Evolution of complex life cycles

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METAMORPHOSIS, AN EVOLUTIONARY DEAD END?

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Abstract

While most animal species undergo metamorphosis, several species have evolved life cycle modifications to avoid complete metamorphosis. Some species, e.g. many salamanders and newts, have deleted the adult stage via a process called paedomorphosis. Others, e.g. some frog species and marine invertebrates, do no longer have a distinct larval stage and reach maturation via direct development. It is not well understood which ecological conditions can lead to the loss of metamorphosis, either via the evolution of paedomorphosis or via the evolution of direct development. Here we show with the use of a size-structured consumer-resource model in conjunction with the adaptive-dynamics approach, that metamorphosis often is an evolutionary dead end which leads to the extinction of a population when the environment deteriorates. Only under limited ecological conditions metamorphosis can disappear via the evolution of paedomorphosis or direct development. When the adult habitat deteriorates, individuals postpone metamorphosis, this will lead to a (partial) paedomorphic population in case the larval habitat is very favorable. Vice versa, in case the larval habitat deteriorates, individuals will produce larger offspring and in concert accelerate metamorphosis, leading to direct development in case the adult habitat is highly favorable. With a phylogenetic approach we furthermore show that among amphibians the evolution of direct development is indeed, as we hypothesize, preceded by the evolution of larger egg sizes.

5.1 Introduction

What do the Puerto Rican tree frog *Eleutherodactylus coqui*, the axolotl (*Ambystoma mexicanum*) and the flat periwinkle (*Littorina obtusata*, a marine sea snail), have in common? They all have lost the ability to metamorphose, something their ancestors still did. Both the tree frog and the sea snail lost metamorphosis via the evolution of direct development, their offspring are born with the adult morphology. The axolotl, on the other hand, retains the larval morphology and lost the adult stage via the evolution of paedomorphosis. In contrast to metamorphosing salamanders, adult axolotls possess gills and remain their whole life aquatic. How did these life-history strategies evolve?

Even though some species have lost the ability to metamorphose, metamorphosis is the dominant life-history strategy in the animal kingdom (Werner 1988). We define metamorphosis here as the morphological change that takes place at the transition from the free-living larval to the juvenile stage. This morphological change allows for the effective exploitation of different niches during an individual's life (Moran 1994). It has been shown before in a theoretical study that metamorphosis is difficult to evolve, but, once evolved it is a very successful strategy that is not lost easily (chapter 4 of this thesis). Since metamorphosing species often depend on multiple niches for their growth and reproduction, they are vulnerable to habitat degradation since a metamorphosing population can already go extinct if only one of the two habitats becomes unsuitable (Rudolf and Lafferty 2011). Metamorphosis is furthermore both a risky and energetically costly process (e.g. Geffen et al. 2007; Wassersug and Sperry 1977). It is therefore likely that under some ecological conditions individuals evolve a life-history strategy without metamorphosis.

The evolution of direct development is one pathway by which metamorphosis can disappear. In direct developing species the adult features form during the embryonic stage and are present at hatching (Callery et al. 2001). Species with direct development lack a free-living larval stage. Direct development evolved at least 10 times in anurans (Hanken 1999) and at least twice in salamanders (in the lungless salamanders, Wake and Hanken 1996). Direct development is also a common life-history strategy among marine invertebrates (e.g. Marshall et al. 2012) and the default strategy among mammals. While there are many studies that describe the morphological and hormonal development of direct developing species (e.g. Callery et al. 2001; Schweiger et al. 2017), from an ecological point of view it is not well understood how and why direct development evolved. It is likely that unfavorable conditions for larvae select for the evolution of direct development. Life-history data of marine invertebrates for example show that aplanktonic species, where individuals are born with the adult morphology, are more common in unproductive environments (Marshall et al. 2012). Empirical

data furthermore show that direct development is associated with the production of larger offspring (e.g. Callery et al. 2001; Marshall et al. 2012; McEdward 2000), but it is unknown if direct development leads to the evolution of larger offspring or the other way around.

Metamorphosis can also be lost via the evolution of paedomorphosis, where individuals retain the larval features during their whole life cycle. Paedomorphosis is common in salamanders (Denöel et al. 2005) but for example absent in frogs (Elinson and del Pino 2012). Paedomorphosis can evolve when individuals change the relative timing of developmental events (heterochrony). When the size at maturation is decreased, while the size at metamorphosis stays the same, individuals mature while keeping the larval morphology (progenesis). Paedomorphosis can also evolve when individuals increase the size at which they metamorphose, such that metamorphosis takes place very late in life after individuals have matured (neoteny) (Bonett et al. 2014*b*). Both progenesis and neoteny can ultimately lead to paedomorphic individuals.

There are several hypotheses regarding the loss of metamorphosis via the evolution of paedomorphosis (Whiteman 1994; Wilbur and Collins 1973). The 'paedomorph advantage hypothesis' states that paedomorphosis evolves under good larval conditions and harsh adult conditions (Whiteman 1994; Wilbur and Collins 1973). Because they occupy different ecological niches in different stages of their development, individuals that optimally use the larval niche, have a higher fitness than individuals that switch to the unfavorable adult niche. It is therefore evolutionary advantageous to skip metamorphosis and always keep the larval morphology. Alternatively, under the 'best of a bad lot' hypothesis paedomorphs originate in case of unfavorable larval conditions. Because larval growth is in this case very slow, individuals never reach the minimum size needed in order to metamorphose (Whiteman 1994). The theoretical models underlying these hypotheses only assume that there is some variation in growth rates among individuals which leads to differences in fitness. They do not include any feedback between the individuals in the population and their environment and are mainly used to explain variation in developmental mode within populations (e.g. Bonett et al. 2014*a*; Whiteman et al. 2012; Wilbur and Collins 1973). Individuals that metamorphose have a different impact on the environment (e.g. food densities) than paedomorphic individuals (e.g. Denöel and Joly 2001), and the success of an individual therefore depends on the strategy of the other individuals in the population. Hence, it is necessary to take this feedback loop between the strategy of individuals and their environment into account when studying the evolution of paedomorphosis.

The aim of this paper is to better understand when paedomorphosis and direct development can evolve in an initially metamorphic population. To do so, we use a fully size-structured consumer resource model where the consumer forages on two types of food. These food sources require different morphologies to be effectively utilized.

While large individuals can feed upon both food sources, small individuals can only feed upon the primary food source, since they are too small to handle the secondary food source. Individuals are born with a morphology specialized in feeding on the primary food source. At a certain size individuals undergo metamorphosis and develop a morphology specialized in feeding on the secondary food source. While metamorphosis allows for the efficient exploitation of the two food sources, we assume that it is an energetically costly process. We will study the evolutionary response of the metamorphosing population in relation to deteriorating food conditions. Since the benefits and costs of metamorphosis depend on the food densities and these densities are in turn affected by the strategy of the consumers, it is important to take into account the feedback loop between the environment and the consumer individuals. We therefore use the framework of adaptive-dynamics (Geritz et al. 1998) to study the evolutionary loss of metamorphosis.

We first study how metamorphosing individuals will respond to changes in the supply rate of the primary food source. We find that there is selection to produce larger offspring when the primary food source becomes less productive. Secondly, we study how changes in the supply rate of the secondary food source affects life-history traits of metamorphosing individuals. We show that diminishing supply rates lead to individuals that postpone metamorphosis. Thirdly, we study under which ecological conditions metamorphosis can disappear through the evolution of direct development or paedomorphosis. In line with the results in chapter 4 of this thesis we find that metamorphosis is hard to loose, even when this leads to the extinction of the population. Paedomorphosis and direct development can only evolve under limited conditions. Finally, we test our predictions regarding the evolution of direct development in amphibians with the use of a phylogenetic comparative framework (Pagel 1994).

5.2 Model and methods

Model

To understand under which ecological conditions metamorphosis can disappear we use an extension of the size-structured consumer-resource model described by Persson et al. (1998). Below we describe the most important aspects of the model, a more detailed model description can be found in appendix 5.A and in chapter 4 of this thesis.

The growth and fecundity of an individual depends on its food intake. We assume that consumers have access to two food sources that each require a different morphology to be effectively utilized by the consumers. The primary food source is available for all consumers while the secondary food source is only available for individuals with a body mass larger than w_{min}. Both the primary and secondary food source follow semi-chemostat dynamics with a turn-over rate of δ and will, in the absence of con-

sumers, reach a maximum density of $X_{1,\text{max}}$ and $X_{2,\text{max}}$, respectively. Metamorphosis decouples the morphologies expressed at different life stages such that an individual can adopt different morphologies before and after metamorphosis. Initially, the consumer has three life stages; larvae (L), juveniles (J) and adults (A). Larvae are born with body mass w_{b} and metamorphose into juveniles at a body mass of w_{J}, juveniles subsequently mature into adults and start reproducing when reaching a body mass of w_{A}. The morphology of an individual is described by the relative degree of specialization ψ_i (i = L, J, or A) on the secondary food source; a value of $\psi_i = 0$ means that individuals are completely specialized in feeding on the primary food source, conversely, a value of $\psi_i = 1$ means that individuals are completely specialized in feeding on the secondary food source.

The morphology of larvae is determined by parameter ψ_{L}. The morphology of postmetamorphs (juveniles and adults) is determined by two traits, the extent of metamorphosis θ and the larval specialization parameter ψ_{L} following

$$\psi_{\text{A}} = \psi_{\text{J}} = \min(1, \psi_{\text{L}} + \theta). \tag{5.1}$$

Note that ψ_{L}, ψ_{J}, and ψ_{A} have values between 0 and 1. Individuals that undergo metamorphosis lose part of their body mass and furthermore have a probability of $\rho\theta$ to die during metamorphosis. We refer to the larval morphology in case a life stage is specialized in feeding on the primary food source ($\psi_i = 0$) and to the adult morphology in case a life stage is (partly) specialized in feeding on the secondary food source ($\psi_i > 0$).

Metamorphosis can disappear in several ways. Paedomorphosis, where all individuals have the larval morphology, can evolve when the degree of metamorphosis θ evolves to a value of 0 or when the body mass at metamorphosis w_{J} evolves to values larger than the body mass at maturation w_{A}. As a consequence, individuals will first mature before they metamorphose or even never reach the size at metamorphosis at all. Direct development, where all individuals adopt the adult morphology, can evolve in case the body mass at birth w_{b} is larger than the body mass at metamorphosis w_{J}, such that metamorphosis takes place before individuals are born. In this case the mothers pay for the costs of the metamorphosis of their offspring (see appendix 5.A).

To study how paedomorphosis and direct development can evolve we study the evolution of four traits; the two traits that determine the morphology of an individual (ψ_{L} and θ), the body mass at metamorphosis w_{J} and the body mass at birth w_{b}. We use the framework of adaptive-dynamics to study the evolution of these four traits (Geritz et al. 1998).

We assume that initially larvae are completely specialized on the primary food source ($\psi_{\text{L}} = 0$) while postmetamorphs are (partly) specialized on the secondary food source ($\theta > 0$), which is the case when the supply rates of both food sources are high

(see chapter 4 of this thesis). To understand which ecological conditions lead to the disappearance of metamorphosis, we track this evolutionary singular strategy (ESS) predicted by the model for decreasing values of the supply rate of either the primary ($\delta X_{1,\mathrm{max}}$) or the secondary ($\delta X_{2,\mathrm{max}}$) food source. We decrease the supply rates by varying $X_{1,\mathrm{max}}$ and $X_{2,\mathrm{max}}$ while keeping δ constant. We assume that the body mass at which the secondary food source becomes available w_{min} does not evolve. Since this parameter is possibly very important in the evolutionary outcome, we also investigate the effect of this parameter.

For most values of w_{min}, the evolutionary singular strategies found possess strong convergence stability and therefore correspond to a CSS (Leimar 2009). In case w_{min} is very low and the supply rates of both food sources are high, the selection gradient vanishes for an ecological steady state that is dynamically unstable (saddle point) and hence not an ecological attractor. We used the canonical equation of adaptive dynamics (Dieckmann and Law 1996; Durinx et al. 2008) to study how the four traits evolve in this case. For simplicity we assume that all evolutionary traits evolve independently from each other, we therefore used the identity matrix for the mutational covariance matrix. In appendix 5.B we show that even though the four evolving traits always vary over evolutionary time, they stay close to the strategy with a vanishing selection gradient that gives rise to an ecologically unstable steady state. We therefore ignore this subtlety in the result section and will refer to the strategy with a vanishing selection gradient as an ESS irrespective of its ecological instability.

Even though there are four traits evolving in our model, for clarity we do not always show how all of these traits change for changing supply rates. We show the evolutionary endpoints of body mass at birth w_{b} and at metamorphosis w_{J} in case of diminishing supply rates of the primary food source and the degree of metamorphosis θ and the body mass at metamorphosis w_{J} in case of diminishing supply rates of the secondary food source. All analyses are performed using the PSPManalysis software package (de Roos 2016). This software package allows for the equilibrium and evolutionary analysis of physiologically structured population models (see chapter 4 of this thesis for more details). A more detailed description of the model and the evolutionary analysis can be found in appendix 5.A.

Phylogenetic comparative analyses

We use a phylogenetic comparative analysis to test the correlation between the evolution of direct development and larger offspring. A dated phylogenetic tree including 2871 amphibian species was obtained from Pyron and Wiens (2013). Data for direct development and egg size were obtained from the AmphiBIO database (Oliveira et al. 2017) and matched against the phylogenetic data. From the entries in this database we used breeding strategy 'Dir' to indicate whether species reproduce via direct devel-

opment or not (binary) and 'Offspring_size_min_mm' as a measure of egg size. As the latter trait is continuous, and our analyses (see below) can only handle binary data, we defined large eggs as ≥ the average across amphibians, and small eggs as < the average. The average was 2.857 mm. In total, we obtained direct development data for 79% of the species (n = 2265) and egg size data for 28% of the species (n = 795) for which we also had phylogenetic data (n = 2871).

We tested for correlated evolution between direct development and large egg sizes in a phylogenetic comparative framework (Pagel 1994). To do so, we calculated the log marginal likelihood of an independent and a dependent model. In the independent model it is assumed that transitions in the two traits (between no direct development and direct development and between no large eggs and large eggs) occur completely independently from each other. The evolution of direct development does in this independent model not depend on the presence of large eggs and, vice versa, the evolution of large eggs is independent of the type of developmental mode. We compare the fit of this model with a dependent model where the two traits are correlated. In this model, the transition rates of both traits depend on the state of the other trait. It is assumed that the probability that two traits change at exactly the same time equals zero (Pagel 1994). There are therefore in total 8 transition rates calculated. These analyses were carried out in BAYESTRAITS v3 (Meade and Pagel 2017).

We ran five replicate Markov chain Monte Carlo (MCMC) chains for models of independent evolution and dependent (correlated) evolution, using a reversible jump hyper prior with an exponential prior between 0 and 100 and using a stepping stone sampler (Xie et al. 2011) to obtain estimates of the log marginal likelihoods. These MCMC chains were run for 5000000 generations and we discarded a 10% burnin. Support for correlated evolution was calculated using log Bayes Factors as follows:

$$2 \cdot (\text{log marginal likelihood (dependent model)} -$$
$$\text{log marginal likelihood (independent model)})$$

(5.2)

in which a log Bayes Factor > 10 indicates strong support for the more complex model (in this case the dependent model, and thus for correlated evolution).

In case we found support for correlated evolution, we evaluated transition rates to assess whether the transition towards direct development is conditional on the evolution of large egg sizes. The significance of this was tested by comparing Bayes Factors of the full, dependent model (no constraints) to a constraint model. In this constraint model we assume that large eggs and small eggs may equally likely be present when direct development evolves. The constraint model therefore only calculates 7 transition rates (in contrast to 8 transition rates in the full, dependent model). We compare again the log marginal likelihoods of both models to test which model fits the data the best (Pagel 1994).

5.3 Results

In chapter 4 of this thesis we found that metamorphosis can evolve as a way to relax the trade-off between early and late foraging success. Metamorphosis is, however, costly and it can therefore only evolve when the secondary food source is very abundant. As soon as the supply rate of this food source reaches a high threshold, metamorphosis evolves abruptly. Once evolved, metamorphosis does often not disappear when the supply rate of the secondary food source diminishes. There is therefore evolutionary bistability; for many supply rates of the secondary food source there are two evolutionary attractors, one where individuals undergo metamorphosis and a second attractor where individuals do not metamorphose. Here, we study the evolutionary response of a metamorphosing population to deteriorating food conditions. We therefore only study how the traits in the CSS of a metamorphosing population respond to decreasing supply rates and we ignore how a non-metamorphosing population responds to changing supply rates.

In the first part of this section we show that individuals produce larger offspring when the primary food source deteriorates. While this sometimes leads to the evolution of direct development, the population often goes extinct when the primary food source becomes too scarce. In the second part we show how a metamorphosing population adapts to deteriorating conditions of the secondary food source. We show that paedomorphosis can evolve but that, again, the population can also go extinct in case the supply rate of the secondary food source becomes too low. In the third section we show that for most parameter settings metamorphosis is an evolutionary trap in the sense that it leads to the extinction of a metamorphosing population when one of the food sources becomes to scarce. In the last section we show with a phylogenetic comparative analysis that the evolution of large egg sizes preceded the evolution of direct development in amphibians.

Evolution of larger offspring when the primary food source deteriorates
When the primary food source deteriorates there is selection to reduce the period where individuals depend on this food source. There is therefore an evolutionary response to a diminishing supply rate of the primary food source such that individuals produce larger offspring and furthermore metamorphose at a smaller body mass (top panels of figure 5.1). By increasing the body mass at birth w_b and decreasing the body mass at which individuals undergo metamorphosis w_J, individuals will metamorphose at an earlier age (bottom panels in figure 5.1).

Since individuals depend crucially on the primary food source when their body mass is less than w_{min}, it is of importance to produce offspring that are large enough to immediately start feeding on the secondary food source when the primary food

source is very scarce or even absent. Producing large offspring is energetically more expensive than producing small offspring. Adults that produce larger offspring therefore need more food in order to produce a single offspring compared to adults that produce smaller offspring. There is thus a trade-off between producing many small individuals that depend on the primary food source for a long time or producing a few big individuals that do not rely on this food at all. For most supply rates of the secondary food source, the density of this food is not high enough for individuals to produce offspring large enough to completely skip the primary food source. The population therefore often goes extinct in case of diminishing supply rates of the primary food source, even though the body mass at birth increases (figure 5.1A).
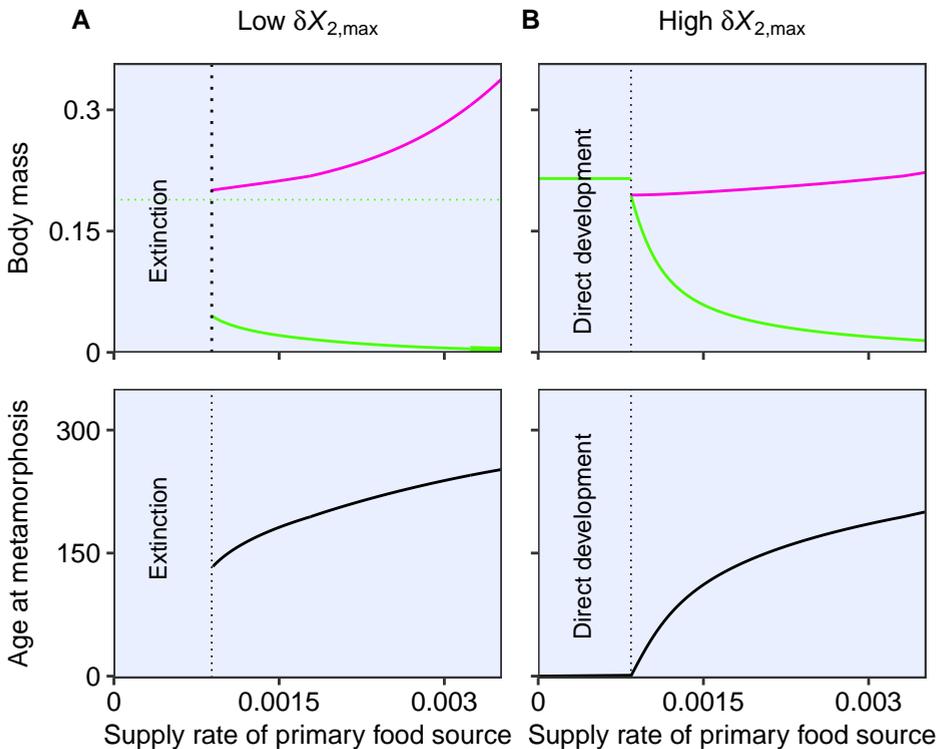

Figure 5.1: Body mass (g) at birth (green), body mass at metamorphosis (light purple) (top panels) and age at metamorphosis (bottom panels) at the CSS for decreasing values of the supply rate of the primary food source (mg l^{-1}day^{-1}) for low (A) and high (B) supply rates of the secondary food source (mg l^{-1}day^{-1}). For low supply rates of the primary food source the population either goes extinct (A) or evolves direct development (B). The dotted green line in the top panel of A shows the minimum body mass at birth that is necessary to skip the primary food source. Parameters: $\delta X_{2,\max} = 0.0066$ (A) or $\delta X_{2,\max} = 0.011$ mg l^{-1} (B); $w_{\min} = 0.1742$ gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

When the supply rate of the secondary food source is very high, direct development can evolve (figure 5.1B and figure 5.2). The body masses at birth and at metamorphosis evolve such that at a certain point individuals metamorphose before they are born (vertical dotted line in figure 5.1B). At this point, individuals do no longer feed on the primary food source. We show in figure 5.2 how the traits change over evolutionary time as soon as metamorphosis takes place before birth. Because metamorphosis is still costly (the costs are now paid by the mother, appendix A), there is selection to reduce the extent of metamorphosis θ (mint-green line) while at the same time it is beneficial to increase specialization parameter ψ_L (orange line) such that all individuals have a morphology fully specialized on the secondary food source (dark purple line). Because individuals no longer pay the costs of metamorphosis, the size at birth will evolve to higher values (figure 5.2) since adults have more energy available to produce large offspring. This results in a sudden jump in the body mass at birth as soon as direct development evolves (top panel in 5.1B). Since we are only interested in how a metamorphosing population responds to decreasing supply rates, we do not show in figure 5.1B when a direct developing species would again re-evolve metamorphosis when the supply rate of the primary food source increases.
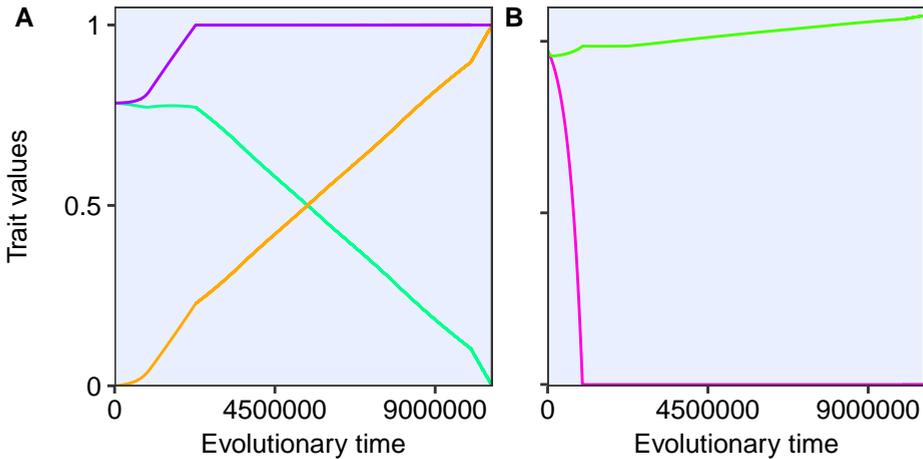

Figure 5.2: Evolutionary dynamics, starting from a metamorphic initial population, of the extent of metamorphosis (θ, mint-green) the larval specialization parameter ψ_L (orange) and the resulting specialization on the secondary food source for all individuals (dark purple) (A) and the body mass at birth (w_b, green) and at metamorphosis (w_J, light purple) (B) in gram. Parameters: $\delta X_{1,max} = 0.00084$, $\delta X_{2,max} = 0.011$ mg l^{-1} and $w_{min} = 0.1742$ gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

Evolution of a postponed metamorphosis when the secondary food source deteriorates

When the supply rate of the secondary food source diminishes, there is an evolutionary response to postpone metamorphosis (top panels in figure 5.3). When the supply rate of the secondary food source decreases, there is less of it available. It is therefore beneficial for individuals to postpone metamorphosis such that they are specialized on the primary food source for longer.

Individuals are, after metamorphosis, very efficient in feeding on the secondary food source. For most supply rates of the primary food source they therefore only feed on the secondary food source after metamorphosis (bottom panel in figure 5.3A). Because of this, there is no selection to reduce the extent of metamorphosis (middle panel in figure 5.3A). Hence, adults rely completely on the secondary food source for their reproduction, such that when this food source becomes too scarce, reproduction diminishes and the population goes extinct (figure 5.3A).

Paedomorphosis, where all individuals adopt the larval morphology, evolves abruptly in case the supply rate of the primary food source is very high while that of the secondary food source is low (figure 5.3B). Even though postmetamorphs are not specialized in feeding on the primary food source, the high availability of the primary resource makes that they now do include this food in their diet when the secondary food source becomes scarce (bottom panel figure 5.3B). For very low supply rates of the secondary food source, a large fraction of the diet of large individuals consists of the primary food source. It is therefore beneficial to specialize on the primary food source. As soon as individuals reduce the extent of their metamorphosis, however, they become less efficient in feeding on the secondary food source and more efficient in feeding on the primary food source (equation 4.10). Therefore, individuals will include more of the primary food source in their diet which in turn selects for a less pronounced metamorphosis. Because of this autocatalytic effect of a decrease in metamorphosis, paedomorphosis evolves abruptly as soon as the supply rate of the secondary resource drops below a certain threshold (dotted line in figure 5.3B).

The results in chapter 4 of this thesis show that metamorphosis can only re-evolve as soon as the supply rate of the secondary food source reaches a high threshold (not shown in figure 5.3). There is therefore a second evolutionary attractor present for many supply rates of the secondary food source where individuals do not metamorphose. Since we are only interested in how a metamorphosing population responds to decreasing supply rates, this attractor is not represented.
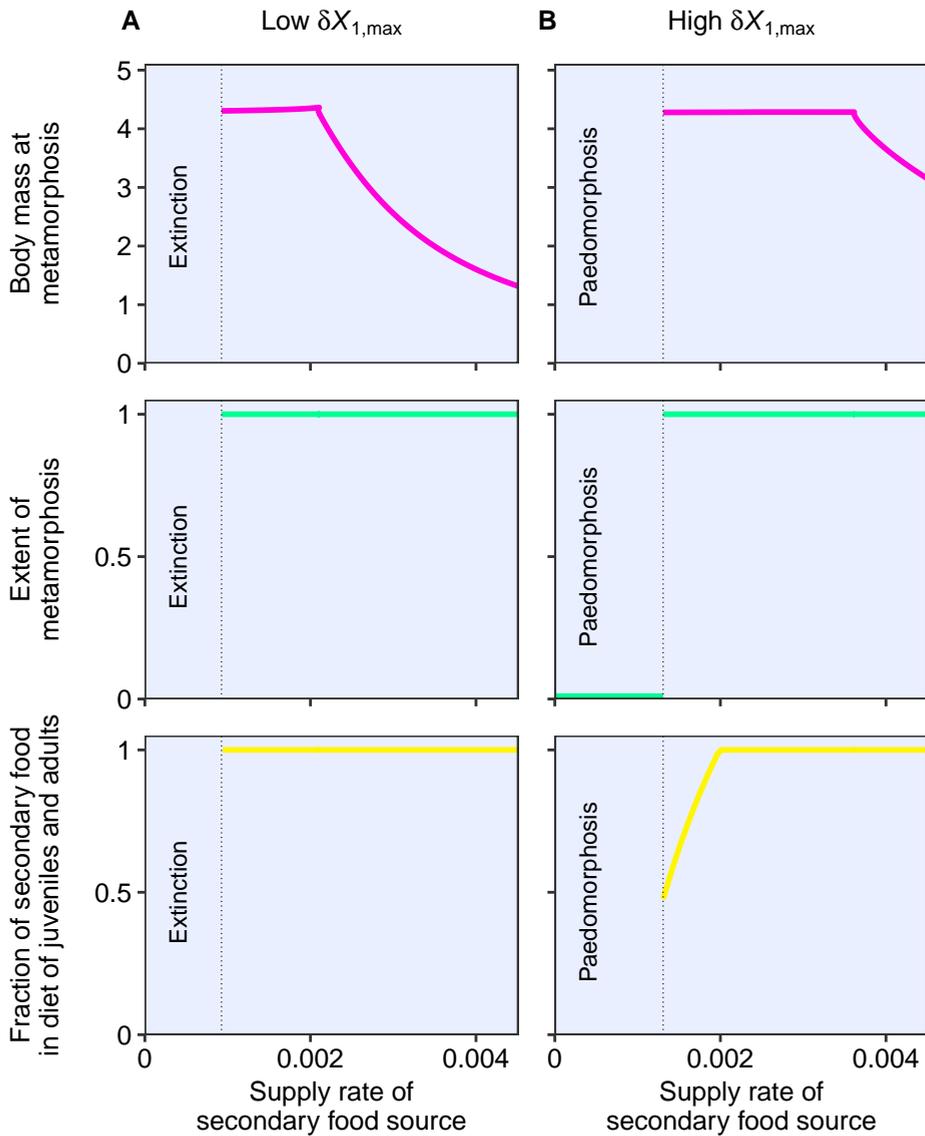
Figure 5.3: Body mass (g) at metamorphosis (top panel), the extent of metamorphosis (middle panel) and the fraction of the secondary food source source in the diet of juveniles and adults (bottom panel) at the CSS as a function of the supply rate of the secondary food source $(\mathrm{mg}\,\mathrm{l}^{-1}\mathrm{day}^{-1})$ for low (A) and high (B) supply rates of the primary food source. Parameters: $\delta X_{1,\max} = 0.0055$ (A) or $\delta X_{1,\max} = 0.011\,\mathrm{mg}\,\mathrm{l}^{-1}\mathrm{day}^{-1}$ (B); $w_{\min} = 0.01742$ gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

In case the secondary food source is only available for very large individuals (high value of $w_{\min}$), there is a second mechanism by which paedomorphosis can evolve. Because only the largest individuals can make use of the secondary food source, metamorphosis takes place relatively late in life (figure 5.4A). When the supply rate of the secondary food source diminishes, individuals postpone metamorphosis (as in figure 5.3), such that metamorphosis takes place just before maturation (vertical dashed line in figure 5.4). In contrast to figure 5.3, figure 5.4 shows that in this case the mass at metamorphosis continues to increase with decreasing supply rates of the secondary resource. When the mass at metamorphosis exceeds the mass at maturation there is a discrete change in the body mass at metamorphosis such that individuals postpone metamorphosis until they have reached a very large body mass. Because of this, most adults die before metamorphosis takes place and only a few actually undergo metamorphosis (figure 5.4B). For even lower values of the supply rate metamorphosis takes place at a body mass that not a single individual actually reaches (vertical dotted line in figure 5.4). Even though metamorphosis has not really disappeared ($\theta > 0$), the population appears to be paedomorphic since not a single individual undergoes metamorphosis. How such a paedomorphic population re-evolves a metamorphosis when the supply rate of the secondary food sources increases, is not investigated.
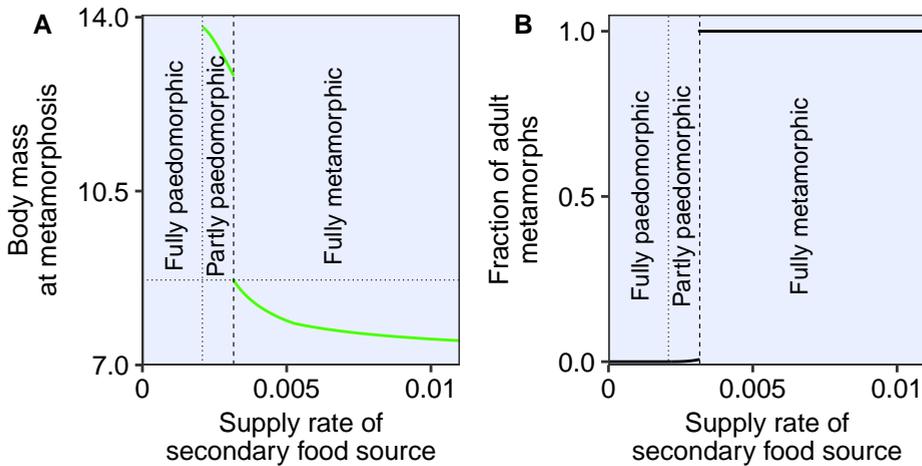
Figure 5.4: Body mass at metamorphosis (A) and the fraction of adults in the population that have metamorphosed (B) at the CSS as a function of the supply rate of the secondary food source ($\mathrm{mg\,l^{-1}day^{-1}}$). The horizontal dotted line in A indicates at which body mass individuals mature. The vertical lines indicate where the population becomes partly (dashed) or fully (dotted) paedomorphic. $\delta X_{1,\max} = 0.055 \ \mathrm{mg\,l^{-1}day^{-1}}$; $w_{\min} = 6.97$ gram. Other parameter values are as shown in tables 5.A3 and 5.A4.

When does metamorphosis disappear?

In the previous two sections we showed that direct development and paedomorphosis can evolve in case of diminishing supply of the primary and the secondary food source, respectively. In this section we show how these results depend on the supply rates of the two food sources and the body mass at which the secondary food source becomes available.

In case individuals have access to the secondary food source very early in life, direct development almost always evolves in case the supply rate of the primary food source diminishes (yellow line figure 5.5A). Because the secondary food source is already available for small individuals, direct development can evolve relatively easy because individuals can skip the primary food source even when they are born with a relatively small body mass. For very low supply rates of the secondary food source, however, adults do not have enough food available to produce offspring large enough to skip the primary food and the population goes extinct in case the supply rate of this food becomes too low (red line in figure 5.5A).

When the secondary food source is available somewhat later in life, direct development can only evolve when the supply rate of the primary food source is high (yellow line in figure 5.5B), otherwise the population goes extinct in case the supply rate of the primary food source becomes too low (red line 5.5B). Adults can only produce offspring large enough to skip the primary food source when there is a lot of the secondary food source available. For even higher values of w_{min} direct development can not evolve at all (e.g. figure 5.5C), even not when the supply rate of the secondary food source is very high. In this case the population always goes extinct when the supply rate of the primary food source diminishes.

For most values of w_{min} paedomorphosis only evolves in case the supply rate of the primary food source is very high (figure 5.5A and 5.5B). In this case postmetamorphs also feed on the primary food source, which leads to selection to reduce the extent of metamorphosis when the supply rate of the secondary food source decreases (figure 5.3B). However, for most supply rates of the primary food source, the population goes extinct in case the secondary food source deteriorates (red lines in figures 5.5A and 5.5B). Only when the secondary food source is available very late in life paedomorphosis evolves easily (blue lines in figure 5.5C).

To summarize, a metamorphosing population often goes extinct in case one of the two food sources diminishes. Direct development can evolve in case the secondary food source is available early in life and when the supply rate of this food source is high. The earlier the secondary food source is available, the lesser the supply rate of this food source that is necessary for the evolution of direct development. Paedomorphosis, on the other hand, evolves when the supply rate of the primary food source is

very high. When the secondary food source is only available for very large individuals paedomorphosis evolves relatively easily.
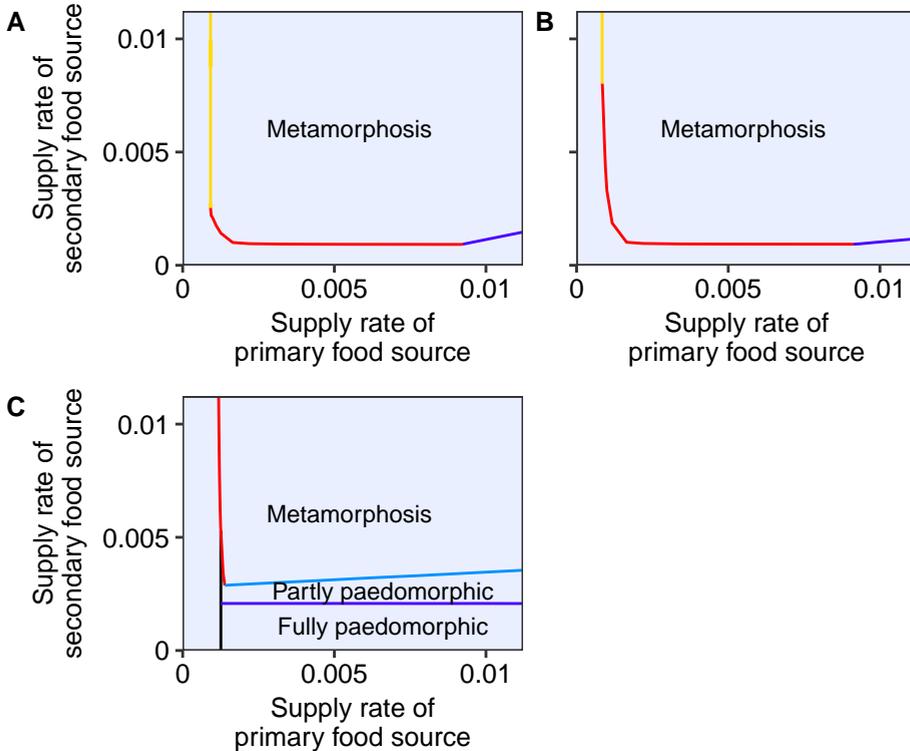

Figure 5.5: Two-parameter plots showing where an initially metamorphic population goes extinct (red lines), becomes (partly) paedomorphic (blue lines) or evolves direct development (yellow lines) as a consequence of decreasing supply rates of the primary and secondary food source ($mg\,l^{-1}day^{-1}$) for different values of the body mass at which the secondary food source becomes available (w_{min}). A (partly) paedomorphic population goes extinct at the black line in C. $w_{min} = 0.01742$ (A), $w_{min} = 0.1742$ (B), or $w_{min} = 6.97$ (C). Other parameter values are as shown in tables 5.A3 and 5.A4.

Direct development only evolves in amphibians after the evolution of large eggs

Our model results show that before direct development evolves, there is selection for increased offspring size (top panels in figure 5.1). While a correlation between developmental mode and offspring size has been observed before (e.g. Callery et al. 2001; Marshall et al. 2012; McEdward 2000), this correlation has not been tested in a phylogenetic framework.

We found very strong support for correlated evolution between direct development and large egg sizes within the amphibians, i.e. the average log Bayes Factor over all five parallel runs was 23.4 in favor of the dependent model (Table 5.C1 in appendix C). To test if the transition to direct development indeed depends on the presence of large eggs, we furthermore compared the Bayes Factor of the fully dependent model to a constrained model where we assumed that the transition rate to direct development does not depend on egg size. The dependent model performed significantly better than the model in which we constrained the transition to direct development to be independent of egg size (Bayes Factor of 11.6).

Table 5.1 shows the conditional transition rates of the two traits, estimated by the dependent model. The presence of direct development is indicated with D=1, the presence of metamorphosis with D=0. Large eggs are referred to as E=1, small eggs as E=0. The parameter $P(E = 1 \rightarrow 0 \mid D = 1)$ for example, is the estimated transition probability per million years from large to small eggs in case individuals mature via direct development. These transition rates strongly support the prediction that direct development cannot evolve unless large egg size has evolved first, i.e. the transition from metamorphosis to direct development is zero if small eggs are present (table 5.1). The transition rates furthermore show that the loss of direct development is extremely rare when the lineage has large egg sizes (table 5.1). All other transition scenarios are equally likely (see Table 5.1). It is therefore for example possible that after direct development has evolved, small eggs evolve again.

Table 5.1: Transition probabilities per million years between developmental modes (trait D) and large egg size (trait E) for the correlated (dependent) model of evolution resulting from Bayesian Markov chain Monte Carlo analyses in BayesTraits. '0' refers to absence of the trait, '1' refers to presence.

Transition rate	Median estimate (Transitions/Million years)
$P(D = 0 \rightarrow 1 \mid E = 0)$	0
$P(D = 0 \rightarrow 1 \mid E = 1)$	0.004462
$P(D = 1 \rightarrow 0 \mid E = 0)$	0.004528
$P(D = 1 \rightarrow 0 \mid E = 1)$	0
$P(E = 0 \rightarrow 1 \mid D = 0)$	0.004783
$P(E = 0 \rightarrow 1 \mid D = 1)$	0.004646
$P(E = 1 \rightarrow 0 \mid D = 0)$	0.004785
$P(E = 1 \rightarrow 0 \mid D = 1)$	0.004485

5.4 Discussion

In this chapter we have shown that a metamorphosing population evolves in response to changing conditions in such a way that individuals reduce their dependence on the deteriorating food source. While this can lead to the evolution of either direct development or paedomorphosis, we also showed that metamorphosis tends to be an evolutionary dead end. Since metamorphosing species often crucially depend on two (or more) habitats for their growth, survival and reproduction, they are hypersensitive to habitat loss (Rudolf and Lafferty 2011) and a metamorphosing population often goes extinct when one of the two food sources becomes too scarce.

We have found that there is selection to produce larger offspring and to decrease the body mass at metamorphosis in case the food source that larvae crucially depend on deteriorates. Larger offspring require less food to reach the metamorphosis size threshold and have therefore an advantage when the larval food source is scarce. In case adults are able to produce large enough offspring to skip this primary food source, direct development can evolve in order to avoid the dependence on the declining food source. It has often been observed in marine invertebrates (e.g. Marshall et al. 2012) and amphibians (e.g Callery et al. 2001) that direct developing species produce larger eggs compared to related indirect developing species. Our phylogenetic analysis indeed strongly supports our hypothesis that among amphibians the evolution of large eggs preceded the origin of direct development. Our finding that before direct development evolves metamorphosis occurs earlier in life remains to be tested.

Instead of producing larger offspring, individuals can also adapt to bad larval conditions by enhancing parental care, for example by nursing their offspring. Parental care can greatly increase survival and growth rates of offspring and is therefore a good strategy when the larval food source is of poor quality. However, taking care of your offspring is energetically costly (e.g. Smith and Wootton 1995) and will reduce the number of offspring an individual can produce. Individuals will therefore face a similar trade-off as is the case for producing larger offspring, they can either produce many offspring without taking care of them or produce a few and spend lots of energy in their upbringing. It is therefore likely that, as in the case for producing large offspring, the evolution of parental care depends on the conditions of the adult habitat. It has been shown in frogs that the evolution of large egg size typically precedes the evolution of parental care (Summers et al. 2006) and it would be interesting for further research to study how these two strategies interact with the evolution of direct development in case ecological conditions change.

We have shown that a deteriorating adult habitat is associated with a delayed metamorphosis, a high risk of extinction and, under some circumstances, the evolution of paedomorphosis. Our results show that a prerequisite for the evolution of paedo-

morphosis is that the ontogenetic niche shift at metamorphosis is incomplete, such that postmetamorphs keep utilizing the larval niche (the primary food source) even after metamorphosis. Part of these results are in line with empirical work that showed with a phylogenetic approach that the occurrence of paedomorphosis in plethodontids salamanders is correlated with inhospitable environments for terrestrial adults (Bonett et al. 2014*a*). Bonett et al. (2014*a*) furthermore showed that the rate of extinction in paedomorphic lineages is much higher than in metamorphic lineages. The authors suspect that the limited dispersal abilities of paedomorphs have caused these high extinction rates. However, our results indicate that these high extinction rates can also be explained by a different mechanism; populations that evolve in the direction of paedomorphosis are very vulnerable to extinction since they depend on the bad adult habitat for their reproduction. While we looked at changes in the supply rate of the postmetamorphic food source, the work of Bonett et al. (2014*a*) looked at the effect of climatic conditions such as temperature and precipitation. However, the effect of an inhospitable environment for postmetamorphs is comparable to low food conditions since both will reduce reproduction and survival. In another paper they furthermore showed, in line with our results, that a delay in the age at metamorphoses preceded the evolution of paedomorphosis (Bonett et al. 2014*b*). A similar phylogenetic approach as used by Bonett et al. 2014*a,b* could be used to test if metamorphosis indeed occurs at relatively larger body masses in case of unfavorable adult habitats, if the evolution of paedomorphosis is related to relative good larval conditions and whether or not paedomorphosis is associated with incomplete niche segregation between larvae and postmetamorphs.

While we found that it is difficult to evolve paedomorphosis, this life-history strategy has evolved several times in salamanders (Hanken 1999). One explanation for this contrasting result is that we only considered the evolution in body mass at metamorphosis. However, paedomorphosis can also evolve when individuals accelerate maturation (i.e. reduce the body mass at maturation), a process known as progenesis (Denöel et al. 2005; McMahon and Hayward 2016). It might be easier to evolve paedomorphosis in case individuals can also mature at a smaller body size. Interestingly, there are no known cases of paedomorphosis in anurans. A possible explanation for this is that it is physically not possible for the tadpole stage to possess characters needed for reproduction (Wassersug 1975). However, tadpoles of *Xenopus laevis* that fail to metamorphose are able to develop gonads. Furthermore, tadpoles of the paradoxical frog *Pseudis paradoxa* also have fully developed gonads (Downie et al. 2009). Metamorphosis takes place at very large body sizes in the paradoxical frog, indicating that this species is evolving in the direction of paedomorphosis (Downie et al. 2009).

Studies of facultative paedomorphosis in salamanders indicate that the onset of metamorphosis is probably not only dependent on body mass but also on age and

growth conditions (Denöel et al. 2005), leading to some plasticity in the timing of metamorphosis. Paedomorphic individuals do not only arise when the larval growth conditions are very favorable (e.g. Denöel and Joly 2001), but also when larvae do not grow fast enough to reach the critical size that is needed to undergo metamorphosis (Whiteman 1994; Whiteman et al. 2012, i.e. best of a bad lot hypothesis). To better understand the conditions under which paedomorphosis can evolve, it would be interesting to also take into account both age and body mass at metamorphosis and maturation.

We found that the body mass at which the secondary food source becomes available (w_{min}) largely influences if direct development and paedomorphosis can evolve or not. When the secondary food source is already available for small individuals, direct development evolves easily while paedomorphosis is often not possible. Vice versa, when the secondary food source is only available for large individuals, direct development can often not evolve but paedomorphosis evolves easily. These results indicate that there is strong selection to change the body mass at which individuals have access to the secondary food source in case one of the two food sources become too scarce. While including this trait in the evolutionary analysis will probably facilitate the evolution of direct development and paedomorphosis, there are certain size limits to what you can do with a certain morphology (Werner 1988) and therefore limits to which extent w_{min} can evolve. Piscivorous fish are for example limited by their gape size and need to be of a certain size before they are large enough to consume other fish (e.g. Mittelbach and Persson 1998). Because of these constraints we have chosen to not let w_{min} evolve and only study how changing this parameter changes the result.

In appendix 5.D we show that changing the ontogenetic scaling of the attack rates changes for which supply rates of the secondary food source direct development can evolve. In case small individuals are very efficient feeders on their food source, direct development can hardly evolve and the population will ultimately go extinct in case the primary food source becomes too scarce. However, because small individuals are very efficient in feeding on the primary food source, the population can deal with very low supply rates of the primary food source. These results show that the ability to evolve direct development do not only depend on the supply rates of the different food sources but are also influenced by the size-dependent ingestion capacity of individuals.

We have assumed a constant mortality rate for all individuals, independent of an individuals body mass. This is of course a very simplistic assumption since mortality is often size dependent, with high mortality rates among the smallest individuals (e.g. Sogard 1997). However, we expect that changing this assumption will not qualitatively change our results. When small individuals experience elevated mortality levels, there is probably a stronger selection to produce large offspring. However, adults will nonetheless need a substantial amount of food to produce those large offspring.

Therefore, the evolution of direct development, which is constraint by the food availability for adults, will probably not evolve more easily in case of size dependent mortality.

Together, our results demonstrate that metamorphosis is a very successful strategy that is not easily lost. However, metamorphosis comes with a risk since it also makes individuals dependent on multiple food sources. An evolutionary response to changing conditions can prevent extinction, but this is often not possible.

Acknowledgments

Appendix 5.A Detailed model description

Model description

We assume that there are two, unstructured, food sources present. Both the primary and secondary food source follow semi-chemostat dynamics with turnover rate δ, and will reach, in the absence of consumers, a density of $X_{1,\max}$ and $X_{2,\max}$ respectively. The primary food source, with density X_1, is available for all individuals while the secondary food source, with density X_2, is only available for large individuals. The two food sources require two different morphologies to be efficiently utilized by the consumers.

We assume that a consumer consists of two different forms of mass, irreversible mass x such as bones and organs and reversible mass y such as fat. The reversible mass of an individual can be invested in metamorphosis or used to cover its basic metabolism under starvation conditions. For simplicity we assume equilibrium conditions and ignore starvation conditions; an individual's reversible mass is therefore fully available for covering the costs of metamorphosis. The body length, attack rate and handling time of an individual depend only on its standardized body mass $w = x + y_{\max} = x(1 + q_J)$ (Persson et al. 1998), where $y_{\max}$ is the maximum attainable amount of reversible body mass. Parameter q_J is a dimensionless scaling constant describing an individual's maximum ratio of reversible to irreversible mass.

Table 5.A1: Model variables

Variable	Description	Range	Unit
X_1	Density of primary food source	From 0 to $X_{1,\max}$	mg l^{-1}
X_2	Density of secondary food source	From 0 to $X_{2,\max}$	mg l^{-1}
x	Irreversible body mass	Larger than x_b	g
y	Reversible body mass	From $q_J x_b$ to $y_{\max}$	g

Newborn larvae (L) are born at an irreversible body mass x_b and the maximum attainable amount of reversible mass $y = q_J x_b$. The total body mass at birth equals $w_b = (1 + q_J)x_b$. The ratio between irreversible and reversible mass is constant until individuals reach standardized body mass w_J and metamorphose into juveniles. Individuals lose an amount $\theta x_J(q_J - q_s)$ of their reversible body mass during metamorphosis. In this equation θ is the extent of the metamorphosis and parameter q_s is the ratio of y over x of an individual immediately after full metamorphosis ($\theta = 1$). After metamorphosis the reversible body mass y is over time restored to $y_{\max} = q_J x$ (see below) such that the total body mass $x + y$ again equals its standardized body mass. We therefore use the term body mass to refer to the standardized body mass w. Juveniles mature into adults (A) and start reproducing when reaching standardized body mass

w_A. The secondary food source X_2 becomes available after individuals have reached standardized body mass w_{min}.

The size-dependent attack rate on the primary and secondary food source are described by two hump-shaped functions following

$$a_1(w) = A_{1i}[\frac{w}{w_0}\exp(1-\frac{w}{w_0})]^\alpha \tag{5.A1a}$$

$$a_2(w) = \begin{cases} 0 & w \leq w_{min} \\ A_{2i}[\frac{w-w_{min}}{w_0}\exp(1-\frac{w-w_{min}}{w_0})]^\alpha & \text{otherwise.} \end{cases} \tag{5.A1b}$$

In these equations α determines how strongly the attack rates on the primary and secondary food sources increase and decrease around the peaks at w_0 and $w_0 + w_{min}$, respectively. Parameters A_{1i} and A_{2i} are the maximum attack rates an individual can reach on the primary and secondary food source when its standardized body mass equals w_0 and $w_0 + w_{min}$, respectively. We assume that there is a linear trade-off between these two maximum attack-rate constants within a certain life stage (i = L, J or A),

$$A_{1i} = (1-\psi_i)(A_{max} - A_{min}) + A_{min},$$
$$A_{2i} = \psi_i(A_{max} - A_{min}) + A_{min}. \tag{5.A2}$$

In these equations, $0 \leq \psi_i \leq 1$ is the relative degree of specialization on the secondary food source of a certain life stage. A value of $\psi_i = 0$ means that individuals in life stage i are completely specialized in feeding on the primary food source and not very efficient in feeding on the secondary food source. Vice versa, a value of $\psi_i = 1$ means that individuals are very efficient in feeding on the secondary food source while they are not very efficient in feeding on the primary food source.

Metamorphosis can decouple the different life stages such that individuals can be specialized on the primary food source as larvae and on the secondary food source as juveniles and adults. Metamorphosis decouples the different life stages as follows

$$\psi_A = \psi_J = \min(1, \psi_L + \theta), \tag{5.A3}$$

in this equation parameter θ is the extent of the metamorphosis. Individuals that undergo metamorphosis lose part of their body mass as described above and furthermore have a probability of $\rho\theta$ to die during metamorphosis.

The food intake of an individual with standardized body mass w can be written as

$$I(X_1, X_2, w) = \frac{\phi(w)a_1(w)X_1 + [1-\phi(w)]a_2(w)X_2}{1 + h(w)\{\phi(w)a_1(w)X_1 + [1-\phi(w)]a_2(w)X_2\}} \tag{5.A4a}$$

whereby the handling time $h(w)$ equals (following Persson et al. 1998)

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3}e^{\zeta_4 w}. \tag{5.A4b}$$

We assume that individuals show optimal foraging behavior and allocate their time searching for each food source in such a way that food intake is maximized. This implies that $\phi(w)$, the fraction of time individuals spend searching for the primary food source equals

$$\phi(w) = \frac{1}{1 + e^{\sigma(a_2(w)X_2 - a_1(w)X_1)}}.$$ (5.A5)

In this equation parameter σ determines the steepness of the sigmoid, food-selection curve at equal food source profitabilities, $a_1(w)X_1 = a_2(w)X_2$ (de Roos et al. 2002). The form of equation 5.A1 and 5.A5 imply that large individuals ($w > w_{min}$) always include both food sources in their diet. We will, however, for convenience state that individuals only feed upon the primary or secondary food source in case the fraction of the secondary food source in the diet of large individuals is graphically indistinguishable from 0 or 1, respectively.

The total energy-intake of an individual equals its food-intake rate multiplied by a conversion factor κ_e. Total net-energy intake is first used to cover maintenance costs. The metabolic demands per unit of time is a function of both irreversible and reversible mass of a consumer and can be described by a power function following

$$E_m(x, y) = p_1(x + y)^{p_2}.$$ (5.A6)

Larvae and juveniles allocate a fraction $\kappa_J(x, y)$ of the net-biomass production (the difference between the food assimilation and maintenance cost of an individual) $E_g(X_1, X_2, x, y) = k_e I(X_1, X_2, w) - E_m(x, y)$ to growth in irreversible mass, following

$$\kappa_J(x, y) = \frac{y}{(1 + q_J)q_J x}.$$ (5.A7a)

The remaining part is allocated to growth in reversible mass. Since adults also invest in reproduction they allocate a lower fraction $\kappa_A(x, y)$ to growth in irreversible mass following

$$\kappa_A(x, y) = \frac{y}{(1 + q_A)q_A x},$$ (5.A7b)

with $q_A > q_J$, the remainder is invested in reversible mass and reproduction. To ensure that individuals will aways invest in reversible mass in such a way that the ratio of y to x either remains or is restored to q_J and that reproduction does not take place when $y < q_J x$ (Persson et al. 1998) we assume that adults invest a fraction $\kappa_R(x, y)$ of their net-energy production in reversible mass according to the function (see chapter 4 of this thesis):

$$\kappa_R(x, y) = \begin{cases} 1 - \kappa_A(x, y) & y < q_J x \\ (1 - \kappa_J(x, y))\frac{\kappa_A(x,y)}{\kappa_J(x,y)} & \text{otherwise.} \end{cases}$$ (5.A8)

The remainder fraction of the adult net-biomass production $(1 - \kappa_A(x, y) - \kappa_R(x, y))$ is invested in reproduction. The number of eggs an individual adult produces per unit of time then equals

$$b(x, y, X_1, X_2) \begin{cases} 0 & y < q_J x \\ (1 - \frac{\kappa_A(x,y)}{\kappa_J(x,y)}) E_g(x, y, X_1, X_2) \eta / w_b & \text{otherwise.} \end{cases} \quad (5.A9)$$

where η is a conversion factor.

Direct development

We assume that in case metamorphosis takes place before individuals are born ($w_J < w_b$), the costs of metamorphosis are paid by the mother. This means that a fraction of the eggs ($\rho\theta$) does not survive. It is furthermore more costly to produce an egg because the energetic costs of metamorphosis have to be paid as well. The number of eggs an individual adults produces per unit of time therefore equals

$$b(x, y, X_1, X_2) \begin{cases} 0 & y < q_J x \\ (1 - \rho\theta)(1 - \frac{\kappa_A(x,y)}{\kappa_J(x,y)}) E_g(x, y, X_1, X_2) \eta / (w_b + \theta x_J(q_J - q_s)) & \text{otherwise.} \end{cases}$$
$$(5.A10)$$

in case metamorphosis takes place before individuals are born. It is likely that metamorphosis is less costly in case the mothers pay for it. However, changing the costs of metamorphosis after birth does not change the results (unpublished results).

Metabolic demands and handling time are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food sources following Persson et al. (1998). The model should, however, be interpreted as a more general consumer-resource model describing the interaction between two food sources and a size-structured consumer. All rates were scaled to a daily basis, all parameter values related to energetics are based on a reference temperature of 19°C. Processes taking place during the winter season are ignored. We assume that eggs have a minimal mass of $1 \ 10^{-4}$ gram, which is the smallest egg size observed for cold-blooded aquatic invertebrates (Hendriks and Mulder 2008). Model variables are listed in table 5.A1, the evolving parameters in table 5.A2 and standard parameter values in tables 5.A3 and 5.A4.

Evolutionary dynamics

To study under which conditions metamorphosis disappears we use the framework of adaptive dynamics (Dieckmann and Law 1996; Geritz et al. 1998). Adaptive dynamics assumes that a population is monomorphic and that evolution in this population occurs because of the fixation of very small and rare mutations. The extent of metamorphosis θ, specialization parameter ψ_L, the the body mass at birth w_b and

the body mass at which metamorphosis takes place w_J can all evolve. For the latter two we assume that the amount of irreversible mass at metamorphosis (x_J) and birth (x_b) evolve while parameter q_J, that determines together with the irreversible mass x the total body mass, does not evolve. We assume that initially both supply rates are high ($\delta X_{1,max} = \delta X_{2,max} = 0.011 \text{mg}\,\text{l}^{-1}\text{day}^{-1}$) and individuals undergo metamorphosis ($\theta > 0$). In this case there is only a single evolutionary singular strategy (ESS), which is defined by the vanishing of the selection gradient of all considered traits. We track this ESS for different values of w_{min} as a function of the supply rate of either the primary or secondary food source and determine whether these strategies are convergence stable and/or evolutionary stable following Geritz et al. (1998) and Leimar (2009).

Table 5.A2: Evolving traits

Variable	Description	Range	Unit
ψ_L	Degree of specialization of larvae on the secondary food source	From 0 to 1	-
θ	Extent of metamorphosis	From 0 to 1	-
w_J	Body mass at which individuals undergo metamorphosis	Larger than w_b	g
w_b	Body mass of newborns	Larger than 0.0001	g

Table 5.A3: Standard parameters of the model from Persson et al. (1998)

Parameter	Description	Default Value	Unit
δ	Food source turnover rate	0.1	day^{-1}
$X_{1,\max}$	Maximum biomass density of primary food source	variable	mg l^{-1}
$X_{2,\max}$	Maximum biomass density of secondary food source	variable	mg l^{-1}
w_A	Standardized body mass at maturation	8.71	g
w_0	Standardized body mass at which maximum attack rate is attained on primary food source	17.42	g
α	Exponent in attack-rate functions	0.93	-
ζ_1	Constant in handling-time function	0.00036*	day mg^{-1}
ζ_2	Constant in handling-time function	0.00745*	$\text{day mg}^{-1}\text{g}^{\zeta_3}$
ζ_3	Slope of decrease in handling time at small consumer sizes	0.68	-
ζ_4	Slope of increase in handling time at large consumer sizes	$1.15\ 10^{-3}$	g^{-1}
p_1	Metabolic constant	0.033	$\text{g}^{1-p_2}\text{day}^{-1}$
p_2	Metabolic exponent	0.77	–
k_e	Metabolic conversion factor	0.00061*	–
q_J	Constant determining maximum reversible body mass	0.742	–
q_A	Constant in adult allocation function	1	–
η	Gonad-offspring conversion factor	0.5	-
μ	Background mortality rate	0.01	day^{-1}

Note: *These values are the original values from Persson et al. (1998) divided by $1.1 \cdot 10^{-2}$ (the weight of a prey individual) to express prey densities in milligram l^{-1} instead of individuals l^{-1}.

Table 5.A4: Parameters related to specialization and metamorphosis

Parameter	Description	Default Value	Unit
A_{max}	Maximum value of the attack rate constants A_1 and A_2	$1\,10^5$	$l\,day^{-1}$
A_{min}	Minimum value of the attack rate constants A_1 and A_2	$1\,10^4$	$l\,day^{-1}$
w_{min}	Standardized body mass at which the secondary food source becomes available	0.01742, 0.1742 or 6.97	g
σ	Constant in habitat-switching rate	10	$day\,mg^{-1}$
q_s	Ratio of reversible to irreversible body mass immediately after full metamorphosis	0.2	–
ρ	Probability to die during full metamorphosis	0.5	-

Appendix 5.B   Evolutionary cycling

In this appendix we show how the four traits evolve in case there is no stable evolutionary endpoint.

In case the secondary food source is already available for very small individuals ($w_{min} = 0.01742$), the evolutionary singular strategy is for many combinations of the two food supply rates absent. The black line in figure B1 indicates the parameter area where this is the case. The reason for this is that there are two stable ecological equilibria, separated by an unstable equilibrium. The life history strategy for which the selection gradient equals 0 is in this case located on the ecologically unstable equilibrium branch and can therefore never be reached (we will refer to this particular life history strategy as an unstable ESS, even though this is in the context of adaptive dynamics somewhat of a misnomer). In each of the two stable equilibrium states evolution takes the evolving strategies to the boundary of the existence of this equilibrium, at which point the system switches to the other ecological stable equilibrium. As a consequence, the four traits keep on changing over evolutionary time. Since there is no stable ESS occurring for these parameter values, the traits stay relatively close to the trait values that characterize the unstable ESS (figure B2). For low supply rates of the secondary food source, the ESS is located on a stable ecological attractor (figure B1).
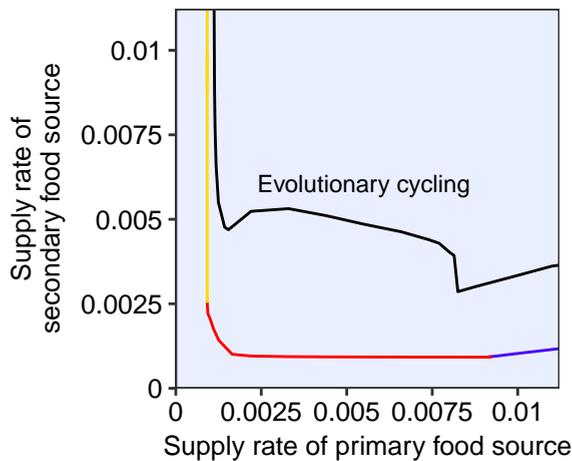

Figure B1: Two-parameter plot showing where the population goes extinct (red lines), becomes paedomorphic (blue lines), evolves direct development (yellow lines) and where the evolutionary singular strategy is absent (above the black line) as a function of the supply rates of the primary and secondary food source ($\mathrm{mg\,l^{-1}day^{-1}}$). $w_{min} = 0.01742$, other parameter values are as shown in tables 5.A3 and 5.A4.
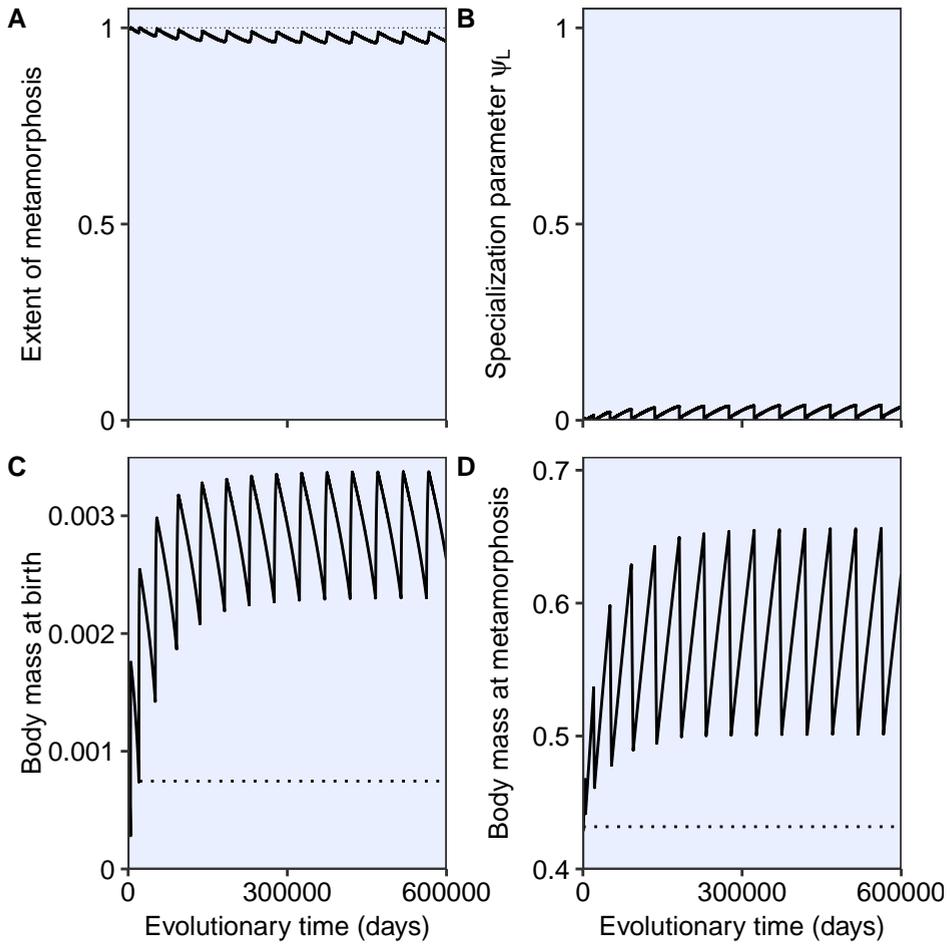
Figure B2: Evolutionary dynamics of the extent of metamorphosis (A), both in gram, the specialization parameter ψ_L (B), the body mass at birth (C) and metamorphosis (D) in case life history strategy for which the selection gradient vanishes corresponds to an unstable ecological equilibrium. The dotted lines indicate the value of the trait in the ESS in the ecologically (and hence evolutionary) unstable equilibrium. $\delta X_{1,max} = 0.0055$, $\delta X_{2,max} = 0.0088$ mg l^{-1}day^{-1}, and $w_{min} = 0.01742$ gram. Other parameters are as shown in tables 5.A3 and 5.A4.

Appendix 5.C Log marginal likelihoods

In this appendix we show the log marginal likelihoods for the three different models. These indicate strong support for the dependent model over the independent model, as well as strong support for the dependent model over the dependent constrained model.

Table 5.C1: Log marginal likelihood for the dependent, independent, and constrained dependent models obtained from Markov chain Monte Carlo (MCMC) in BayesTraits, for the evolution of direct development and large egg size on the amphibian phylogeny. For each of the models, five independent MCMC chains were run for 5000000 generations, discarding 10% as burnin. The average log marginal likelihoods for the dependent, independent and constrained dependent models were used to calculate a log Bayes Factor.

	Dependent model	Independent model	Constrained dependent model
MCMC 1	-597.05	-610.12	-602.74
MCMC 2	-598.05	-608.1	-603.72
MCMC 3	-599.87	-610.31	-603.24
MCMC 4	-596.35	-608.8	-606.66
MCMC 5	-598.65	-611.24	-603.17
Average log marginal likelihood	-597.99	-609.71	-603.91
Log Bayes Factor (dependent vs independent)	23.44		
Log Bayes Factor (dependent vs constrained dependent $P(D = 0 \rightarrow 1 \mid E = 0) =$ $P(D = 0 \rightarrow 1 \mid E = 1))$	11.6		

Appendix 5.D   The effect of α

In this appendix, we study how changing parameter α affects our result. Parameter α determines how fast the attack rates on the primary and secondary food source increase and decrease around the peaks at w_0 and $w_0 + w_{min}$, respectively. This parameter affects, among other things, how effectively the smallest individuals can forage on the primary food source. The lower α, the higher the attack rates of the smallest individuals. When $\alpha = 0.6$, small individuals need less food to survive compared to larger individuals. In case $\alpha = 1.1$, it is the other way around and small individuals need more food in order to survive compared to large individuals. When $\alpha = 0.93$ individuals require more or less the same amount of food for their survival (Persson et al. 1998).

Figure 5.D1 shows that changing parameter α does affect the evolutionary response to decreasing supply rates of the primary food source but hardly affects how the population responds to decreases in the supply rate of the secondary food source. Changing α affects the attack rate of small individuals more strongly than that of large individuals (equation 5.A1), which explains why α hardly influences how the population responses to changes in the supply rate of the secondary food source, since this food source is only eaten by larger individuals.

For low values of α, the population will ultimately go extinct in case the primary food source becomes too scarce. Direct development does not evolve. When the primary food source is very low there is hardly an evolutionary response to produce larger offspring. Because small offspring are very efficient on the primary food source, they can grow even when this food source is scarce. Producing larger offspring is therefore not profitable because it will decrease the number of offspring an individual produces while it hardly decreases the time until metamorphosis. Only when the supply rate of the secondary food source is very high (e.g. $0.02 \, \text{mg} \, \text{l}^{-1} \text{day}^{-1}$) direct development will evolve (not shown in the figure). Note that because small individuals are very efficient in feeding, the population can survive for much lower supply rates of the primary food source compared to higher α values.

In case $\alpha = 1.1$ direct development evolves for lower supply rates of the primary food source compared to the situation where $\alpha = 0.93$. Because for high values of α small individuals are much less efficient on the primary food source, the selection pressure to produce large individuals is higher.
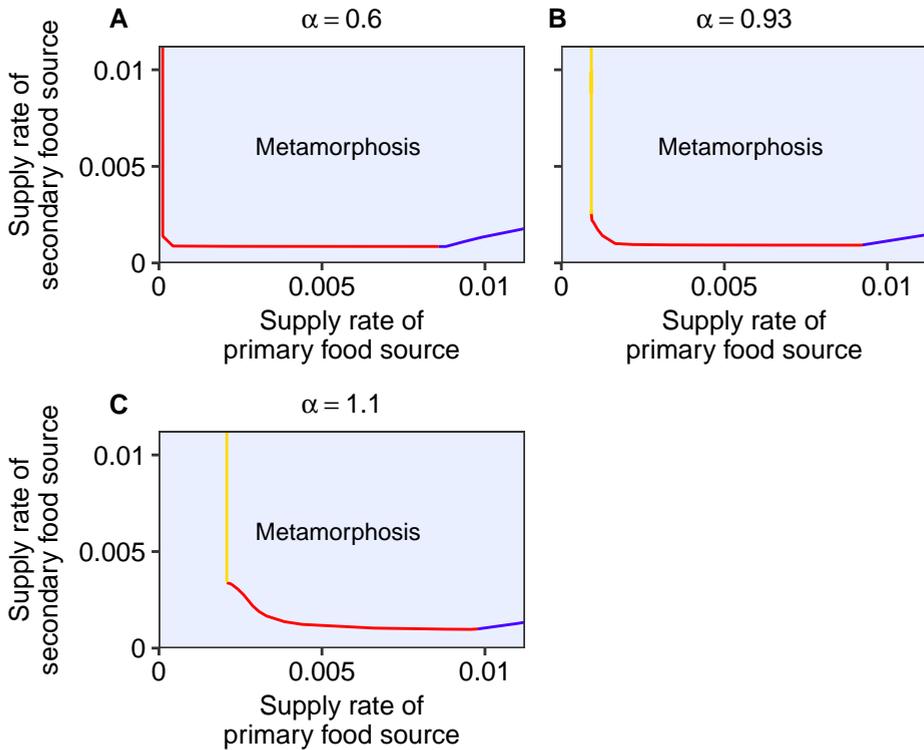
Figure 5.D1: Two-parameter plots showing where the population goes extinct (red lines), becomes paedomorphic (blue lines) and evolves direct development (yellow lines) as a consequence of decreasing the supply rates of the primary and secondary food source $(\mathrm{mg}\,\mathrm{l}^{-1}\mathrm{day}^{-1})$ for different values of α, which determines the competitive ability of an individual of a given size. $\alpha = 0.6$ (A), $\alpha = 0.93$ (B), or $\alpha = 1.1$ (C); $w_{\min} = 0.01742$, other parameter values are as shown in tables 5.A3 and 5.A4.