The Evolutionary Ecology of Metamorphosis

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ABSTRACT: Almost all animal species undergo metamorphosis, even though empirical data show that this life-history strategy evolved only a few times. Why is metamorphosis so widespread, and why has it evolved? Here we study the evolution of metamorphosis by using a fully size-structured population model in conjunction with the adaptive-dynamics approach. We assume that individuals compete for two food sources; one of these, the primary food source, is available to individuals of all sizes. The secondary food source is available only to large individuals. Without metamorphosis, unresolvable tensions arise for species faced with the opportunity of specializing on such a secondary food source. We show that metamorphosis can evolve as a way to resolve these tensions, such that small individuals specialize on the primary food source while large individuals specialize on the secondary food source. We find, however, that metamorphosis evolves only when the supply rate of the secondary food source exceeds a high threshold. Individuals postpone metamorphosis when the ecological conditions under which metamorphosis originally evolved deteriorate but will often not abandon this life-history strategy, even if it causes population extinction through evolutionary trapping. In summary, our results show that metamorphosis is not easy to evolve but that, once evolved, it is hard to lose. These findings can explain the widespread occurrence of metamorphosis in the animal kingdom despite its few evolutionary origins.

Keywords: metamorphosis, evolution, adaptation, size structure, evolutionary trapping.

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Introduction

Metamorphosis is widespread in the animal kingdom (Werner 1988). Salamanders, frogs, butterflies, and ants all abruptly change their morphology at a certain point during their lives. Also many other species—for example, salmon and flatfish (McMenamin and Parichy 2013), crustaceans such as lobsters and barnacles (Haug and Haug 2013), and jellyfish (Holstein and Laudet 2014)—undergo a period of postembryonic remodeling of their body plan. In this article, we aim to understand which ecological conditions promote the evolution of metamorphosis in free-living species that change their diet over their life cycle. Metamorphosis is here defined as the morphological change that takes place at the transition from the larval to the juvenile life stage.

It is commonly thought that metamorphosis has evolved to decouple different life stages, such that larvae and adults can evolve independently of each other in response to different selection pressures (Werner 1988; Ebenman 1992; Moran 1994). This allows individuals to adopt different phenotypes during their life cycle, each specialized on different tasks such as dispersal, mate finding, or food acquisition (Moran 1994). A body plan that is needed for efficient mate finding, for example, may often be very different from a body plan needed for efficient feeding (Moran 1994). However, genetic correlations among the phenotypes expressed during different life stages prevent their independent evolution (Schluter et al. 1991). This is because adaptations beneficial for one life stage can be disadvantageous for another life stage. The adaptive-decoupling hypothesis predicts that metamorphosis breaks up these genetic correlations and therefore permits the independent evolutionary response of phenotypes expressed during different life stages (Werner 1988; Ebenman 1992; Moran 1994). Although many studies have shown that genetic correlations persist, to some extent, across the metamorphic boundary, so that larval traits keep influencing postmetamorphic performance (Crean et al. 2011; Fellous and Lazzaro 2011;

Aguirre et al. 2014), there is considerable evidence that meta-morphosis allows for the decoupling of phenotypic evolution (Moran 1994; Parichy 1998; Saenko et al. 2012; Aguirre et al. 2014; Sherratt et al. 2017). While metamorphosis can therefore be highly beneficial for organisms, it typically is a costly process. For instance, during metamorphosis species not only often lose body mass but also tend to be more vulnerable to predation (Wassersug and Sperry 1977; Geffen et al. 2007). This raises the question of under which ecological conditions the benefits of metamorphosis can outweigh its disadvantages.

Metamorphosis is likely to be especially advantageous in species that change diet during ontogeny. It has even been suggested that ontogenetic changes in diet constituted the first steps in evolutionary history toward life cycles with metamorphosis (Wassersug 1975; Wilbur 1980; Werner 1988; Ebenman 1992; Nielsen 1998; Schoch 2009). Species with an ontogenetic diet shift face a fundamental trade-off between their performance early in life and that late in life, since different food types often require different morphologies (Werner 1977; Ebenman 1992; Svanbäck and Eklov 2003). Recent research has shown that individuals will change their diet during ontogeny when this increases their energy intake (ten Brink and de Roos 2017). However, it is not possible for individuals to specialize on a new food source when this excessively reduces their performance on the food source they depended on early in life (ten Brink and de Roos 2017). These results suggest that strong selection pressures exist toward decoupling the phenotypes expressed during different life stages, so that an individual's performance on different food sources can be maximized as independently as possible.

Although most animal species undergo metamorphosis, only a few theoretical studies have investigated the origin of metamorphosis in species exhibiting ontogenetic diet shifts during their life cycle (Istock 1967; Werner 1988; Ebenman 1992). One of the first analyses of this problem is presented in the paper by Istock (1967). Using an age-structured model, Istock (1967) examined whether a population in which individuals undergo metamorphosis could invade and persist in a community of species without metamorphosis. In his model, the two different life stages interfaced by metamorphosis occupy separate niches and evolve independently of each other. Istock (1967) argued that a population in which individuals undergo metamorphosis can invade in a community of species without metamorphosis. However, natural selection will favor the elimination of either the adult or the larval stage, such that on an evolutionary timescale metamorphosis ultimately disappears. On this basis, he concluded that metamorphosis is an evolutionarily unstable strategy. In contrast to Istock, Ebenman (1992) considered fitness maximization at the individual level in an age-structured model and concluded that metamorphosis easily evolves in species that change resources during ontogeny. Other theoretical studies of the evolution of metamorphosis have mainly focused on the optimal timing of metamorphosis (Werner and Gilliam 1984; Werner 1988) and not on the question of under which conditions metamorphosis evolves in the first place.

An important shortcoming of all the aforementioned studies is that they do not take into account the feedback between individuals and their environment. In most species, growth and reproduction, which crucially influence fitness, are largely determined by food intake (de Roos and Persson 2013). Diet shifts and metamorphosis change this food intake and thus also the densities of the different food sources. This change in food densities, in turn, alters the food intake of individuals and therefore their fitness. Hence, the feedback loop between individuals and their environment cannot be ignored in studies of the evolution of metamorphosis.

Here we study the origin of metamorphosis in species that undergo an ontogenetic diet shift, taking into account the just-highlighted feedback loop between individuals and their environment. To do so, we use a size-structured consumer-resource model in conjunction with the adaptive-dynamics approach. Adaptive-dynamics theory enables the exploration of evolution in realistic ecological contexts (Metz et al. 1992; Dieckmann and Law 1996; Geritz et al. 1998). We assume that individuals are limited to foraging on a primary food source when they are small. Larger individuals additionally have access to a secondary food source, occurring in a different habitat. Individuals prefer the habitat where their food intake is the highest. Furthermore, we assume that individuals can specialize on the consumption of either the primary food source or the secondary food source, leading to a trade-off between their foraging success early in life and that late in life. Metamorphosis allows for the decoupling of the different life stages, such that small and large individuals can evolve independently of each other. However, since metamorphosis is costly, we assume that metamorphosing individuals lose body mass and have a high probability of dying.

To understand the ecological conditions that allow for the evolution of metamorphosis, we first study how specialization on the secondary food source is hindered by the aforementioned trade-off. On this basis, we examine whether and to what extent metamorphosis evolves, depending on the supply rate of the secondary food source. Finally, we investigate whether and when metamorphosis disappears when the ecological conditions under which it has evolved change.

Methods

Population Dynamics

We use a size-structured consumer-resource model based on the model described by Persson et al. (1998) to study

the evolution of metamorphosis in species changing their diet during ontogeny. In contrast to Persson et al. (1998), we assume, for the sake of simplicity, continuous reproduction and equilibrium conditions. Extending the model by Persson et al. (1998), we introduce a second food source. Both food sources are assumed to be unstructured. The primary food source, with population density X_1, is available to all individuals, whereas the secondary food source, with population density X_2, is available only to individuals exceeding a threshold size. Both food sources follow semi-chemostat dynamics and reach densities of $X_{1, max}$ and $X_{2, max}$ in the absence of the consumer population. It is assumed that the two food sources occur in two distinct habitats of equal size (it has been shown that relaxing this assumption has little impact on results; ten Brink and de Roos 2017).

The feeding, growth, reproduction, and mortality of an individual are functions of two individual-state variables, measuring an individual's irreversible mass (such as bones and organs) and its reversible mass (such as fat, gonads, or liver tissue), denoted x and y, respectively. The maximum attainable reversible body mass is given by $y_{max} = q_J x$, where q_J is a dimensionless scaling constant describing an individual's maximum fraction of reversible to irreversible mass (Persson et al. 1998). An individual's total body length, attack rate, and handling time are assumed to depend only on its standardized body mass $w = x + y_{max} = x(1 + q_J)$ (Persson et al. 1998). In general, an individual's reversible mass can be used, and thus decrease below y_{max}, for two purposes: to cover its basic metabolism under starvation conditions and to be invested in metamorphosis (see "Evolving Traits and Life-History Trade-Offs"). When population dynamics are equilibrated, starvation conditions do
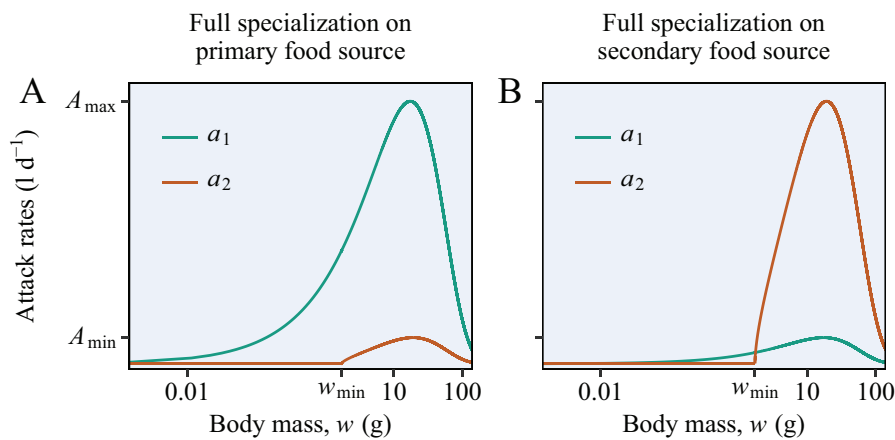
not occur, so an individual's reversible mass is fully available for covering its costs of metamorphosis.

Newborn individuals are born at an irreversible body mass x_b and are assumed to possess the maximum amount $q_J x_b$ of reversible body mass. Since starvation conditions do not occur, the ratio between irreversible and reversible mass is constant until individuals reach the threshold body mass at which metamorphosis can occur: larvae (L) potentially undergo metamorphosis and become juveniles (J) when reaching the standardized body mass w_J. Juveniles mature into adults (A) and start reproducing when reaching the standardized body mass w_A. The secondary food source becomes available to individuals after they reach the standardized body mass w_{min}.

The foraging rates of individuals initially increase with their body mass, because of enhanced visual capacity and locomotion ability, but then decrease with body mass when individuals are larger, because of a reduced ability to perceive small prey and to make fine-tuned maneuvers. To describe this fundamental dependence of an individual's attack rates on its standardized body mass in foraging on the primary and secondary food sources, we use the following hump-shaped functions (fig. 1), respectively,

$$a_1(w) = A_1 \left(\frac{w}{w_0} \exp\left(1 - \frac{w}{w_0} \right) \right)^\alpha, \tag{1a}$$

$$a_2(w) = \begin{cases} 0 & \text{if } w \leq w_{min}, \\ A_2 \left(\frac{w - w_{min}}{w_0} \exp\left(1 - \frac{w - w_{min}}{w_0} \right) \right)^\alpha & \text{otherwise.} \end{cases} \tag{1b}$$

Figure 1: In the absence of metamorphosis, individuals can specialize on either the primary food source (*A*) or the secondary food source (*B*). The figure shows the attack rates (L day^{-1}) on the primary food source (green) and secondary food source (orange) as functions of a consumer's body mass (g) *A*, Individuals do not undergo metamorphosis and are fully specialized on the primary food source ($\psi_i = 0$ for all life stages $i = $ L, J, A). *B*, Individuals do not undergo metamorphosis and are fully specialized on the secondary food source ($\psi_i = 1$ for all life stages i). Parameter values are as shown in tables 2 and 3.

In these equations, A_1 and A_2 are the maximum attack rates individuals can reach when their body mass equals w_0 and $w_0 + w_{min}$ on the primary and secondary food sources, respectively. The parameter 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. In the absence of an ontogenetic diet shift and all else being equal, α determines the competitive ability of an individual of a given size, which can be characterized by the food density at which the individual can just meet its maintenance requirements (Persson et al. 1998). By choosing the value $\alpha = 0.6$, we assume that small individuals have, in the absence of an ontogenetic diet shift, a higher competitive ability than large individuals (Persson et al. 1998).

We assume a Holling type 2 functional response for individuals feeding on two food sources that occur in different habitats, following McCann et al. (2005; see app. A for the derivation; apps. A–G are available online). The food intake of an individual with standardized body mass w can be written as

$$I(w, X_1, X_2) = \frac{\phi(w, X_1, X_2)a_1(w)X_1 + (1 - \phi(w, X_1, X_2))a_2(w)X_2}{1 + h(w)[\phi(w, X_1, X_2)a_1(w)X_1 + (1 - \phi(w, X_1, X_2))a_2(w)X_2]},$$ (2a)

with handling time

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3} e^{\zeta_4 w}.$$ (2b)

In equation (2a), $\phi(w, X_1, X_2)$ is the relative preference of consumers for the primary food source, which depends on the profitability of this food compared to the secondary food source. Since we assume that both food sources have the same nutritional value and handling time, the relative profitabilities of the food sources depend only on the resource densities and the size-dependent attack rates. The relative preference for the primary food source is then calculated as

$$\phi(w, X_1, X_2) = \frac{1}{1 + \exp(\sigma(a_2(w)X_2 - a_1(w)X_1))}.$$ (3)

In this equation, the parameter σ determines the steepness of the sigmoid curve at equal food source profitabilities, $a_2(w)X_2 = a_1(w)X_1$ (de Roos et al. 2002). The higher the parameter σ, the better consumers are in choosing the most profitable habitat and the larger the fraction of the corresponding food source is in their diet.

The energy intake rate of an individual equals its food intake rate multiplied by a conversion factor k_e. Assimilated energy is first used to cover maintenance costs. An individual's metabolic-cost rate allometrically increases with its total body mass $x + y$,

$$E_m(x, y) = p_1(x + y)^{p_2}.$$ (4)

The biomass production rate of larvae and juveniles is given by the difference between their energy intake rate and their maintenance cost rate,

$$E_g(x, y, X_1, X_2) = k_e I(w, X_1, X_2) - E_m(x, y).$$ (5)

Of this biomass production, larvae and juveniles allocate a fraction $\kappa_J(x, y)$ to growth in irreversible mass,

$$\kappa_J(x, y) = \frac{y}{(1 + q_J)q_J x},$$ (6a)

with the remaining fraction being allocated to growth in reversible mass. If the amount of reversible mass is at its maximum ($y = q_J x$), a fraction $1/(1 + q_J)$ is therefore allocated to growth in irreversible mass and a fraction $q_J/(1 + q_J)$ to growth in reversible mass (eq. [6a]), keeping the amount of reversible mass equal to its maximum ($y = q_J x$). When the amount of reversible mass, y, is less (more) than the maximum amount, the allocation function distributes more (less) of the biomass production to reversible mass. This allocation function therefore ensures that individuals always approach a constant ratio of irreversible to reversible mass, such that $y = y_{max} = q_J x$. Since adults also invest in reproduction, they allocate a lower fraction $\kappa_A(x, y)$ to growth in irreversible mass,

$$\kappa_A(x, y) = \frac{y}{(1 + q_A)q_A x},$$ (6b)

with the remainder being allocated to growth in reversible mass and reproduction. To ensure that individuals always invest in reversible mass in such a way that the ratio of y to x either remains at 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 allocate a fraction $\kappa_R(x, y)$ to reversible mass, according to

$$\kappa_R(x, y) = \begin{cases} 1 - \kappa_A(x, y) & \text{if } y < q_J x, \\ (1 - \kappa_J(x, y))\dfrac{\kappa_A(x, y)}{\kappa_J(x, y)} & \text{otherwise.} \end{cases}$$ (7)

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

$$b(x, y, X_1, X_2)$$
$$= \begin{cases} 0 & \text{if } y < q_J x, \\ \left(1 - \dfrac{\kappa_A(x, y)}{\kappa_J(x, y)}\right)\dfrac{\eta E_g(x, y, X_1, X_2)}{(1 + q_J)x_b} & \text{otherwise,} \end{cases}$$ (8)

where the factor η converts from energy to body mass.

Because an individual's total body mass $x + y$ equals its standardized body mass w before metamorphosis and since its reversible body mass y is restored to $y_{max} = q_J x$ soon after metamorphosis, so that its total body mass again equals

its standardized body mass, we from now on simply use the term "body mass" to refer to the standardized body mass w.

Following Persson et al. (1998), metabolic costs and handling times are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food sources. Our 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 parameter values related to energetics are based on a reference temperature of 19°C. Processes taking place during the winter season are ignored.

Model variables are listed in table 1, and model parameters are listed in table 2, together with their default values.

Evolving Traits and Life-History Trade-Offs

We assume that the two food sources require different morphologies to be effectively utilized. This means that a morphology that is optimal for feeding on the primary food source is not very efficient in feeding on the secondary food source, and vice versa. We furthermore assume that metamorphosis can decouple the morphologies at different life stages such that an individual can adopt different morphologies before and after metamorphosis. To incorporate this, we consider a linear trade-off between the two attack rate constants A_{1i} and A_{2i} within a certain life stage (larvae, juveniles, or adults; $i = L, J, A$), assuming that these constants can vary between A_{min} and A_{max},

$$A_{1i} = (1 - \psi_i)(A_{max} - A_{min}) + A_{min},$$
$$A_{2i} = \psi_i(A_{max} - A_{min}) + A_{min}. \tag{9}$$

In these equations, $0 \leq \psi_i \leq 1$ is the relative degree of specialization of a life stage ($i = L, J, A$) on the secondary food source. The value $\psi_i = 0$ means that individuals in life stage i are completely specialized on the primary food source and not very efficient in feeding on the secondary food source (fig. 1A). Conversely, the value $\psi_i = 1$ means that individuals in life stage i are completely specialized on the secondary food source and not very efficient in feed-

ing on the primary food source (fig. 1B). In the absence of metamorphosis, the degree of specialization is equal for all three life stages ($\psi_L = \psi_J = \psi_A$).

Because larger individuals can feed on the secondary food source, whereas smaller individuals cannot, there is a possible conflict between maximizing feeding performance across all life stages. For small individuals, it is important to be specialized on the primary food source, while later in life it becomes important to be specialized on the secondary food source as well. Metamorphosis can decouple the different life stages such that they can adapt independently of each other—it unlinks the specialization between the different life stages. In other words, individuals with metamorphosis that specialize on the secondary food source later in life are not specialized on the primary food source, but this does not affect their offspring. Metamorphosis decouples the different stages as follows:

$$\psi_A = \psi_J = \min(1, \psi_L + \theta), \tag{10}$$

where θ represents the extent of the metamorphosis. Individuals without metamorphosis have the same morphology over their lifetime ($\psi_L = \psi_J = \psi_A$), whereas individuals with full metamorphosis can specialize on the primary food source when small and on the secondary food source when large. Since the benefits of metamorphosis depend on an individual's body mass, we examine the body mass at metamorphosis w_J as one of the evolving traits.

Metamorphosis is an energetically costly process (Sheridan and Kao 1998; Thiyagarajan et al. 2003; Geffen et al. 2007). We therefore assume that individuals have to invest reversible mass to cover those costs. When individuals reach the body size at which they may undergo metamorphosis ($w_J = x + y$, with $x = x_J$ and $y = q_J x_J$), they lose $\theta x_J(q_J - q_s)$ of their reversible body mass. In this equation, the parameter q_s is the ratio of y to x of an individual immediately after full metamorphosis ($\theta = 1$). The lower q_s, the more expensive is the metamorphosis.

Metamorphosis not only is energetically costly but can also be risky. For example, in some species, metamorphosing individuals are more vulnerable to predation, compared

Table 1: Model variables and evolving traits

Variable	Description	Unit	Range
X_1	Density of primary food source	g L^{-1}	$0 - X_{1, max}$
X_2	Density of secondary food source	g L^{-1}	$0 - X_{2, max}$
x	Irreversible body mass	g	$\geq x_b$
y	Reversible body mass	g	$q_J x_b - y_{max}$
ψ_i	Degree of specialization at life stage i on the secondary food source[a]	...	$0 - 1$
θ	Extent of metamorphosis	...	$0 - 1$
w_J	Standardized body mass at metamorphosis	g	$\geq (1 + q_J)x_b$

[a] Life stage $i = $ L (larva), J (juvenile), or A (adult).

Table 2: Model parameters and their default values from Persson et al. (1998)

Parameter	Description	Unit	Default value
δ	Food source turnover rate	day^{-1}	.1
$X_{1,\,max}$	Maximum biomass density of primary food source	g L^{-1}	.000055
$X_{2,\,max}$	Maximum biomass density of secondary food source	g L^{-1}	Variable
x_b	Irreversible body mass of newborns	g	.000804
w_A	Standardized body mass at maturation	g	8.71
w_0	Standardized body mass at which maximum attack rate is attained on primary food source	g	17.42
α	Exponent in attack rate functions	. . .	.6
ζ_1	Constant in handling-time function	days	.36[a]
ζ_2	Constant in handling-time function	days g$^{\zeta_3}$	7.45[a]
ζ_3	Slope of decrease in handling time at small consumer sizes	. . .	.68
ζ_4	Slope of increase in handling time at large consumer sizes	g^{-1}	1.15×10^{-3}
p_1	Metabolic constant	g$^{1-p_2}$ day^{-1}	.033
p_2	Metabolic exponent	. . .	.77
k_e	Metabolic conversion factor	. . .	.61[a]
q_J	Constant determining maximum reversible body mass	. . .	.742
q_A	Constant in adult energy allocation function	. . .	1
η	Gonad-offspring conversion factor	g	.5
μ	Background mortality rate	day^{-1}	.01

[a] These are the original values from Persson et al. (1998) divided by 1.1×10^{-5} g (the mass of a prey individual) to express prey densities in g L^{-1} instead of individuals L^{-1}.

to pre- and postmetamorphic individuals (Wassersug and Sperry 1977; Hadfield 2000). Furthermore, during metamorphosis there is a high risk of developmental mistakes in phenotypic expression. Therefore, we assume that individuals may die during metamorphosis with probability $\rho\theta$. The parameter ρ is the probability of dying during metamorphosis when undergoing full metamorphosis ($\theta = 1$).

Parameters related to specialization and metamorphosis are listed in table 3, and the corresponding evolving traits are listed in table 1. The equations and functions describing the full model are listed in appendix G.

Evolutionary Dynamics

We use adaptive-dynamics theory (Metz et al. 1992; Dieckmann and Law 1996; Geritz et al. 1998) to study how the

specialization of larvae ψ_L, the extent of metamorphosis θ, and the body mass at metamorphosis w_J evolve. Specifically, we consider populations that evolve through the fixation of small and rare mutations in these traits while otherwise being monomorphic. This gives rise to evolutionary rates that are proportional to the selection gradient (Dieckmann and Law 1996). We thus use the canonical equation of adaptive-dynamics theory (Dieckmann and Law 1996; Durinx et al. 2008) to determine the resultant evolutionary trajectories.

For the numerical illustrations shown in our figures, we assume that mutations in the three evolving traits ψ_L, θ, and w_J are uncorrelated and have the same standard deviation (the mutational variance-covariance matrix is thus proportional to the identity matrix). Since all evolutionary end points we have found in this study can be shown to possess strong convergence stability, changing the mutational

Table 3: Model parameters and their default values related to specialization and metamorphosis

Parameter	Description	Unit	Default value
A_{max}	Maximum value of attack rate constants A_1 and A_2	L day^{-1}	10^5
A_{min}	Minimum value of attack rate constants A_1 and A_2	L day^{-1}	10^4
w_{min}	Standardized body mass at which the secondary food source becomes available	g	1.742
σ	Constant in habitat-switching rate	days g^{-1}	10
q_s	Ratio of reversible to irreversible body mass immediately after full metamorphosis	. . .	.2
ρ	Probability of dying during full metamorphosis	. . .	.5

variance-covariance matrix, by considering nonuniform variances or nonvanishing covariances among the three evolving traits, has no effect on the location and convergence stability of these evolutionary end points (Leimar 2009).

Evolutionarily singular strategies (Geritz et al. 1998) are defined by the vanishing of the evolutionary rates of all considered traits, corresponding to the absence of any directional selection. We continue trait combinations at these potential evolutionary outcomes as functions of the supply rate of the secondary food source and determine whether the evolutionarily singular strategies are convergence stable and/or evolutionarily stable, following Geritz et al. (1998) and Leimar (2009). To study how the evolution of metamorphosis depends on the supply rate $\delta X_{2,\max}$ of the secondary food source, we vary $X_{2,\max}$ while keeping δ constant.

Model Analysis

All analyses are performed with the R package PSPManalysis (de Roos 2017). Based on the computational approach described by Kirkilionis et al. (2001), Diekmann et al. (2003), and de Roos (2008), the PSPManalysis package numerically computes the ecological equilibrium of physiologically structured population models as a function of any model parameter, by iteratively computing the food source densities for which the lifetime reproductive success R_0 of an individual equals 1. In nonlinear size-structured models, R_0 depends on an individual's size-specific rates of feeding, growth, mortality, and fecundity, so the PSPManalysis package numerically integrates a set of coupled ordinary differential equations that describe how these rates change over an individual's lifetime.

The PSPManalysis package can automatically detect and classify evolutionarily singular strategies according to the classification of Geritz et al. (1998). The package can numerically continue these evolutionarily singular strategies as functions of any (second) model parameter (de Roos 2017). The package can furthermore calculate derived quantities such as the expected food intake of an individual during its lifetime. We use these quantities to calculate the expected fraction of the secondary food source in the diet of juveniles and adults ($w > w_J$, or $w > w_{\min}$ in the absence of metamorphosis) to characterize the degree of the ontogenetic diet shift. The model-specific file needed for the PSPManalysis can be found in the supplementary information, available online, together with an R script that executes all calculations made in our analyses.[1]

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1. Code that appears in the *American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

Results

In the first part of this section, we show that—in the absence of metamorphosis—the trade-off between foraging success early in life and that late in life impedes specialization on the secondary food source. In the second part, we show that metamorphosis can evolve to allow individuals to specialize on the primary food source when small and on the secondary food source when large. In the last part, we show that metamorphosis can evolve only under limited ecological conditions; however, once evolved, it is a very robust life-history strategy.

Without Metamorphosis, Individuals Specialize on the Primary Food Source

It has been shown that, even when it is beneficial for individuals to change diet during their ontogeny, specialization on a new food source is not possible in the absence of metamorphosis (ten Brink and de Roos 2017). These results are mostly corroborated by the analysis of our model, and therefore we describe our corresponding analysis only briefly.

In contrast to ten Brink and de Roos (2017), we assume that food choice is a behavioral trait and does not evolve. Because of the choice of the trade-off function (eq. [9]) and the preference function (eq. [3]), large individuals ($w > w_{\min}$) always include both food sources in their diet. However, when the fraction of the secondary food source in the diet is graphically indistinguishable from 0 or 1, we state, for convenience, that large individuals completely feed on the primary or the secondary food source, respectively. In this section, we assume that metamorphosis is absent ($\theta = 0$) and that only specialization evolves. Without metamorphosis, all individuals have the same morphology ($\psi_L = \psi_J = \psi_A$, which we denote by ψ), so body mass at metamorphosis w_J disappears from the model formulation. For low values of both the specialization trait ψ and the supply rate of the secondary food source, there are two stable ecological equilibria, separated by an unstable one. Nevertheless, for the parameter settings at which this ecological bistability occurs, evolution always reaches the same evolutionary outcome, independent of the initially realized ecological equilibrium. We therefore ignore this ecological bistability, since it is inconsequential on the evolutionary timescale. All evolutionary outcomes described in this subsection are continuously stable strategies (CSSs) and therefore locally evolutionarily stable (Geritz et al. 1998).

Specialization on a secondary food source is not possible when individuals are initially specialized on the primary food source (fig. 2A), independent of the supply rate of the secondary food source. When individuals are initially specialized on the secondary food source, they evolutionarily lose
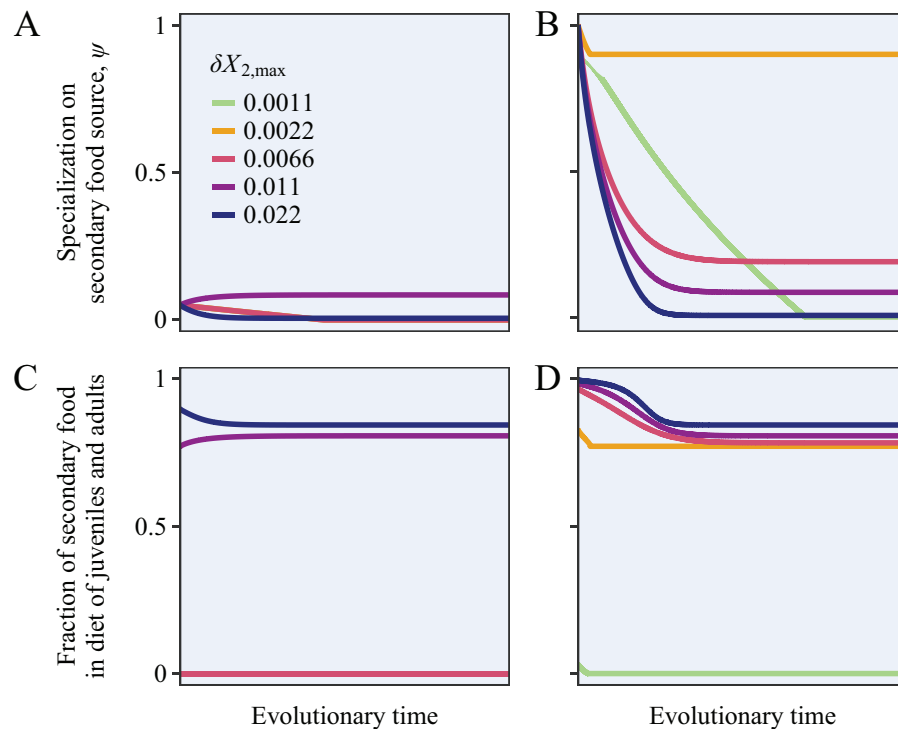
Figure 2: Evolutionary dynamics of specialization in the absence of metamorphosis for five different supply rates of the secondary food source. Specialization on the secondary food source is possible only for intermediate supply rates of the secondary food source (*B*) and not for low or high supply rates (see app. B, available online, for an explanation), even when large individuals feed mainly on the secondary food source (*C*, *D*). *A*, *B*, Evolutionary dynamics of specialization when individuals are initially specialized on the primary food source (*A*) or the secondary food source (*B*). *C*, *D*, Resultant changes in the fraction of the secondary food source in the diet of large individuals when individuals are initially specialized on the primary food source (*C*) or the secondary food source (*D*). Light-colored lines indicate lower supply rates of the secondary food source, whereas dark-colored lines indicate higher supply rates: $\delta X_{2,\max} = 0.0011$ (green), 0.0022 (orange), 0.0066 (pink), 0.011 (purple), or 0.022 (blue) mg L^{-1} day^{-1}. In *A* and *C*, the green, orange, and pink lines lie on top of each other. The initial value of $\psi = \psi_L = \psi_J = \psi_A$ equals 0.05 (*A*, *C*) or 1 (*B*, *D*). Other parameter values are as shown in tables 2 and 3.

this specialization in case of low or high supply rates of the secondary food source but not in case of intermediate supply rates (fig. 2*B*). Even though specialization is often not possible, large individuals do include the secondary food source in their diet for intermediate or high supply rates (fig. 2*C*, 2*D*).

These results underscore that, without metamorphosis, unresolvable tensions arise for species faced with the opportunity of specializing on a secondary food source. Even though large individuals mainly feed on this food source, specialization is possible only for a narrow range of conditions, in which case small individuals pay high costs, as they end up having poor foraging capacity (see app. B for more details). Accordingly, a decoupling of the morphologies expressed during different life stages is favored by strong selection pressures, such that large individuals can specialize on the secondary food source without negatively affecting their offspring's specialization on the primary food source. Even in the rare cases in which specialization on the secondary food source evolves without metamorphosis, there still is selection for metamorphosis, so as to allow small individuals to specialize again on the primary food source.

Metamorphosis Evolves to Enable Independent Specialization

In this and the following subsection, we study the joint evolution of the extent of metamorphosis θ, the body mass at metamorphosis w_J, and the specialization of larvae ψ_L.

Metamorphosis breaks up the trade-off between the attack rates on the two food sources, so that small individuals can be specialized on the primary food source even when large individuals are specialized on the secondary food source (fig. 3*A*). We find that metamorphosis can evolve either to enable large individuals to specialize on the secondary food source (fig. 3*B*) or to enable small individuals to specialize on the primary food source (fig. 3*C*).

Figure 3*B* shows an evolutionary time series that is typical when individuals initially are mainly specialized on the
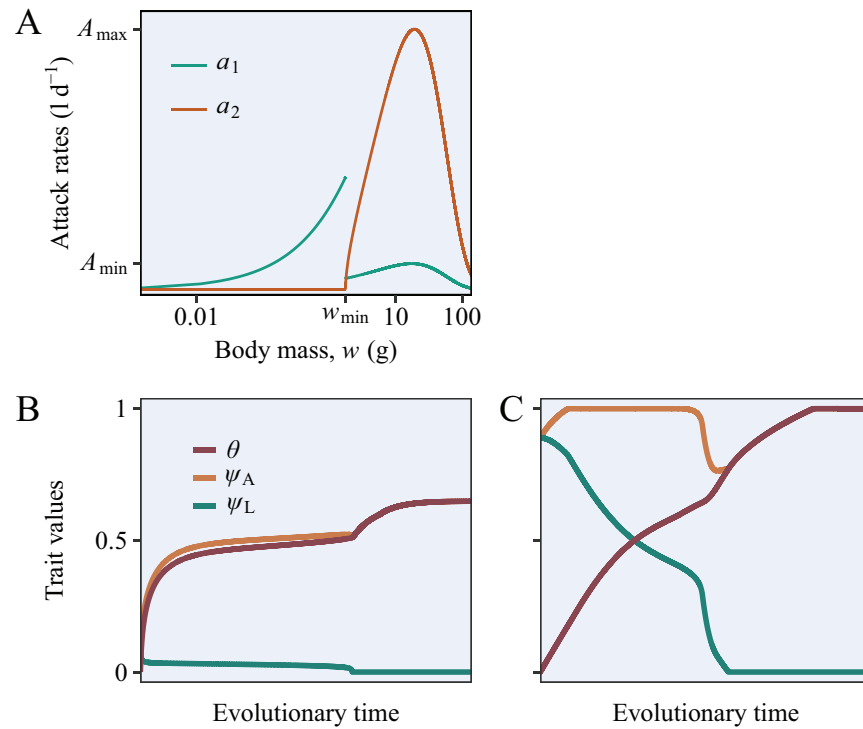
Figure 3: Metamorphosis can evolve such that individuals are specialized on the primary food source when small and on the secondary food source when large. *A*, Attack rates (L day^{-1}) on the primary food source (green) and the secondary food source (orange), as functions of a consumer's body mass (g) when individuals undergo full metamorphosis. *B*, *C*, Evolutionary dynamics of the extent of metamorphosis (dark red) and of the specialization on the secondary food source for larvae (green) and for juveniles and adults (orange) when individuals are initially specialized on the primary food source (*B*) or the secondary food source (*C*). At the kinks in *B* and *C* the system switches to a different ecological attractor, where the selection gradient is slightly stronger than before. Parameters: $\delta X_{2, max} = 0.011$ (*B*) or 0.0022 (*C*) mg L^{-1} day^{-1}. The body mass at metamorphosis is $w_J = w_{min} = 1.742$ g in *A*, which approximately equals the body mass to which metamorphosis eventually evolves in *B* and *C*. Other parameter values are as shown in tables 2 and 3.

primary food source and the supply rate of the secondary food source is high enough for large individuals to include the secondary food source in their diet. The extent of metamorphosis (dark red line in fig. 3*B*) increases over evolutionary time, while the specialization trait of larvae ψ_L (green line in fig. 3*B*) slightly decreases over evolutionary time. Large individuals therefore partly specialize on the secondary food source (orange line in fig. 3*B*), whereas small individuals fully specialize on the primary food source ($\psi_L = 0$).

Figure 3*C* shows an evolutionary time series that is typical when individuals are initially specialized on the secondary food source. We find that even in this case, metamorphosis evolves such that small and large individuals can specialize on the primary and secondary food sources, respectively. The extent of metamorphosis θ (dark red line in fig. 3*C*) increases over evolutionary time, while larvae become more and more specialized on the primary food source as their specialization trait ψ_L decreases (green line in fig. 3*C*). Since ψ_L evolves faster than θ, as the former is subject to stronger selection than the latter, adults become temporarily less specialized on the secondary food source

(orange line fig. 3*C*). Ultimately, however, a full metamorphosis evolves, so that small individuals are fully specialized on the primary food source ($\psi_L = 0$), whereas large individuals are fully specialized on the secondary food source ($\psi_J = \psi_A = 1$). In this case, large individuals thus invest in metamorphosis not to improve their own performance but to improve the performance of their offspring. Accordingly, the morphology of small individuals, which was initially specialized on feeding on the secondary food source, diverges over evolutionary time from that of large individuals.

In summary, metamorphosis can evolve either to enable large individuals to specialize on the secondary food source (fig. 3*B*) or to enable small individuals to specialize on the primary food source (fig. 3*C*).

Metamorphosis Evolves Only When the Supply Rate Exceeds a High Threshold

In the previous subsection, we showed that specialization on the secondary food source is hardly possible without

metamorphosis. For simplicity, we now therefore focus on the conditions under which metamorphosis evolves when individuals are initially specialized on the primary food source (fig. 3*B*). In appendix C, we analogously show under which conditions metamorphosis evolves when individuals are initially specialized on the secondary food source.

The extent of metamorphosis θ and the larval specialization on the secondary food source ψ_L jointly determine the specialization on the secondary food source of juveniles and adults according to equation (10). We find that, for an initial value 0, ψ_L never evolves away from 0, so $\psi_J = \psi_A = \theta$ (eq. [10]). It is hence sufficient to study and discuss the joint evolution of θ and the body mass at metamorphosis w_J. Whether or not metamorphosis starts to evolve is hardly influenced by the initial body mass at metamorphosis w_J. We therefore assume that the body mass at metamorphosis, w_J, initially equals the body mass at which the secondary food source becomes available, w_{min}.

Figure 4*A* shows that metamorphosis originates abruptly when the supply rate of the secondary food source becomes sufficiently high. Surprisingly, however, metamorphosis is not lost when the supply of the secondary food source decreases, which results in population extinction through evolutionary trapping when this supply becomes too low. These results can be explained by the trade-off between the attack rates and the feedback between the food sources and the consumers, as follows. We have seen above that, in a population in which individuals do not undergo metamorphosis, specialization on the secondary food source is not possible; therefore, individuals have a low foraging efficiency on this food source. For low values of the supply rate of the secondary food source $\delta X_{2,max}$, individuals barely feed on it (fig. 4*B*), and therefore it does not pay to evolve a metamorphosis, since the costs are very high while the benefits are low. The fraction of secondary food in the diet of large individuals increases with increasing supply rates, even though individuals are not specialized in feeding on this food source ($\psi_L = \psi_J = \psi_A = 0$; fig. 4*B*). After $\delta X_{2,max}$ has reached a certain threshold such that the secondary food source is a substantial part of the diet of large individuals (after the vertical dotted line in fig. 4*B*), it becomes beneficial to invest in metamorphosis. A small investment in metamorphosis increases the feeding efficiency on the secondary food source, which in turn increases the absolute amount of this food source in the diet of large individuals. Because of this, it is beneficial to invest even more in metamorphosis. Therefore, the degree of metamorphosis can suddenly evolve from 0 to high values, so that small individuals have a morphology specialized on feeding on the primary food source while large individuals have a morphology specialized on feeding on the secondary food source.

While increasing the extent of metamorphosis will increase the food intake of large individuals and therefore
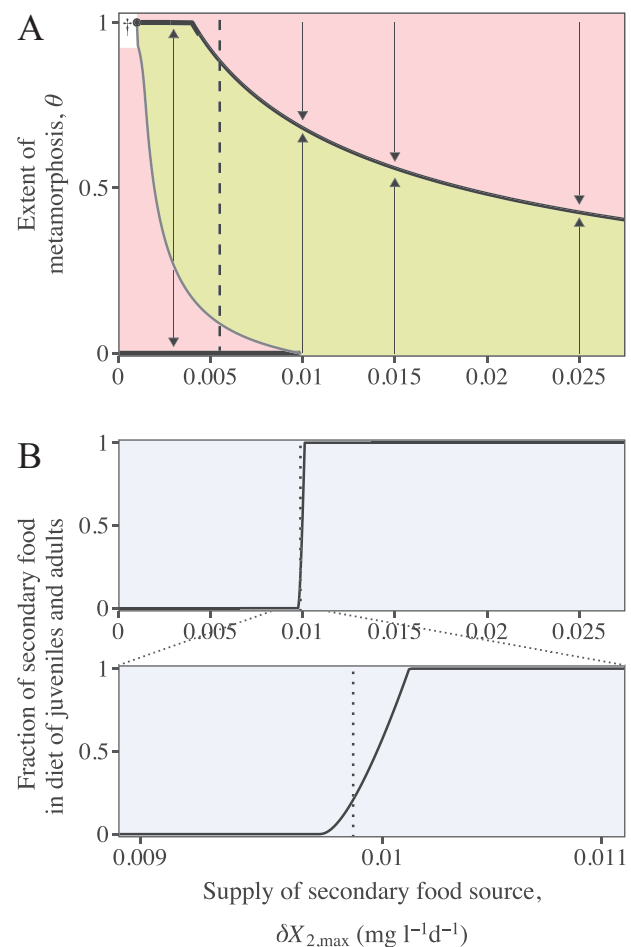
Figure 4: Metamorphosis originates abruptly when the supply rate of the secondary food source becomes sufficiently high (*A*), so that a significant fraction of the diet of large individuals consists of the secondary food source (*B*). When metamorphosis has evolved, it is not lost when the supply rate of the secondary food source decreases, which results in population extinction through evolutionary trapping when this supply becomes too low. *A*, Evolution of the extent of metamorphosis as a function of the supply rate of the secondary food source (mg L^{-1} day^{-1}). Thick black lines indicate continuously stable strategies, whereas the thin gray line indicates evolutionary repellers. Arrows show the direction of evolution. In the red area, evolution decreases the extent of metamorphosis, whereas in the green area, evolution increases the extent of metamorphosis. The population cannot persist in the white area marked with a dagger (†). The dashed line indicates the supply rate of the primary food source. *B*, Fraction of the secondary food source in the diet of juveniles and adults in the absence of metamorphosis ($\psi_L = \psi_J = \psi_A = 0$), as a function of the supply rate of the secondary food source. The vertical dotted line indicates the critical supply rate at which the extent of metamorphosis evolves away from 0. This happens when a significant fraction of the diet of juveniles and adults consists of the secondary food source. Parameter values are as shown in tables 2 and 3.

their birth rate, metamorphosis is always costly: metamorphosis decreases the probability that an individual survives until adulthood and slows down maturation, because of the energy investment metamorphosis requires. When the supply rate of the secondary food sources increases, the extent of metamorphosis evolves to lower values because of these costs (fig. 4*A*). When the supply rate of the secondary food source is high, there is plenty of food available for the metamorphosed individuals. In this case, the gains of increased efficiency do not outweigh the costs of investing more in metamorphosis; in other words, the necessity for changing morphology decreases with increasing supply rate of the secondary food source.

Once Evolved, Metamorphosis Does Not Disappear When Conditions Change

Once metamorphosis has evolved, it does not disappear when the secondary food source becomes less productive. Remarkably, the extent of metamorphosis even increases when the supply rate of the secondary food source decreases (fig. 4*A*). This seemingly paradoxical result can be explained by the fact that metamorphosed individuals are specialized on the secondary food source and do not feed on the primary food source at all. Individuals investing less in metamorphosis thereby increase their foraging efficiency on the primary food source when large but do not benefit from this, since this food source is not used after metamorphosis. Conversely, individuals investing more in metamorphosis increase their foraging efficiency on the secondary food source, which is beneficial when the supply rate of this food source diminishes.

Surprisingly, when the supply rate of the secondary food source is very low, metamorphosis does not disappear. Instead, the population ultimately becomes extinct (fig. 5*B*). We show in figure 5*A* that the less productive the secondary food source, the later in life metamorphosis occurs. With decreasing values of the supply rate of the secondary food source, there is less of it available, which makes it beneficial for individuals to postpone their metamorphosis and feed on the primary food source for longer. Because metamorphosed individuals are very efficient in feeding on the secondary food source, they will continue to feed on it even though its supply rate decreases. Our findings indicate that there is no selection to reduce the extent of metamorphosis when the supply rate of the secondary food source is decreasing. However, we find that the size at metamorphosis is always smaller than the size at maturation. Adults therefore rely mainly on the secondary food source for their reproduction. When the supply of this food source becomes too low, adults do not have enough food to reproduce, and the population becomes extinct. Since the population's evolutionary attractor collides with its extinction boundary, metamorphosis can be an evolutionary trap (Dieckmann and Ferrière 2004; Ferrière and Legendre 2013).

Robustness and Generality of Results

Our results turn out to be robust under many different parameter combinations. Different values of the model param-
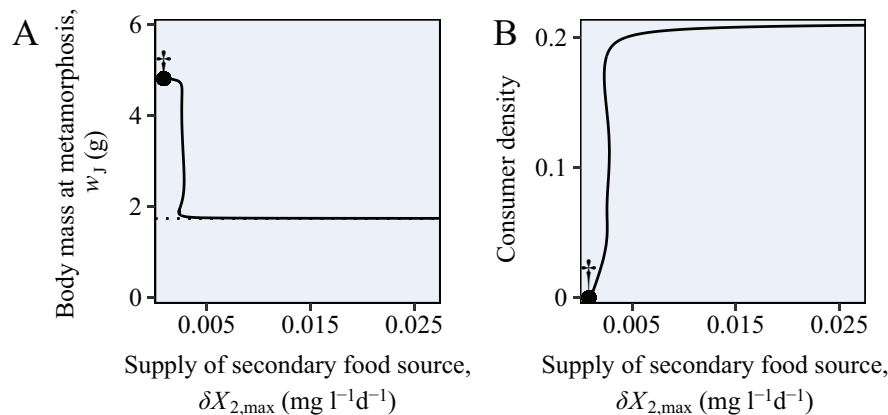
Figure 5: The lower the supply rate of the secondary food source, the later in life individuals undergo metamorphosis (*A*). Because metamorphosis does not disappear with a diminishing supply of the secondary food source, the population experiences evolutionary trapping and becomes extinct when the secondary food source becomes too scarce (*B*). In that case, population extinction occurs at the circles marked with a dagger (†). *A*, Body mass (g) at which individuals undergo metamorphosis at the continuously stable strategies (CSSs) shown in fig. 4*A*, as a function of the supply rate of the secondary food source (mg L^{-1} day^{-1}). The dotted line indicates the body mass at which the secondary food source becomes available to individuals. *B*, Consumer density (per 1,000 L) at the CSSs shown in fig. 4*A*, as a function of the supply rate of the secondary food source (mg L^{-1} day^{-1}). The nonsmooth points are due to switches in the ecological attractor. Parameter values are as shown in tables 2 and 3.

eters $X_{1,\mathrm{max}}$, w_{min}, ρ, q_s, and α all give the same qualitative pattern (app. D).

Interestingly, for very high values of $X_{1,\mathrm{max}}$, metamorphosis ceases to be an evolutionary trap. Because of our assumption that individuals always have a positive feeding rate on the primary food source (eqq. [1], [9]), large individuals can survive on the primary food source alone when its supply rate is sufficiently high, even though they are not specialized in doing so. When the secondary food source becomes scarce while the primary food source is sufficiently abundant, individuals feed solely on the primary food source, metamorphosis disappears, and the population persists (fig. D1*D*; figs. B1, C1, D1–D5, E1, E2, and F1 are available online).

When metamorphosis does not cost any energy ($q_s = q_J = 0.742$), the metamorphosing population does not become extinct for low supply rates of the secondary food source. Instead, the size at metamorphosis (w_J) evolves to such high values that metamorphosis takes place after maturation (fig. D4). Ultimately, when the supply rate of the secondary food source becomes very low, not a single individual reaches the body mass at which metamorphosis takes place, and all individuals are therefore specialized in feeding on the primary food source.

In appendix E, we show that our results also hold for two other types of models that differ substantially with regard to parameterization and model structure. We first study the evolution of metamorphosis in the Kooijman-Metz model (Kooijman and Metz 1984), which is a so-called gross-production allocation model, or a kappa-rule model. This type of model assumes that a fraction κ of the ingested energy is used for maintenance and somatic growth and a fraction $1 - \kappa$ for reproduction. This is qualitatively different from the model analyzed above, which is a net-production allocation model and assumes that energy intake is first used to cover maintenance costs before it is divided between growth and reproduction. Second, we test the generality of our results in a general size-structured population model, parameterized for an invertebrate species. In this model, we also study how different trade-off functions affect our results.

The results in appendix E show that the evolutionary bistability of metamorphosis is robust against major changes in model structure, parameters, and trade-off strengths. The results of the general size-structured model differ in one interesting aspect from those of other models: in this model, metamorphosis disappears and individuals are fully specialized on the primary food source when the secondary food source becomes scarce (fig. E2), which in the model analyzed above occurs only for very high values of $X_{1,\mathrm{max}}$ or when metamorphosis does not cost any energy. It is, however, beyond the focus of this article to study why the models differ in this aspect.

Discussion

Here we have shown that metamorphosis can evolve to break up the phenotypic correlation between different life stages, such that small individuals are specialized on a primary food source while large individuals are specialized on a secondary food source. Our findings suggest that metamorphosis can evolve only when the secondary food source is highly abundant. When the supply rate of the secondary food source is very high, such that the density of this food source is much higher than that of the primary food source, large individuals switch to feeding on the secondary food source even though they do not have the morphology ideally suited to utilizing it. Metamorphosis then evolves to allow large individuals to specialize on the secondary food source without negatively affecting the performance of their offspring in feeding on the primary food source. When the supply rate of the secondary food source is lower, metamorphosis can evolve only when individuals are initially specialized in feeding on it. Specialization on the secondary food source can evolve only under limited conditions, but if these are met, metamorphosis evolves to allow small individuals to specialize on the food source available early in life.

Although it has been shown that metamorphosis evolves in species with an ontogenetic diet shift as soon as its benefits outweigh its costs (Ebenman 1992), we have additionally shown here that a population with metamorphosis does not easily lose this life-history strategy when the ecological conditions under which it evolved change. Moreover, when the ecological conditions for metamorphosed individuals become very unfavorable, the population will often become extinct. Metamorphosis can therefore be an evolutionary trap. Since this evolutionary trap co-occurs with a viable evolutionary attractor, it is possible, in principle, that the population escapes extinction by evolving back to a non-metamorphosing life-history strategy. However, we show in appendix F why this is rather unlikely. A population in which individuals undergo metamorphosis can rarely be invaded by a mutant, recombinant, or immigrant that does not undergo metamorphosis. Conversely, a population that does not undergo metamorphosis can almost always be invaded by individuals undergoing full metamorphosis. Metamorphosis changes the efficiencies of the consumers on the different food sources, which in turn change the food densities and therefore the benefits and costs of metamorphosis. Hence, this feedback loop between individuals and their environment is crucial for understanding the evolution of metamorphosis and should not be ignored.

The model analyzed here consists of specific and parameter-rich functions based on the interaction between roach (*Rutilus rutilus*) and two small-bodied zooplankton species. Although the model therefore has a clear basis in biological reality, not all assumptions may apply to other systems.

In appendix E, we therefore analyze the evolution of metamorphosis in two different models. The analyses in this appendix show that our main result—that metamorphosis is not easily gained but, once evolved, does not easily disappear when conditions change—does not depend on the parameterization or model-specific assumptions, such as a linear trade-off function or hump-shaped attack-rate functions.

The common ancestor of all animal species probably had a complex life cycle, with a pelagic larva stage and a benthic adult stage separated by metamorphosis (Jägersten 1972). There is a long-standing debate in evolutionary biology about the origin of these pelagobenthic life cycles. While the dominant view is that the ancestral metazoan was a pelagic larva-like animal and that later in evolutionary history a benthic juvenile/adult stage was added to its life cycle (e.g., Jägersten 1972; Nielsen 2013), there is an alternative view suggesting that the ancestral metazoan was a benthic adult-like animal (e.g., Sly et al. 2003; Raff 2008; Page 2009). Here we have assumed that the ancestral state of the consumer had a larval morphology and that the adult morphology evolved later through the evolution of metamorphosis. However, we have also shown that when individuals start with the adult morphology (after specialization on the secondary food source), metamorphosis can evolve as a way to include a specialized larval morphology in their life cycle. Therefore, even though we have assumed the larval morphology as the ancestral state, our results suggest that it is also possible that the adult morphology is ancestral and that the larval state evolved only later in evolutionary history.

While metamorphosis is widespread in the animal kingdom, the loss of the premetamorphic life stage has occurred in several species, for example, in many marine invertebrates (Pechenik 1999) and some frog species (Callery et al. 2001), via the evolution of direct development. In our model, a loss of the larval stage is impossible, since the smallest individuals need to feed on the primary food source in order to metamorphose. To test under which conditions metamorphosing individuals evolve toward a life history with direct development, a different approach is therefore needed. In species with direct development, the elimination of the larval stage occurred in association with the production of larger offspring (Moran 1994; Callery et al. 2001). In marine invertebrates, for example, species that undergo metamorphosis produce smaller offspring than related species that skip the larval stage (Marshall et al. 2012). For future studies, it would be interesting to see under which ecological conditions adults evolve to produce larger offspring, such that the larval stage can be skipped and species evolve direct development.

Another pathway by which metamorphosis can disappear is the evolution of paedomorphosis, through which individuals mature while keeping the larval morphology (as happens, e.g., in many newts and salamanders). We have found that individuals evolve to paedomorphosis when the supply rate of the primary food source is very high or when metamorphosis does not cost energy (app. D). In the first case, metamorphosis disappears when the secondary food source becomes scarce, so individuals evolve to retain the same larval morphology throughout their ontogeny. This is in line with empirical work that shows that paedomorphosis evolves when conditions for the postmetamorphic stage are unfavorable (Bonett et al. 2014). In the second case, when metamorphosis does not cost any energy, the size at metamorphosis evolves to very high values when the supply rate of the secondary food source is low (app. D). Eventually, not a single individual reaches the body mass at which metamorphosis would take place, and the population becomes paedomorphic.

We find that in the main model paedomorphosis can evolve only under limited conditions. Surprisingly, we show in appendix E that paedomorphosis easily evolves in the general size-structured model examined there. It is, however, beyond the scope of this article to further investigate the conditions under which paedomorphosis evolves. In this study, we have assumed that the body mass at maturation is fixed. In future research, it would be interesting to study whether paedomorphosis could evolve more easily in a model in which the body mass at maturation evolves as well.

In this study, we have examined the evolution of metamorphosis in species changing their diet during their life cycle. However, factors other than diet could also explain the origin of metamorphosis, such as dispersal, mate finding, predator avoidance, or habitat selection (Moran 1994). Many insects have, for example, a nonfeeding adult stage that is specialized on dispersal and mate finding. The traits needed for these tasks may be maladaptive during the feeding stage (Moran 1994). Metamorphosis could therefore evolve to separate tasks over the life cycle. In addition, predators might force species to change their habitat during their life cycle. For example, results of a recent experiment suggest that the transition from water to land in marine blenny fish has been promoted by the presence of aquatic predators (Ord et al. 2017). In future research, it would be interesting to study whether metamorphosis is more likely to evolve because of a diet shift or because of other factors, such as dispersal or predation pressure. Further work could also address the question of under which ecological conditions either the larval or the adult stage evolves into a nonfeeding stage.

Here we have modeled metamorphosis as a discrete life-history transition. While metamorphosis can occur within a few minutes or hours (e.g., in marine invertebrates; Hadfield 2000), it is often a relatively slow process that may take weeks or months (e.g., in amphibians; Downie et al. 2004). Taxa that nowadays exhibit a sharp and abrupt metamor-

phosis between different life stages have evolved from situations in which the changes from newborn to adult were more continuous. For example, in insects and marine invertebrates, it has been shown that the morphological divergence between different life stages has increased during the course of evolution (Brown 1977; Nielsen 1998). Furthermore, the ancestors of frogs looked more like the metamorphosing stage than the larvae or adults of present-day species (Wassersug and Hoff 1982). Gradually, the different life stages became morphologically distinct, and ultimately, a metamorphosis evolved. Since the transitory stage cannot be well adapted to the needs addressed by either the larval or the adult morphology, there is probably a high selection pressure to concentrate the developmental events during this transition, so as to decrease the duration of the transformation. In our study, the duration of metamorphosis is not taken into account, while in reality it is an important aspect of metamorphosis—suggesting another avenue of promising future research.

Fossil evidence and phylogenetic distributions of metamorphosis indicate that metamorphosis evolved more than 200 million years ago in insects (Labandeira and Sepkoski 1993) and amphibians (Wassersug 1975). In marine invertebrates, this evolution occurred earlier, in the Cambrian period, 500 million years ago (Strathmann 1993), which indicates that the common ancestor of all animals had already undergone a metamorphosis, with a pelagic larva stage and a benthic adult stage (Jägersten 1972). This early metamorphosis got lost in some phyla, for example, the Ctenophora and the Chaetognata, while it reevolved in only a few cases (Jägersten 1972). The abundant occurrence of metamorphosis is thus due not to a high frequency of origination but to its persistent ecological success (Moran 1994). Our findings here are in line with these observations. We have shown that metamorphosis can evolve only under limited ecological conditions. However, once evolved, it is a very successful life-history strategy that will not easily disappear through further evolution.

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