models under this assumption (Gross, 1985; Wakano *et al.*, 2002; Wakano, 2004). However, observational and experimental studies have shown that the phenotype, in many cases, is not solely genetic but is a result of interactions with the environment (Lively, 1986c; Pfennig, 1992; Whiteman, 1994a; for reviews, see Roff, 1996; West-Eberhard, 2003). In this case, the strategy is not the phenotype itself but rather a rule (or algorithm) that selects the optimal phenotype under given environmental conditions, which is called a *conditional strategy* (Gross, 1996).

One feature of such polyphenism is that the fitness of each phenotype is not always equal among individuals (Roff, 1996; West-Eberhard, 2003). The simplest example occurs when the optimal phenotype is solely determined by relative body size. If larger males become fighters and smaller males become sneakers, the co-existence of fighter and sneaker males is expected as long as each male chooses the optimal phenotype even though the fitness of fighter males is always greater than that of sneaker males. A more complex and thus interesting case is when the optimal phenotype depends on both environmental factors (food availability, density, habitat, etc., all of which may impact body size) and the frequency of the phenotype in the population. Such a polyphenism can be studied using evolutionary game theory by considering it as the evolution of the conditional strategy. Here we present such a game-theoretical approach to polyphenism using facultative paedomorphosis in salamanders as a model system.

Although polyphenic phenotypes exist in a wide range of taxa, including shell dimorphism in barnacles (Lively, 1986a, 1986b), wing dimorphism in insects (Roff and Fairbairn, 1991, 1993), and alternative male morphologies in insects and fish (Eberhard, 1979; Gross, 1985, 1991; Emlen, 1997a, 1997b), facultative paedomorphosis in salamanders provides a unique system among vertebrates in which to study the evolution of phenotypic plasticity. Facultative paedomorphosis occurs when individuals either transform into terrestrial, ‘metamorphic adults’ or achieve sexual maturity while remaining within the larval form, termed ‘paedomorphic adults’, depending on the environmental conditions experienced during larval development (Whiteman, 1994a; Denoël *et al.*, 2005). This polyphenism appears to be a response to the individual’s expected success in the aquatic versus terrestrial environment (Wilbur and Collins, 1973; Whiteman, 1994a).

There is considerable support for the hypothesis that the origin and maintenance of facultative paedomorphosis is a result of selection, including between- and within-population variation in paedomorph production in nature (Sprules, 1974a; Collins, 1981; Semlitsch, 1985; Denoël *et al.*, 2001) and under experimental conditions (Snyder, 1956; Sprules, 1974b; Harris, 1987; Semlitsch, 1987a; Ryan and Semlitsch, 2003), evidence for heritable phenotypic variation (Semlitsch and Gibbons, 1985, Semlitsch and Wilbur, 1989; Semlitsch *et al.*, 1990), and results from molecular comparisons and interspecific crosses that are consistent with a genetic basis to paedomorphosis (Shaffer and Voss, 1996; Voss and Shaffer, 1997). A variety of proximate environmental factors have been shown to influence the production of each morph, but only recently have the fitness consequences of paedomorphosis been studied in earnest (for reviews, see Whiteman, 1994a; Denoël *et al.*, 2005).

## PREVIOUS MODELS OF FACULTATIVE PAEDOMORPHOSIS

Previous modelling efforts have provided testable hypotheses for these and other studies of facultative paedomorphosis. Metamorphosis models by Wilbur and Collins (1973) and Werner (1986, 1988) provided the basis for understanding the conditions under which individuals might delay metamorphosis. These models also led to the creation of two alternative hypotheses for the production and maintenance of facultative paedomorphosis, which can be separated by the proximate conditions that produce paedomorphs and the resulting fitness payoffs to each morph (Whiteman, 1994a).

The Paedomorph Advantage (PA) hypothesis suggests that paedomorphic adults have higher fitness than metamorphic adults because of the good growing conditions in the aquatic environment. This hypothesis predicts that large larvae become paedomorphic to take advantage of the good growth conditions; small larvae metamorphose to escape competition with large larvae and paedomorphic adults (Wilbur and Collins, 1973). Note that this hypothesis assumes that the aquatic environment is relatively better for growth than the terrestrial environment.

In contrast, the Best of a Bad Lot (BOBL) hypothesis assumes that paedomorphic adults have lower fitness than metamorphic adults because aquatic habitats are not conducive to growth (e.g. because of strong competition). Under such conditions, larvae large enough to reach a minimum critical size for metamorphosis (Wilbur and Collins, 1973; Wilbur, 1980) metamorphose to escape competition; larvae that cannot reach this size but can mature sexually become paedomorphic. Paedomorphosis is maintained because the fitness benefits of becoming paedomorphic at an early age and small size outweigh the consequences of foregoing another reproductive season to attain large size and subsequent metamorphosis or metamorphosing at the current small size. Thus, some larvae are 'forced' into paedomorphosis through unfavourable aquatic conditions, because the remaining alternatives confer even lower fitness. This hypothesis also predicts that paedomorphosis will be more frequent under unfavourable aquatic conditions.

It is also possible that both mechanisms operate in the same population – the Dimorphic Paedomorph (DP) hypothesis. For example, during years of strong competition it may be best for small individuals to become paedomorphic and large individuals to metamorphose (BOBL), whereas during years of weak competition the largest larvae may maximize fitness if they become paedomorphic, while smaller larvae metamorphose (PA). The DP hypothesis predicts that the size distribution of paedomorphic adults should be 'dimorphic' because they are produced by two different mechanisms.

Previous studies on larval growth and fitness consequences to each morph are consistent with the predictions of the PA and BOBL hypotheses in different species or populations; no published studies have provided evidence that both mechanisms can operate in a single population [DP (Whiteman, 1994a; Denoël *et al.*, 2005; but see H.H. Whiteman *et al.*, unpublished)]. These results suggest that facultative paedomorphosis can be produced and maintained through two disparate mechanisms in different environments, stimulating interest into whether similar polyphenisms might also be produced and maintained through multiple mechanisms (Whiteman, 1994a; Denoël *et al.*, 2005).

All current models of facultative paedomorphosis are heuristic and thus we focused on developing explicitly quantitative models for understanding the production and maintenance of this polyphenism, using the above hypotheses as a framework. Facultative paedomorphosis can be considered as an optimal strategy for utilizing aquatic and terrestrial resources effectively. According to ideal free distribution (IFD) theory, the proportion of individuals in one habitat is determined so that the amount of resource per individual is equal for all habitats. However, previous studies have found that the proportion of animals that become paedomorphic within a cohort increases as the density of that cohort increases, consistent with the BOBL hypothesis (Whiteman, 1994b, unpublished). Since high density primarily increases competition in the aquatic environment more than in the terrestrial environment, this result contradicts IFD theory. Moreover, a clear relationship between relative body size and morph determination has been observed. Larger salamander larvae tend to become paedomorphic in some environments [supporting the PA (Harris, 1987; Semlitsch, 1987a, 1987b)], while smaller animals become paedomorphic in others [BOBL (Whiteman, 1994b, unpublished; Doyle and Whiteman, 2008)]. IFD theory cannot explain these observed relationships within facultative paedomorphosis, perhaps because organisms are not subject to frequency dependence alone, but also must interact with other condition-dependent factors such as density, body size, and other cues (West-Eberhard, 2003).

Thus, we propose a simple mathematical model of facultative paedomorphosis that incorporates density, body size variation, and resource competition in the aquatic environment. Each of these factors is closely related to the production and maintenance of the polyphenism (Whiteman, 1994a; Denoël *et al.*, 2005). We evaluate the evolutionary dynamics of the conditional strategy, and compare the evolutionarily stable frequency of paedomorphs as a function of density and the predicted relationship between body size and morph determination with observational and experimental results from the literature. We also discuss the utility of this model for use in understanding the production and maintenance of other polyphenisms.

## MODEL AND RESULTS

We consider a population that consists of both large and small animals. Individual body size is ecologically determined without any genetic basis. Assume that each animal develops into a large animal with probability $p$ and a small animal with probability $1-p$. Each animal chooses one of two phenotypes: to become paedomorphic or to metamorphose. We allow the choice to be conditional on body size. We consider the conditional strategy $(x, y)$ by which an animal becomes paedomorphic with probability $x/p$ and $y/(1-p)$ when it is large and small, respectively. When all animals adopt the same strategy, the frequencies of large and small paedomorphs in the population are $x$ and $y$, respectively (Fig. 1). As the frequencies of large and small animals are $p$ and $1-p$, the constraints $0 \le x \le p$ and $0 \le y \le 1-p$ must hold.

When larvae choose to remain in the aquatic environment to become paedomorphs, they compete for limited resources with other paedomorphs. In addition, the existence of larger paedomorphs might have considerable effects on the growth, survival or reproductive success of smaller paedomorphs. Let the density of animals be $\rho$ and the amount of resources in the aquatic environment be $\alpha$. Then resource $\alpha$ is shared by $\rho x$ large paedomorphs and $\rho y$ small paedomorphs. Consistent with the PA hypothesis, we assume that large paedomorphs are $k$ times as competitive as small paedomorphs, because of the advantages of large body size on competition. Then, the amount of resource per large paedomorph is given by

$$F_{LP} = \frac{k\alpha}{\rho(kx+y)},$$

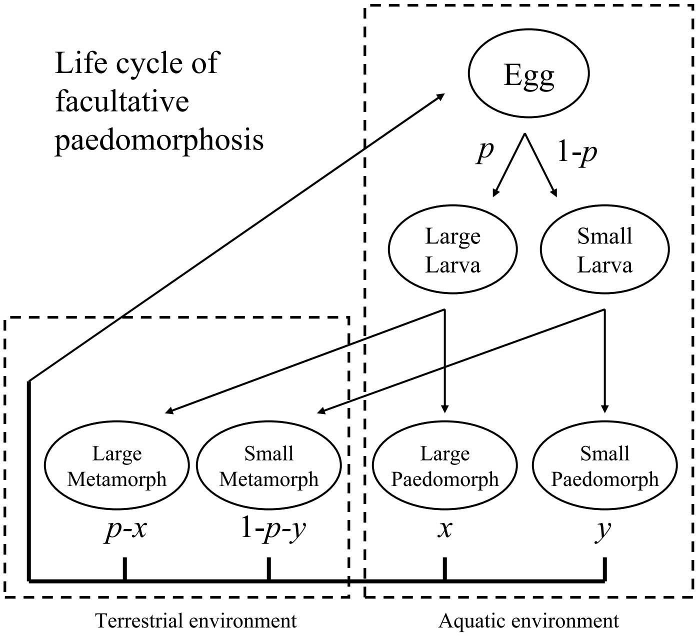

**Fig. 1.** Schematic illustration of the model based on the life cycle of the polyphenism.

which we consider to be the fitness of a large paedomorph. The fitness of a small paedomorph is given by

$$F_{SP} = \frac{\alpha}{\rho(kx + y)}(1 - \gamma\rho x),$$

where $\gamma$ represents the intensity of the interaction with large paedomorphs per large paedomorph. If they interact competitively – that is, if large paedomorphs suppress the growth or reproductive success of small paedomorphs – as might typically be assumed through intraspecific competition or cannibalism, then $\gamma$ is positive. If, in contrast, the existence of large paedomorphs benefits smaller paedomorphs, for example by reducing interspecific competitors, then $\gamma$ is negative.

Compared with the aquatic environment, the terrestrial environment is very large and intraspecific competition might be much weaker; for example, this is the reason why large animals escape from a crowded and unfavourable aquatic habitat under the BOBL hypothesis. To model this situation, the essential assumption is that the density effect is weaker for large animals in the terrestrial environment than in the aquatic environment. To avoid confusion, we consider a simple case in which the fitness of large metamorphs is independent of density. As is also assumed under the BOBL hypothesis, higher densities of larvae and paedomorphs in a pond would result in a smaller larval body size, which might result in failure of metamorphosis (Wilbur and Collins, 1973; Wilbur, 1980). Thus, we assume that the fitness of small metamorphs is decreased if the density is high. Formally, we assume

$$F_{LM} = L$$

$$F_{SM} = S(1 - \rho)$$

where $\rho = 1$ indicates the critical density at which a small animal cannot survive metamorphosis. We only consider cases in which $0 < \rho < 1$.

Strategy, or genotype, $(x, y)$ expresses four phenotypes with the following probabilities: large paedomorph with $x$, large metamorph with $p - x$, small paedomorph with $y$, and small metamorph with $1 - p - y$. As a genotype produces those phenotypes in a single generation, the fitness of this genotype is an arithmetic average denoted by

$$F = xF_{LP} + (p - x)F_{LM} + yF_{SP} + (1 - p - y)F_{SM}.$$

To consider the evolution of $(x, y)$, we compare fitness of a rare mutant with that of the wild-type [i.e. we consider invasion fitness (Geritz *et al.*, 1997)]. In our calculation of fitness of a rare mutant, the fitness of four phenotypes ($F_{LP}$, $F_{LM}$, $F_{SP}$, $F_{SM}$) depends only on the strategy of wild-type animals in the population. Thus these values are constants when we differentiate invasion fitness with respect to a mutant genotype $(x, y)$. We obtain the fitness gradient

$$\frac{\partial}{\partial x}F = F_{LP} - F_{LM},$$

and thus mutants with larger $x$ will invade when $F_{LP} > F_{LM}$. Similarly, mutants with larger $y$ will invade when $F_{SP} > F_{SM}$. Therefore, we can track the evolutionary dynamics of $(x, y)$ by simply comparing the fitness of paedomorphs and metamorphs for each body size. (See Appendix 1 for a more direct and rigorous derivation of this result.)

Large animals receive higher fitness by becoming paedomorphs when

$$F_{LP} > F_{LM} \Leftrightarrow \frac{k\alpha}{\rho(kx + y)} > L,$$

which yields

$$y < -kx + \frac{k\alpha}{L\rho}.$$

For small animals, the condition is denoted by

$$F_{SP} > F_{SM} \Leftrightarrow \frac{\alpha}{\rho(kx + y)}(1 - \gamma\rho x) > S(1 - \rho),$$

which yields

$$y < -(k + \frac{\alpha\gamma}{S(1 - \rho)})x + \frac{\alpha}{S\rho(1 - \rho)}.$$

These inequalities divide a $(x, y)$ plane space into four regions (Fig. 2). Since both isoclines are straight lines, the global behaviour of this system can be easily determined. The system has three equilibria in general: *Ec* (internal equilibrium of co-existence), *Ex* (only $x$), and *Ey* (only $y$). Due to the constraints ($x \le p$ and $y \le 1 - p$), the coordinates of these equilibria sometimes depend on $p$ (see Appendix 2) and *Ex* (*Ey*) is not always on the $x$-axis ($y$-axis). However, the qualitative behaviour of the system can be understood without considering the constraints. In a neutral case where only resource competition occurs ($\gamma = 0$), the two isoclines are parallel and *Ex* (*Ey*) is globally stable if $\rho < 1 - \frac{L}{kS}$ ($\rho > 1 - \frac{L}{kS}$). When

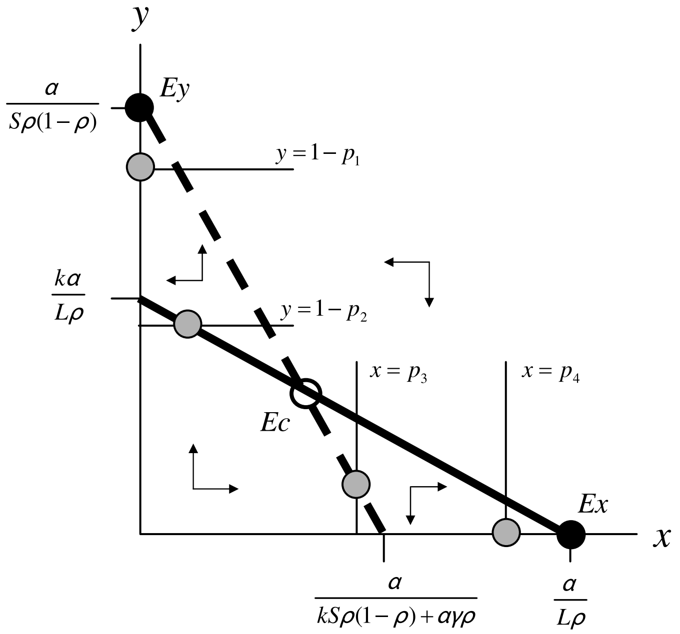

**Fig. 2.** Isoclines of the model and the direction of evolution. Solid and dotted lines are isoclines for large ($x$) and small animals ($y$), respectively. According to the locations and slopes of the isoclines, the system can be monostable or bistable. A bistable case is shown in this figure. $Ex$ and $Ey$ (solid circles) are stable, while $Ec$ (open circle) is unstable. As $x \leq p$ and $y \leq 1 - p$ must hold, sometimes $Ex$ or $Ey$ is impossible. For example, if $p = p_1$ satisfies $\frac{k\alpha}{L\rho} < 1 - p_1 < \frac{\alpha}{S\rho(1-\rho)}$, then $Ey$ is impossible and the grey dot on the line $y = 1 - p_1$ becomes a stable equilibrium instead of $Ey$. If $1 - p$ is even smaller such that $p = p_2$ satisfies $\frac{k\alpha}{L\rho} < 1 - p_2$, then $Ey$ moves to the grey dot on the line $y = 1 - p_2$. All grey dots are stable. For details, see Appendix 2.

interactions among small and large paedomorphs exist ($\gamma \neq 0$), an internal equilibrium $Ec$ may exist. $Ec$ is stable or unstable depending on the relationship between the slopes of the isoclines. It can be shown that $Ec$ is, if it exists, unstable if $\gamma > 0$ and stable if $\gamma < 0$. $Ey$ is stable if $\rho > 1 - \frac{L}{kS}$. This condition is more likely satisfied when $k$ is small or $L/S$ is large. $Ex$ is stable if $\rho < 1 - \frac{L - \alpha\gamma}{kS}$, which is always true when $L \leq \alpha\gamma$, since $\rho < 1$. Given $L > \alpha\gamma$, this condition is more likely satisfied when $k$ is large, $L/S$ is small, or $\alpha\gamma$ is large. When $\gamma > 0$, a region $\rho > 1 - \frac{L}{kS}$ and a region $\rho < 1 - \frac{L - \alpha\gamma}{kS}$ have a common part in which the system is bistable, e.g. whether $Ex$ or $Ey$ is realized depends on their initial frequencies. When $\gamma < 0$, there exists a region $1 - \frac{L - \alpha\gamma}{kS} < \rho < 1 - \frac{L}{kS}$ in which $Ec = (x^*, y^*)$ is stable where

$x^* = \dfrac{L - kS(1-\rho)}{\rho\gamma L}$ and $y^* = \dfrac{k}{\rho\gamma L}(\alpha\gamma + kS(1-\rho) - L)$. The co-existence region or the bistable region is large when $k$ is small, α is large, or $\gamma$ is large in the absolute value.

As a summary of the above analysis, large animals tend to become paedomorphic when densities are low, while small animals tend to become paedomorphic when densities are high. Figure 3 shows numerical examples of the frequency of small and large paedomorphs as a function of density. In a bistable case ($\gamma > 0$; Fig. 3a), either small or large paedomorphs are produced depending on the initial state when density is intermediate $(1 - \dfrac{L}{kS} < \rho < 1 - \dfrac{L - \alpha\gamma}{kS})$. The frequency of large paedomorphs is always a *decreasing* function of density. The frequency of small paedomorphs, in contrast, takes the minimum

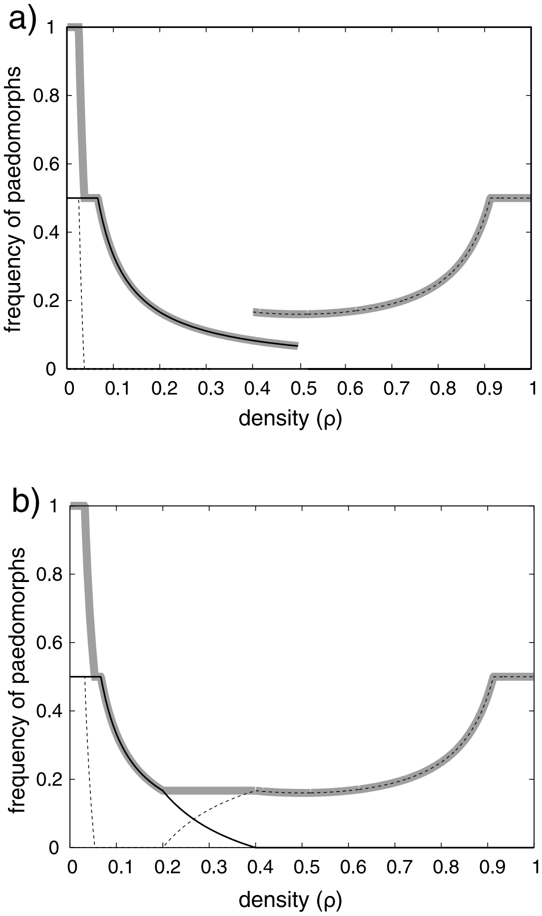

**Fig. 3.** Evolutionarily stable frequency of paedomorphs as a function of density ($\rho$). Solid and dotted curves indicate the evolutionarily stable frequency of large ($x^*$) and small ($y^*$) paedomorphs, respectively. Grey bold curve indicates the total frequency of paedomorphs. Common parameters: $\alpha = 0.04$, $\gamma = 5$, $k = 2$, $L = 1.5$, $S = 1$, and $p = 0.5$. (a) $\gamma = 5$. Only large or small animals become paedomorphs unless density is very low. The system is bistable for an intermediate value of $\rho$. (b) $\gamma = -10$. Large and small paedomorphs co-exist for an intermediate value of $\rho$.

value at $\rho = 0.5$ and *increases* as density increases. Thus, the total frequency of paedomorphs is low at intermediate density and high when density is lower or higher. In a co-existence case ($\gamma < 0$; Fig. 3b), the frequency of paedomorphs shows the same tendency as in a bistable case.

The stable equilibrium in the above analysis represents a convergent stable strategy, which is a different concept from an evolutionarily stable strategy (ESS) (Eshel, 1983; Christiansen, 1991; Britton, 2003). A strategy is convergent stable when evolution will lead the population to reach it, while an ESS occurs such that no mutant can invade the population when it prevails. The internal equilibrium (*Ec*) is not an ESS because the higher derivatives $(\frac{\partial^2 F}{\partial x^2}, \frac{\partial^2 F}{\partial y^2}, \frac{\partial^2 F}{\partial x \partial y}, \ldots)$ are all zero (i.e. neutrally stable). However, the stable equilibrium is an ESS in a finite population because $F_{LP}$ and $F_{SP}$ are decreasing functions of $x$ and $y$, respectively, and increasing or decreasing the probability by which a mutant becomes paedomorphic always results in lower fitness than a wild-type.

## DISCUSSION

We developed an evolutionary game model of facultative paedomorphosis to provide more specific predictions for the production and maintenance of polyphenism than previous models. In this model, the size advantage of large paedomorphs is denoted by $k$ and that of large metamorphs is denoted by $L/S$. We found that the relationship between these variables, salamander density ($\rho$), and the relative effect of large paedomorphs on small paedomorphs ($\gamma$) all play an important role in the evolutionary dynamics of the two morphs.

Although our model makes specific predictions about the conditions producing each morph (see above), our results also provide qualitative descriptions of the relationship between environmental factors and the conditional strategy.

- Small animals tend to become paedomorphs and large animals tend to metamorphose; that is, BOBL occurs when (1) the density is high or (2) the size advantage of metamorphs is larger than that of paedomorphs (i.e. body size is more important to metamorph fitness than to paedomorph fitness).
- Large animals tend to become paedomorphs and small animals tend to metamorphose; that is, PA occurs when (1) the density is low, (2) the size advantage of metamorphs is smaller than that of paedomorphs, (3) the interaction among large and small paedomorphs is competitive and the aquatic environment is favourable, or (4) large paedomorphs have a positive impact on the fitness of small paedomorphs and the aquatic environment is not favourable.
- Both some small animals and some large animals become paedomorphs; that is, DP occurs in the same cohort of salamanders only when the interaction among them is not competitive and the density is at an intermediate level. Such co-existence is more likely when the size advantage of paedomorphs is small, the aquatic environment is favourable, or the positive impact of large paedomorphs on small paedomorphs is large.

Our findings go beyond those of previous models (Whiteman, 1994a), which did not consider the possibility that large paedomorphs might have a positive impact on the fitness of small paedomorphs, given that it is more likely that they exhibit a negative impact via competition and/or cannibalism (Whiteman and Wissinger, 2005). However, it is certainly possible that a positive impact could occur, through indirect community-level effects. For example, large paedomorphs have larger gape widths and thus consume larger prey, potentially including smaller conspecifics. However, they also prey on large invertebrates, including species that may be involved in interspecific competitive interactions with small paedomorphs, such as odonates (Wissinger *et al.*, 1999, unpublished). As long as the potential for cannibalism is low, a reduction of invertebrate competitors could provide a positive impact on the fitness of small paedomorphs (i.e. a negative $\gamma$), thus small individuals would become paedomorphic rather than metamorphose.

One way to lower the potential of cannibalism is to reduce encounter rates through low densities of large paedomorphs or refugia. The effects of large paedomorph densities and the abundance of refugia can be tested directly, both through observation and experimentation. For example, oligotrophic, high-alpine lakes have little vegetation (Wissinger *et al.*, 1999) and thus minimal potential for spatial refuges, while eutrophic wetlands at lower elevations are often packed with aquatic plants (Sharitz and Gibbons, 1982), providing maximal refugia. Because the latter situation should produce negative $\gamma$, we predict that the DP, particularly within a single cohort of larvae, will be much more common in such environments (e.g. in *Ambystoma talpoideum* from Carolina bays in the southeastern USA vs. *A. tigrinum nebulosum* and *Triturus alpestris* from alpine lakes of the Colorado Rocky Mountains and European Alps, respectively). Mesocosm experiments would allow direct testing of both mechanisms, by allowing manipulation of refugia and densities of large and small salamanders as well as competitive invertebrates.

Our model also shows that the frequency of paedomorphs as a function of density is ‘U-shaped’ where PA occurs at low density and BOBL occurs at high density. Although Whiteman’s (1994a, 1994b) models predict both negative (PA) and positive (BOBL) density dependence, the shape of this relationship and the subtle interplay of the two mechanisms at intermediate densities was unknown. This U-shaped distribution is a testable hypothesis since density can be recorded in the field or manipulated in experiments. Several experimental studies have shown that the frequency of paedomorphs decreases with density when larger animals become paedomorphic [i.e. PA (Harris, 1987; Semlitsch, 1987a, 1987b)]. An observational study shows the opposite relationship when larger animals metamorphose [i.e. BOBL (Whiteman, 1994b, unpublished)]. Both of these results are consistent with our model. However, further testing is required to evaluate the precision of the U-shaped density-dependent relationship.

Other researchers have studied the evolution of polyphenism using simple game models. In Lively’s (1986c) model, two morphs and two habitats are assumed where one morph is a generalist while the other morph is specialized to a single habitat. Lively compared a genetically determined polymorphism to a conditional strategy, and found that the conditional strategy can be an ESS if it chooses the right morph for the correct habitat with probability larger than 50%. Moran (1992) performed a more advanced analysis, including consideration of a generalist morph, cost of conditional strategy, and spatial versus temporal variation. She found qualitatively the same result, that polyphenism is favoured when phenotype–environment matching is accurate but revealed that the accuracy threshold depends on the frequency of each environment. Pfennig (1992) also proposed a model with two morphs and two types of resource, with each morph consuming each resource type. One type of resource is limited while the other is constantly supplied.

He showed that a mixed strategy is an ESS under these conditions. Our model can be considered as an extension of these previous works. In addition to some factors proposed by these studies, we incorporated the effect of body size, which is known to play an important role in both morph determination and fitness. The accuracy of choosing a correct morph is not given *a priori* but each animal uses its body size as a cue to determine its morph. We performed convergence stability analysis as well as evolutionary stability analysis. As a result, we found evidence that a conditional strategy can evolve to promote the co-existence of two morphs. Moreover, whether large or small animals become paedomorphic under a given condition can also be predicted by our model.

The results of this model are likely to be generally applicable to other polyphenisms, because of the importance of density/frequency dependence or relative size to the production and maintenance of alternative morphs (Collins and Cheek, 1983; Roff and Fairbairn, 1991; Gross, 1996; Emlen, 1997b; Whiteman *et al.*, 2003). For example, the potential positive impact of large paedomorphs on small paedomorphs might similarly be applied to 'cannibal' morphs, in which larger amphibian larvae consume smaller conspecifics (Crump, 1992; Pfennig and Collins, 1993; Kohmatsu *et al.*, 2001; Wakano *et al.*, 2002; Wakano, 2004). In such systems, cannibals are known to feed on alternative (heterospecific) prey, including large invertebrates (Whiteman *et al.*, 2003), which may release alternative morphs from competitive or predatory interactions. Additionally, the U-shaped density-dependence curve described above is generally applicable to any situation in which one morph can be produced through two divergent mechanisms. Wing polymorphisms in insects (Roff and Fairbairn, 1991) might provide such a case, because of the energetic costs of flight muscles (analogous to metamorphosis) and the trade-offs between fecundity (higher in wingless morphs) and dispersal (Roff and Fairbairn, 1991; Roff, 1994).

We assume that population density ($\rho$) is kept constant during evolutionary time by some population regulation mechanism that is not part of this model. In salamanders, much regulation is known to occur in the larval stages (e.g. Pechmann *et al.*, 1991; Whiteman and Wissinger, 2005), yet there are no data to date showing a relationship between facultative paedomorphosis and population regulation. Thus, our assumption is a reasonable simplification. In addition, we could consider a model where a strategy is conditional not only on body size but also on the other parameters like population density or aquatic resources. Then a strategy is given by a set of functions and the question is: Which function is selected by evolution? The strategy could be a multivariate function that inputs all information (size, density, etc.) as its arguments and returns the probability of metamorphosis. Under this assumption, population density does not need to be constant and the model predicts that PA/BOBL occurs when the density in a focal year is low/high even in a pond where the density varies from year to year. Our current mathematical analysis is not robust enough to consider our result in this way; however, we predict that such an analysis might yield similar results.

To keep the model tractable, we made several simplifications. First, we classified body size into two categories when in fact actual body size distributions are continuous. Second, we did not explicitly model growth dynamics. Thus, the model does not allow the option for a small larva to remain in the pond, delay sexual maturation, and metamorphose during the next reproductive season. These assumptions might be relaxed by explicitly modelling the dynamics of body size distributions through a size-structured model. Hazel *et al.* (1990) modelled the evolution of conditional strategies in which the fitness of alternative phenotypes is determined by a continuous environment. However, body size is determined not only by the environment (in this case, the relative body sizes of others) but also by life-history strategy (i.e. when to metamorphose and/or mature). Furthermore, in facultative paedomorphosis, fitness is dependent on the frequency of alternative morphs as well as body size. Therefore, modelling the dynamics of body size distributions of polyphenisms such as this one will be a challenge for future research.

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## REFERENCES

Britton, N.F. 2003. *Essential Mathematical Biology*. London: Springer.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. *Am. Zool.*, **23**: 35–46.

Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **138**: 37–50.

Collins, J.P. 1981. Distribution, habitats, and life history variation in the tiger salamander, *Ambystoma tigrinum*, in east-central and southeast Arizona. *Copeia*, **1981**: 666–675.

Collins, J.P. and Cheek, J.E. 1983. Effect of food density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum. Am. Zool.*, **23**: 77–84.

Crump, M.L. 1992. Cannibalism in amphibians. In *Cannibalism: Ecology and Evolution among Diverse Taxa* (M.A. Elgar and B.J. Crepsi, eds.), pp. 256–276. Oxford: Oxford University Press.

Denoël, M., Duguet, R., Dzukic, G., Kalezic, M. and Mazzotti, S. 2001. Biogeography and ecology of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *J. Biogeogr.*, **28**: 1271–1280.

Denoël, M., Joly, P. and Whiteman, H.H. 2005. Evolutionary ecology of facultative paedomorphosis in newts and salamanders. *Biol. Rev.*, **80**: 1–9.

Doyle, J.M. and Whiteman, H.H. 2008. Paedomorphosis in *Ambystoma talpoideum*: effects of initial body size variation and density. *Oecologia*, **156**: 87–94.

Eberhard, W.G. 1979. The function of horns in *Podischus agenor* and other beetles. In *Sexual Selection and Reproductive Competition in Insects* (M.S. Blum and N.A. Blum, eds.), pp. 231–258. New York: Academic Press.

Emlen, D.J. 1997a. Alternative reproductive tactics and male dimorphism in the horned beetle *Onthophagus acuminatus*. *Behav. Ecol. Sociobiol.*, **41**: 335–341.

Emlen, D.J. 1997b. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proc. R. Soc. Lond. B*, **264**: 567–574.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.*, **103**: 99–111.

Feldman, M.W. and Cavali-Sforza, L.L. 1984. Cultural and biological evolutionary processes: gene–culture disequilibrium. *Proc. Natl. Acad. Sci. USA*, **81**: 1604–1607.

Geritz, S.A.H., Metz, J.A.J., Kisdi, E. and Meszena, G. 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, **78**: 2024–2027.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature*, **313**: 47–48.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology*, **72**: 1180–1186.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends. Ecol. Evol.*, **11**: 92–98.

Harris, R.N. 1987. Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. *Ecology*, **68**: 705–712.

Hazel, W.N., Smock, R. and Johnson, M.D. 1990. A polygenetic model for the evolution and maintenance of conditional strategies. *Proc. R. Soc. Lond. B*, **242**: 181–187.

Kohmatsu, Y., Nakano, S. and Yamamura, N. 2001. Effects of head shape variation on growth, metamorphosis and survivorship in larval salamanders (*Hynobius retardatus*). *Ecol. Res.*, **16**: 73–83.

Lively, C.M. 1986a. Competition, comparative life histories, and maintenance of shell dimorphism in a barnacle. *Ecology*, **67**: 858–864.

Lively, C.M. 1986b. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution*, **40**: 232–242.

Lively, C.M. 1986c. Canalization versus developmental conversion in a spatially variable environment. *Am. Nat.*, **128**: 561–572.

Maynard-Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Moran, N.A. 1992. The evolutionary maintenance of alternative phenotypes. *Am. Nat.*, **139**: 971–989.

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J. and Gibbons, J.W. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science*, **253**: 892–895.

Pfennig, D.W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. *Evolution*, **46**: 1408–1420.

Pfennig, D.W. and Collins, J.P. 1993. Kinship affects morphogenesis in cannibalistic salamanders. *Nature*, **362**: 836–838.

Roff, D.E. 1994. Evidence that the magnitude of the trade-off in a dichotomous trait is frequency-dependent. *Evolution*, **48**: 1650–1656.

Roff, D.A. 1996. The evolution of threshold traits in animals. *Quart. Rev. Biol.*, **71**: 3–35.

Roff, D.A. and Fairbairn, D.J. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the insects. *Am. Zool.*, **31**: 243–251.

Roff, D.A. and Fairbairn, D.J. 1993. The evolution of alternative morphologies: fitness and wing morphology in male sand crickets. *Evolution*, **47**: 1572–1584.

Ryan, T.J. and Semlitsch, R.D. 2003. Growth and the expression of alternative life cycles in the salamander *Ambystoma talpoideum* (Caudata: Ambystomatidae). *Biol. J. Linn. Soc.*, **80**: 639–646.

Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.*, **24**: 35–68.

Semlitsch, R.D. 1985. Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia*, **65**: 305–313.

Semlitsch, R.D. 1987a. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. *Ecology*, **68**: 1003–1008.

Semlitsch, R.D. 1987b. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. *Ecology*, **68**: 994–1002.

Semlitsch, R.D. and Gibbons, J.W. 1985. Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. *Ecology*, **66**: 1123–1130.

Semlitsch, R.D. and Wilbur, H.M. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution*, **43**: 105–112.

Semlitsch, R.D., Harris, R.N. and Wilbur, H.M. 1990. Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. *Evolution*, **44**: 1604–1613.

Shaffer, H.B. and Voss, S.R. 1996. Phylogenetic and mechanistic analysis of a developmentally integrated character complex: alternate life history modes in ambystomatid salamanders. *Am. Zool.*, **36**: 24–35.

Sharitz, R.R. and Gibbons, J.W. 1982. *The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: A Community Profile*. Washington, DC: U.S Fish and Wildlife Service, Division of Biological Services.

Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. *Am. Zool.*, **23**: 47–55.

Snyder, R.C. 1956. Comparative features of the life histories of *Ambystoma gracile* (Baird) from populations at low and high altitudes. *Copeia*, **1956**: 41–50.

Sprules, W.G. 1974a. The adaptive significance of paedogenesis in the North American species of *Ambystoma* (Amphibia: Caudata): an hypothesis. *Can. J. Zool.*, **52**: 393–400.

Sprules, W.G. 1974b. Environmental factors and the incidence of neoteny in *Ambystoma gracile* (Baird) (Amphibia: Caudata). *Can. J. Zool.*, **52**: 1545–1552.

Voss, S.R. and Shaffer, H.B. 1997. Adaptive evolution via a major gene effect: paedomorphosis in the Mexican axolotl. *Proc. Natl. Acad. Sci. USA*, **94**: 14185–14189.

Wakano, J.Y. 2004. Drastic growth effect may explain sympatric cannibalistic polymorphism. *J. Theor. Biol.*, **226**: 69–77.

Wakano, J.Y., Kohmatsu, Y. and Yamamura, N. 2002. Evolutionary dynamics of frequency-dependent growth strategy in cannibalistic amphibians. *Evol. Ecol. Res.*, **4**: 719–736.

Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Am. Nat.*, **128**: 319–341.

Werner, E.E. 1988. Size, scaling, and the evolution of complex life cycles. In *Size-Structured Populations* (B. Ebenman and L. Persson, eds.), pp. 60–81. Berlin: Springer.

West-Eberhard, M.J. 1986. Alternative adaptations, speciation, and phylogeny (a review). *Proc. Natl. Acad. Sci. USA*, **83**: 1388–1392.

West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press.

Whiteman, H.H. 1994a. Evolution of facultative paedomorphosis in salamanders. *Quart. Rev. Biol.*, **69**: 205–221.

Whiteman, H.H. 1994b. Evolution of alternative life histories in the tiger salmander, *Ambystoma tigrinum nebulosum*. PhD dissertation, Purdue University, West Lafayette, IN.

Whiteman, H.H., Sheen, J.P., Johnson, E., VanDeusen, A., Cargille, R.T. and Sacco, T. 2003. Heterospecific prey and trophic polyphenism in larval tiger salamanders. *Copeia*, **2003**: 56–67.

Whiteman, H.H. and Wissinger, S.A. 2005. Amphibian population cycles and long-term data sets. In *Amphibian Declines: Conservation Status of U.S. Species* (M.L. Lanoo, ed.), pp. 177–184. Berkeley, CA: University of California Press.

Wilbur, H.M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.*, **11**: 67–93.

Wilbur, H.M. and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. *Science*, **182**: 1305–1314.

Wissinger, S.A., Bohonak, A.J., Whiteman, H.H. and Brown, W.S. 1999. Habitat permanence, salamander predation, and invertebrate communities. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (D.P. Batzer, R.B. Rader and S.A. Wissinger, eds.), pp. 757–790. New York : Wiley.

## APPENDIX 1: DIRECT ANALYSIS OF EVOLUTIONARY DYNAMICS

In the text, we argue by invasion fitness. Here we justify our results by studying a model based on population genetics. Let genotypes 1 and 2 co-exist with the frequencies $z$ and $1 - z$, respectively. Assume that genotype 1 develops into a large paedomorph when its body size is large with probability $q_{LP1}$. We introduce $q_{LM1}$, $q_{SP1}$, $q_{SM1}$ in a similar way. Note that $q_{LP1} + q_{LM1} = 1$ and $q_{SP1} + q_{SM1} = 1$ hold. As body size is large with probability $p$, genotype 1 develops four phenotypes (LP, SP, LM, SM) with probabilities ($pq_{LP1}$, $(1-p)q_{SP1}$, $pq_{LM1}$, $(1-p)q_{SM1}$), respectively. A similar assumption holds for genotype 2. Thus the population consists of eight phenogenotypes [genotype–phenotype combinations (Feldman and Cavali-Sforza, 1984)]. The frequency of large paedomorphs with genotype 1 and 2 is $x_1 = zpq_{LP1}$ and $x_2 = (1-z)pq_{LP2}$, respectively. Similarly, the frequency of small paedomorphs with genotype 1 and 2 is $y_1 = z(1-p)q_{SP1}$ and $y_2 = (1-z)(1-p)q_{SP2}$, respectively. The fitness of each genotype is written as

$$F_i = pq_{LPi}F_{LP} + (1-p)q_{SPi}F_{SP} + pq_{LMi}F_{LM} + (1-p)q_{SMi}F_{SM},$$

where $i = 1, 2$ and

$$F_{LP} = \frac{k\alpha}{\rho(kx+y)},\ F_{SP} = \frac{\alpha}{\rho(kx+y)}(1-\gamma\rho x)$$

$$F_{LM} = L,\ F_{SM} = S(1-\rho)$$

$$x = x_1 + x_2 = zpq_{LP1} + (1-z)pq_{LP2}$$

$$y = y_1 + y_2 = z(1-p)q_{SP1} + (1-z)(1-p)q_{SP2}$$

The frequency of genotype 1 in the next generation is written as

$$z' = \frac{zF_1}{zF_1 + (1-z)F_2},$$

where the numerator becomes

$$z[p\{q_{LP1}F_{LP} + (1-q_{LP1})F_{LM}\} + (1-p)\{q_{SP1}F_{SP} + (1-q_{SP1})F_{SM}\}]$$

$$= (F_{LP} - F_{LM})x_1 + (F_{SP} - F_{SM})y_1 + zpF_{LM} + z(1-p)F_{SM}$$

and the denominator yields

$$(F_{LP} - F_{LM})x_1 + (F_{SP} - F_{SM})y_1 + zpF_{LM} + z(1-p)F_{SM}$$

$$+ (F_{LP} - F_{LM})x_2 + (F_{SP} - F_{SM})y_2 + (1-z)pF_{LM} + (1-z)(1-p)F_{SM}$$

$$= (F_{LP} - F_{LM})x + (F_{SP} - F_{SM})y + pF_{LM} + (1-p)F_{SM}$$

and we obtain

$$z' = \frac{(F_{LP} - F_{LM})x_1 + (F_{SP} - F_{SM})y_1 + zpF_{LM} + z(1-p)F_{SM}}{(F_{LP} - F_{LM})x + (F_{SP} - F_{SM})y + pF_{LM} + (1-p)F_{SM}}.$$

Assume two genotypes differ only in $q_{LPi}$, i.e. their strategies are different only when body size is large. Then $y_1 = zy$ is true, and we can assume $q_{LP1} > q_{LP2}$ without loss of generality. Then $z' > z$ holds true if and only if $F_{LP} > F_{LM}$. In biological terms, if the fitness of large paedomorphs (averaged over all animals in the population) is larger than that of large metamorphs, then a genotype that has a greater probability of becoming a paedomorph when its body size is large increases and replaces the other genotype. A similar result holds for the case of small body size. As a consequence of successive replacement of genotypes, the population should evolve towards such a state that $F_{LP} = F_{LM}$ and $F_{SP} = F_{SM}$ hold.

## APPENDIX 2: ANALYSIS OF EQUILIBRIA WITH CONSIDERATION OF CONSTRAINTS

Constraints $x \le p$ and $y \le 1 - p$ must hold because the frequency of large (small) paedomorphs cannot exceed the frequency of large (small) animals. Thus, the coordinates of the equilibria may depend on $p$. As shown in Fig. 2, for example, if $\frac{\alpha}{L\rho} > p$, then $x^* = \frac{\alpha}{L\rho}$ is impossible and $Ex$ moves so that $x^* = p$. If $\frac{\alpha}{kS\rho(1-\rho) + \alpha\gamma\rho} < p < \frac{\alpha}{L\rho}$, then $Ex = (p, 0)$ is realized. If $p$ is even smaller,

$$F_{SP} > F_{SM} \Leftrightarrow \frac{\alpha}{\rho(kp + y)}(1 - \gamma\rho p) > S(1 - \rho),$$

which yields $y^* = \frac{\alpha(1 - \gamma\rho p) - kS(1-\rho)\rho p}{S(1-\rho)\rho}$. Thus, $Ex = (p, y^*)$ is realized. Local stability of $Ex$ does not change (unless $p$ becomes so small to go beyond $Ec$) because the vector field is independent of $p$. Small animals partly become paedomorphic when the frequency of large animals is smaller than the frequency of paedomorphs that would be realized if they were abundant enough. In this model, however, there is a region where all large animals become paedomorphic and all small animals metamorphose. This is because the fitness of small paedomorphs is influenced by both the per capita resource level and suppression by large paedomorphs. Similar logic holds when small animals are not abundant (i.e. $y^* = 1 - p$).

Another constraint we must consider is

$$F_{SP} = \frac{\alpha}{\rho(kx + y)}(1 - \gamma\rho x) > 0 \Leftrightarrow \gamma\rho x < 1,$$

which could be violated if $\gamma$ or $\rho$ is a large positive number. Since the maximum value of $x$ is $p$, we require $\gamma\rho p < 1$. In a numerical example in Fig. 3a, we set $\gamma = 2$ and $p = 0.5$ so that this holds for $\rho < 1$.