

Appendix A from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Derivation of a Two-Habitat Consumer-Resource Model

Here, we derive the functional response for consumers that forage on two food sources occurring in different habitats. The primary food source, with density X_1 , occurs in habitat 1, while the secondary food source, with density X_2 , is in habitat 2. Individuals move from habitat 1 to habitat 2 at a rate $D_{1\rightarrow 2} = D(1 - \phi)$ and from habitat 2 to habitat 1 at a rate $D_{2\rightarrow 1} = D\phi$. The parameter D scales the diffusion rate of the consumers, and the parameter ϕ is the relative preference of the consumer for the primary food source. When consumers do not have a preference (i.e., $\phi = 0.5$), the movement rates are equal, $D_{1\rightarrow 2} = D_{2\rightarrow 1} = 0.5D$. We furthermore assume that consumers start handling prey immediately after capturing one. All searching, handling, and moving processes occur on a relatively fast timescale; we therefore neglect growth, birth, and death processes of the consumer when deriving the functional response. The following differential equations describe the change in the food source densities and in the numbers of consumers searching for (S_i) or handling (H_i) the primary or secondary food source ($i = 1, 2$):

$$\frac{dX_1}{dt} = \delta(X_{1, \max} - X_1) - a_1 X_1 S_1, \quad (\text{A1})$$

$$\frac{dX_2}{dt} = \delta(X_{2, \max} - X_2) - a_2 X_2 S_2, \quad (\text{A2})$$

$$\frac{dS_1}{dt} = -a_1 X_1 S_1 + H_1 \omega - D[(1 - \phi)S_1 - \phi S_2], \quad (\text{A3})$$

$$\frac{dH_1}{dt} = a_1 X_1 S_1 - H_1 \omega, \quad (\text{A4})$$

$$\frac{dS_2}{dt} = -a_2 X_2 S_2 + H_2 \omega - D[\phi S_2 - (1 - \phi)S_1], \quad (\text{A5})$$

$$\frac{dH_2}{dt} = a_2 X_2 S_2 - H_2 \omega. \quad (\text{A6})$$

In these equations, X_1 and X_2 are the densities of the primary and secondary food sources, respectively, a_i is the attack rate on food source i , and ω is the inverse of the handling time (h) for the food sources.

We show below that the total numbers of prey items of the primary and secondary food sources eaten per unit of time equal, respectively,

$$\frac{\phi a_1 X_1 C}{1 + h[\phi a_1 X_1 + (1 - \phi) a_2 X_2]}, \quad (\text{A7})$$

$$\frac{(1 - \phi) a_2 X_2 C}{1 + h[\phi a_1 X_1 + (1 - \phi) a_2 X_2]},$$

where $C = S_1 + S_2 + H_1 + H_2$ is the total number of consumers.

We assume that consumer behavior (searching, handling, and moving) is faster than the change in food densities. Equations (A3)–(A6) therefore all reach a pseudosteady state and track the slower processes. Solving equation (A6) for H_2 and using $H_1 = C - S_1 - S_2 - H_2$, we get

$$H_1 = C - S_1 - S_2 - \frac{a_2 X_2 S_2}{\omega}. \quad (\text{A8})$$

Substituting this equation into equation (A3) yields

$$\frac{dS_1}{dt} = -a_1X_1S_1 + \left(C - S_1 - S_2 - \frac{a_2X_2S_2}{\omega} \right) \omega - D[(1 - \phi)S_1 - \phi S_2] = 0. \quad (\text{A9})$$

By solving equation (A4) for H_1 and using $H_2 = C - S_1 - S_2 - H_1$, we get

$$H_2 = C - S_1 - S_2 - \frac{a_2X_2S_2}{\omega}. \quad (\text{A10})$$

Substituting this equation into equation (A5) yields

$$\frac{dS_2}{dt} = -a_2X_2S_2 + \left(C - S_1 - S_2 - \frac{a_1X_1S_1}{\omega} \right) \omega - D[\phi S_2 - (1 - \phi)S_1] = 0. \quad (\text{A11})$$

Solving equation (A9) for S_1 results in

$$S_1 = \frac{a_2X_2S_2 + \omega(S_2 - C) - DS_2\phi}{D(\phi - 1) - a_1X_1 - \omega}. \quad (\text{A12})$$

Substituting this solution into equation (A11) and solving for S_2 results in the following explicit solution:

$$S_2 = \frac{(1 - \phi)C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}. \quad (\text{A13})$$

Likewise, solving equation (A11) for S_2 and substitution of this solution into equation (A9) yields

$$S_1 = \frac{\phi C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}. \quad (\text{A14})$$

Substitution of the solutions in equations (A13) and (A14) into equations (A1) and (A2) results in

$$\begin{aligned} \frac{dX_1}{dt} &= \delta(X_{1, \max} - X_1) - \frac{\phi a_1X_1C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}, \\ \frac{dX_2}{dt} &= \delta(X_{2, \max} - X_2) - \frac{(1 - \phi)a_2X_2C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}. \end{aligned} \quad (\text{A15})$$

The total numbers of prey items of the primary and secondary food sources eaten per unit of time therefore equal, respectively,

$$\begin{aligned} &\frac{\phi a_1X_1C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}, \\ &\frac{(1 - \phi)a_2X_2C}{1 + h[\phi a_1X_1 + (1 - \phi)a_2X_2]}. \end{aligned} \quad (\text{A16})$$

Appendix B from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Specialization on a Secondary Food Source Is Hardly Possible

In the absence of metamorphosis, the degree of specialization on the secondary food source is equal for all three life stages ($\psi_L = \psi_J = \psi_A$). In this appendix, we show and briefly discuss the evolutionary bifurcations of this uniform degree of specialization, which we denote ψ , as a function of the secondary food source’s supply rate (fig. B1).

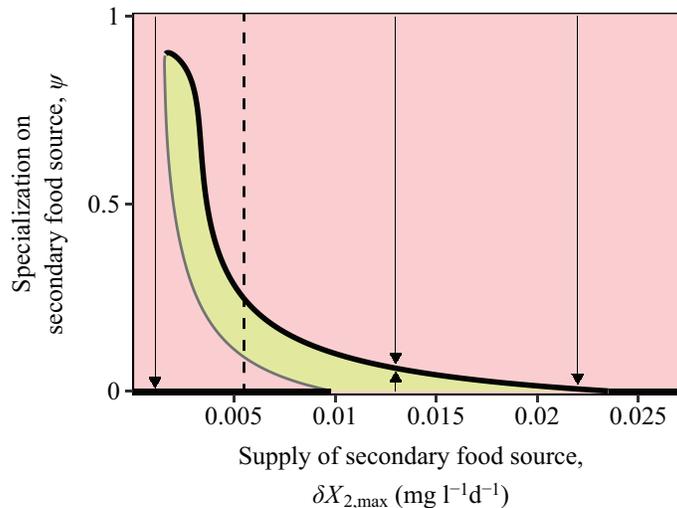


Figure B1: Evolution of specialization on the secondary food source as a function of the supply rate of the secondary food source in the absence of metamorphosis. Black lines indicate continuously stable strategies (CSSs), whereas the thin gray line indicates evolutionary repellers. Arrows show the direction of evolution. In the red area, evolution decreases the degree of specialization on the secondary food source, whereas in the green area, evolution increases this degree of specialization. For intermediate values of the supply rate of the secondary food source, there are two CSSs, one with no specialization and the other with partial specialization on the secondary food source. The dashed line indicates the supply rate of the primary food source. Parameter values are as shown in tables 2 and 3.

When the supply rate of the secondary food source is low, individuals evolve to be fully specialized on the primary food source ($\psi = 0$). Since the secondary food source is very scarce in this case, individuals do not change diet during their ontogeny and feed only on the primary food source. There is therefore no reason for them to specialize on the secondary food source (fig. B1). For high supply rates of the secondary food source, the specialization parameter ψ evolves away from 0 but remains low (fig. B1). The reason for this is subtle but can be understood as follows. Because large individuals have access to the secondary food source, they have high rates of growth and reproduction. This leads to a high number of offspring and therefore to strong competition among those offspring for the primary food source. Individuals that are more specialized on the secondary food source produce offspring that are not very efficient in their feeding early in life. Such individuals are therefore outcompeted by individuals that are more specialized in feeding on the primary food source early in life (ten Brink and de Roos 2017, 2018).

For intermediate supply rates of the secondary food source, two alternative evolutionary outcomes are separated by an evolutionary repeller. Depending on the initial value of the specialization trait ψ , individuals either fully specialize on the primary food source ($\psi = 0$) or specialize on the secondary food source to some extent ($0 < \psi < 1$). When individuals are initially fully specialized on the primary food source, they hardly include the secondary food source in their diet, and therefore ψ does not evolve away from 0. In contrast, above the threshold value of ψ associated with the evolutionary repeller, a substantial fraction of the diet of large individuals consists of the secondary food source, and in this case

further specialization on the secondary food source evolves. For intermediate supply rates of the secondary food source, this food is not too abundant. Therefore, competition among the smallest individuals is not severe enough to promote specialization on the primary food source. Note that, as a consequence, the smallest individuals end up in this case being poor foragers on the food source that is available to them.

When individuals are initially fully specialized on the primary food source, this second evolutionary outcome is realized only when mutational steps are large enough for a mutant to arise with a value of ψ that exceeds that of the evolutionary repeller. Alternatively, when mutational steps are small, a high degree of specialization on the secondary food source can evolve from a full specialization on the primary food source only when the supply rate of the secondary food source is initially so high that ψ evolves away from 0, and this is followed by a decrease in the supply rate of the secondary food source, so that ψ increases further, causing individuals to become even more specialized on the secondary food source (fig. B1).

Appendix C from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Evolution of Metamorphosis When Individuals Are Initially Specialized on the Secondary Food Source

In this appendix, we examine the conditions under which metamorphosis can evolve when individuals are initially specialized on the secondary food source.

Figure C1 illustrates when metamorphosis starts to evolve as a function of the supply rate of the secondary food source and the initial value of the specialization trait $\psi = \psi_L = \psi_J = \psi_A$. Metamorphosis evolves when individuals are not specialized on the secondary food source ($\psi = 0$) and the supply rate of the secondary food source is high or when this supply rate is low (but not too low) and some initial specialization on the secondary food source exists. Whether or not metamorphosis starts to evolve is hardly influenced by the body mass at metamorphosis w_j (not shown). When metamorphosis can evolve (green area in fig. C1), the extent of metamorphosis θ evolves to a high value (upper branch of CSSs in fig. 4A).

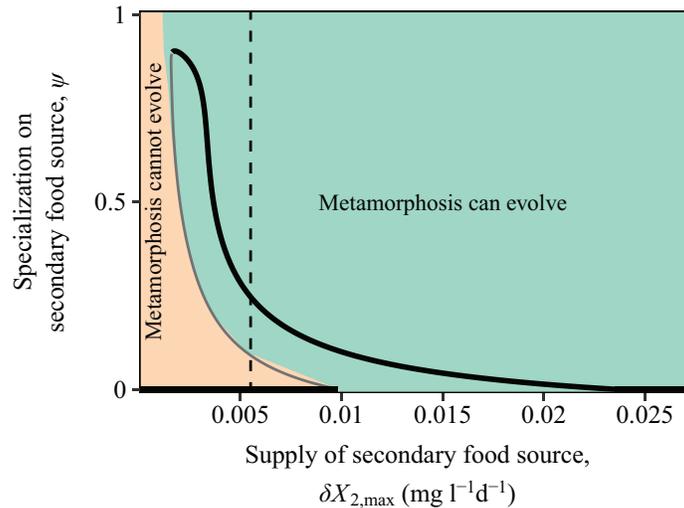


Figure C1: Overview of conditions under which metamorphosis starts to evolve as a function of the supply rate of the secondary food source and the initial degree of specialization on the secondary food source, $\psi_L = \psi_J = \psi_A$, when $\theta = 0$. The figure also shows the outcomes of evolution when the specialization trait $\psi = \psi_L = \psi_J = \psi_A$ evolves in the absence of metamorphosis (as in fig. B1), demonstrating that metamorphosis evolves approximately when the initial value of ψ exceeds the value of the evolutionary repeller in figure B1 and, in particular, when it equals the value of the positive continuously stable strategy in figure B1. The dashed line indicates the supply rate of the primary food source. The initial value of w_j is $w_{\min} = 1.742$ g; other parameter values are as shown in tables 2 and 3.

Appendix D from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Robustness of Results

In this appendix, we study the robustness of our results by investigating the evolution of specialization and metamorphosis for different parameter combinations.

Figure D1 shows how two different choices of the supply rate of the primary food source affect the evolution of specialization and metamorphosis (decreased in *A* and *C*, increased in *B* and *D*). Decreasing this supply rate does not qualitatively change the evolutionary outcomes (fig. D1*A*, D1*C*). In contrast, when this supply rate is increased, a small interval of the supply rate of the secondary food source appears in which evolutionary branching can occur when only the specialization trait ψ evolves (thick gray line in fig. D1*B*). Since evolutionary branching can occur only when the population is initially specialized on the secondary food source and only for a limited range of conditions (when $X_{1,\max}$ is high and $X_{2,\max}$ is intermediate), we do not study this potential for evolutionary branching in further detail. Figure D1*B* also shows a discontinuous change in the CSS of the specialization trait ψ (vertical edge of green area). This happens because two alternative stable ecological equilibria exist for intermediate supply rates of the secondary food source. One of these ecological equilibria disappears when the supply rate of the secondary food source is increased, which leads to an abrupt transition in the evolutionary outcome.

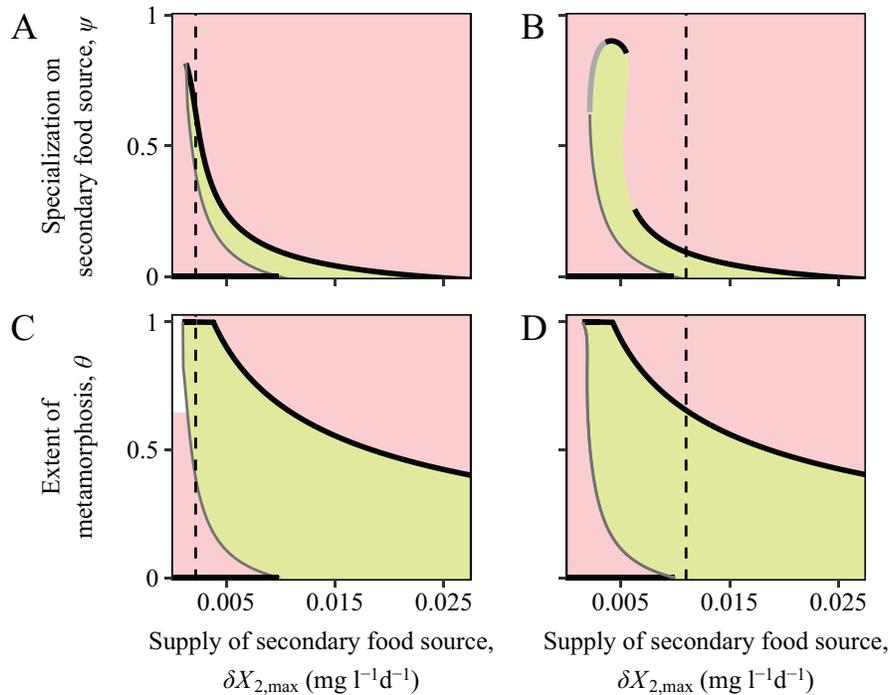


Figure D1: Effects of changing the supply rate of the primary food source. Evolution of specialization on the secondary food source (*A*, *B*) in the absence of metamorphosis, and evolution of metamorphosis (*C*, *D*) when there initially is no specialization on the secondary food source, as functions of the supply rate of the secondary food source (mg L⁻¹ day⁻¹) for two different values of the supply rate of the primary food source (decreased relative to main text in *A* and *C*; increased relative to main text in *B* and *D*). Thick black lines indicate continuously stable strategies, thin gray lines indicate evolutionary repellers, and the thick gray line in *B* indicates evolutionary branching points. In the red areas, evolution decreases the degree of specialization (*A*, *B*) or the extent of metamorphosis (*C*, *D*), whereas in the green areas, evolution increases the degree of specialization or the extent of metamorphosis. The population cannot persist in the white area in *C*. The dashed line indicates the supply rate of the primary food source. Parameters: $X_{1,\max} = 0.022$ (*A*, *C*) or 0.11 (*B*, *D*) mg L⁻¹. Other parameter values are as shown in tables 2 and 3.

When the supply rate of the primary food source is very high, metamorphosis disappears when the supply rate of the secondary food source is decreased, which implies that metamorphosis in this case is not an evolutionary trap (fig. D1D). For high supply rates of the primary food source, metamorphosed individuals can survive and reproduce while feeding only on the primary food source, even though they have a morphology that is not specialized on doing so. When the supply rate of the secondary food source diminishes, the food available to metamorphosed individuals decreases, but there is always enough of the primary food source left for them to survive. Since individuals have a preference for the most profitable food source (eq. [3]), individuals will almost exclusively forage on the primary food source when the secondary food source is rare. At this point, the selection pressure on metamorphosis is negative because of the associated costs, and metamorphosis disappears (fig. D1D). Note that this evolutionary outcome occurs only because we assume that large individuals (with body masses $w > w_{\min}$) can always forage on both food sources, independent of their morphology.

Figure D2 shows that changing the body mass at which the secondary food source becomes available to individuals (decreased in *A* and *C*, increased in *B* and *D*) does not qualitatively change either the evolution of specialization or the evolution of metamorphosis. When the secondary food source is available only to large individuals, specialization on it is not possible (fig. D2B). Because individuals need to grow a lot before the secondary food source becomes available to them, it is even more important for them to be specialized on the primary food source than when the secondary food source is available already to small individuals (fig. D2A). Decreasing the body mass at which the secondary food source becomes available to individuals decreases the supply rate of the secondary food source at which metamorphosis can start to evolve (fig. D2C). Because the secondary food source is available early in life, it is beneficial to invest in metamorphosis already when the supply rate of the secondary food source is relatively low.

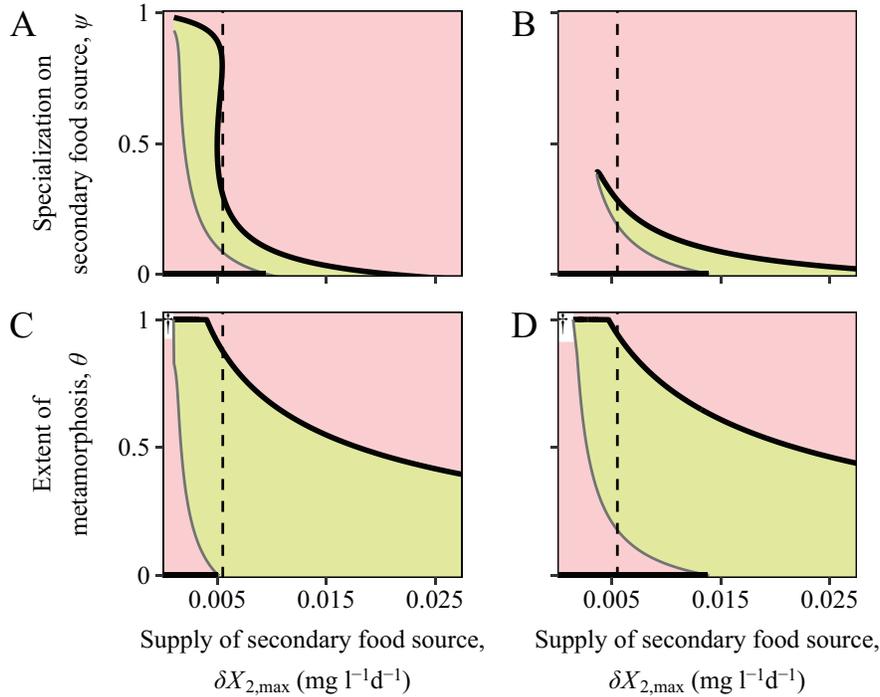


Figure D2: Effects of changing the body mass at which the secondary food source becomes available to individuals. Evolution of specialization on the secondary food source in the absence of metamorphosis (*A*, *B*) and evolution of metamorphosis when there initially is no specialization on the secondary food source (*C*, *D*), as a function of the supply rate of the secondary food source ($\text{mg L}^{-1} \text{day}^{-1}$) for two different values of the body mass at which the secondary food source becomes available to individuals (decreased relative to main text in *A* and *C*; increased relative to main text in *B* and *D*). Note that specialization on a secondary food source is not possible when individuals gain access to it late in life (*B*). Thick black lines indicate continuously stable strategies, whereas thin gray lines indicate evolutionary repellers. In the red areas, evolution decreases the degree of specialization (*A*, *B*) or the extent of metamorphosis (*C*, *D*), whereas in the green areas, evolution increases the degree of specialization or the extent of metamorphosis. The population cannot persist in the white areas marked with a dagger (\dagger). The dashed line indicates the supply rate of the primary food source. Parameters: $w_{\min} = 0.88$ (*A*, *C*) or 6 (*B*, *D*). Other parameter values are as shown in tables 2 and 3.

Since changing the costs of metamorphosis does not affect the evolution of specialization, we show in figure D3 only how changing these costs (increased in *A* and *C*, decreased in *B* and *D*) affects the evolution of metamorphosis. We consider in turn the mortality costs of metamorphosis and the energetic costs of metamorphosis. The risk of dying during metamorphosis largely determines to which extent metamorphosis can evolve (fig. D3*A*, D3*B*) but does not affect the supply rate of the secondary food source at which metamorphosis can start to evolve. The energetic costs of metamorphosis influence only slightly the extent to which metamorphosis evolves (fig. D3*C*, D3*D*).

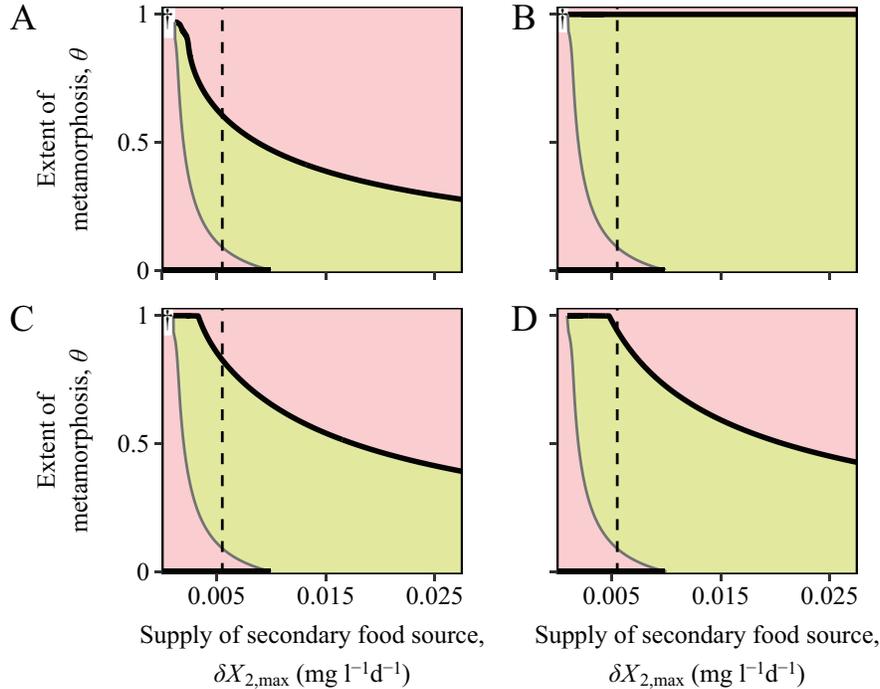


Figure D3: Effects of changing the costs of metamorphosis. Evolution of metamorphosis when there initially is no specialization on the secondary food source, as a function of the supply rate of the secondary food source ($\text{mg L}^{-1} \text{day}^{-1}$) for two different mortality costs (*A*, *B*) and two different energetic costs (*C*, *D*) of metamorphosis (increased relative to main text in *A* and *C*; decreased relative to main text in *B* and *D*). *A*, $\rho = 0.9$, which means that individuals undergoing full metamorphosis ($\theta = 1$) have a probability of 0.1 of surviving metamorphosis. *B*, $\rho = 0$, which means that metamorphosis does not decrease survival. *C*, $q_s = 0$, which means that full metamorphosis requires individuals to invest all their reversible body mass into metamorphosis. *D*, $q_s = 0.742 = q_j$, which means that metamorphosis does not require an investment of reversible body mass. Other parameter values are as shown in tables 2 and 3. Thick black lines indicate continuously stable strategies, whereas thin gray lines indicate evolutionary repellers. In the red areas, evolution decreases the extent of metamorphosis, whereas in the green areas, evolution increases the extent of metamorphosis. The population cannot persist in the white areas marked with a dagger (\dagger). The dashed line indicates the supply rate of the primary food source.

When metamorphosis does not require an energy investment ($q_s = q_j = 0.742$), the population does not become extinct for low supply rates of the secondary food source but becomes paedomorphic. For decreasing values of the supply rate of the secondary food source, the body mass at which metamorphosis takes place increases such that individuals metamorphose after maturation (fig. D4). The population hence becomes partially paedomorphic, as the population includes reproducing individuals with the larval phenotype. Since there is, with decreasing supply rates of the secondary food source, less and less food available for metamorphic individuals, the maximum body mass that individuals reach decreases (fig. D4). When the supply rate of the secondary food source becomes very low, individuals no longer reach the body mass at which metamorphosis takes place, and the population becomes fully paedomorphic (left of the vertical line in fig. D4).

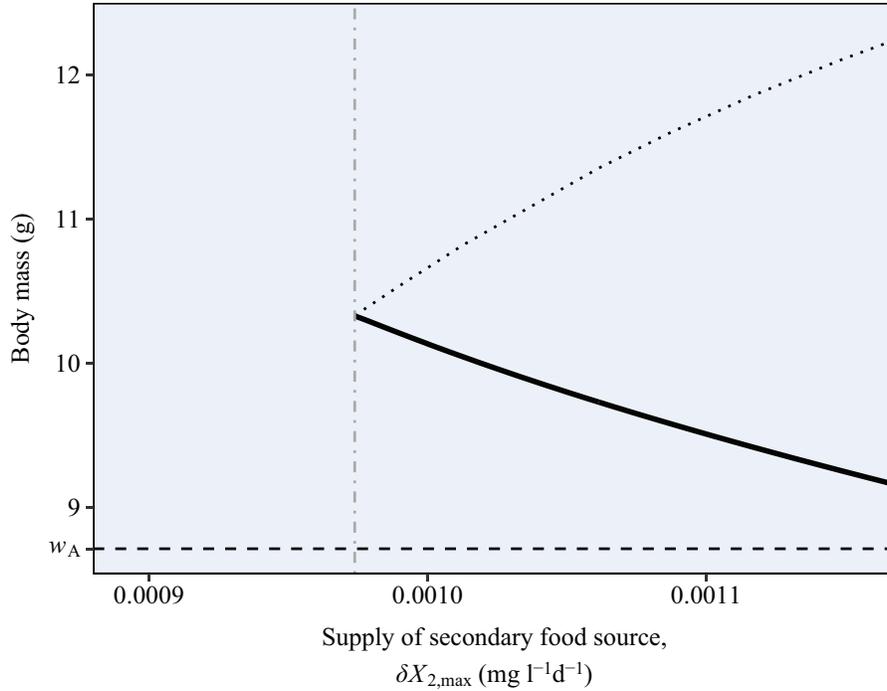


Figure D4: When metamorphosis does not cost energy, paedomorphosis evolves for low supply rates of the secondary food source. The solid line indicates the body mass (g) at which individuals undergo metamorphosis at the continuously stable strategies shown in fig. D3D, as a function of the supply rate of the secondary food source ($\text{mg L}^{-1} \text{day}^{-1}$). The black dotted line indicates the maximum body mass (g) individuals reach. The black dashed line indicates the body mass at which individuals mature. The dash-dotted line indicates the supply rate at which metamorphosis disappears. Parameter values are as shown in tables 2 and 3, except for $q_s = 0.742$.

In figure D5, we show the evolution of specialization and metamorphosis for $\alpha = 0.93$, which is increased relative to the value $\alpha = 0.6$ used in the main text. The parameter α determines how strongly the attack rates on the primary and secondary food sources increase and decrease around their 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 body mass, which can be characterized by the food density at which the individual can just meet its maintenance requirements (Persson et al. 1998). A value of $\alpha = 0.93$ means that in the absence of an ontogenetic diet shift, differently sized consumers have more or less similar competitive abilities. In this case, specialization on the secondary food source is never possible (fig. D5A). For this higher value of α , small individuals are much more affected by the trade-off between specialization on the primary and secondary food sources. Nevertheless, the evolution of metamorphosis is not influenced by α (fig. D5B).

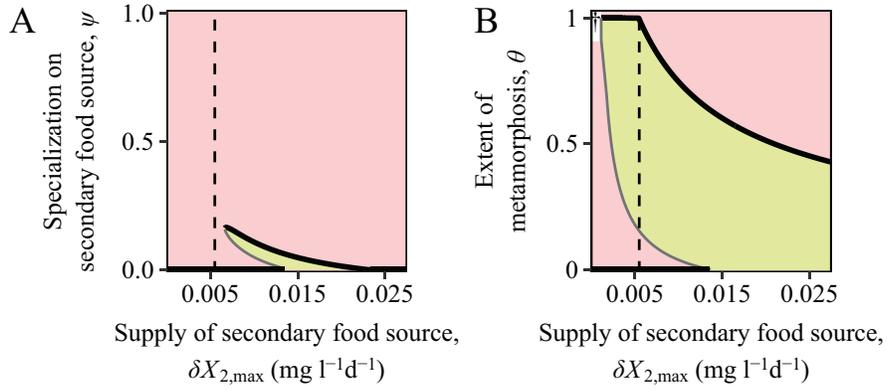


Figure D5: Effects of changing how strongly the attack rates on the primary and secondary food sources increase and decrease around their peaks. Evolution of specialization on the secondary food source in the absence of metamorphosis (*A*) and evolution of metamorphosis when there initially is no specialization on the secondary food source (*B*), as functions of the supply rate of the secondary food source (mg L⁻¹ day⁻¹) for $\alpha = 0.93$ (increased relative to main text). Specialization on the secondary food source is never possible in this case (*A*). Other parameter values are as shown in tables 2 and 3. Thick black lines indicate continuously stable strategies, whereas thin gray lines indicate evolutionary repellers. In the red areas, evolution decreases the degree of specialization (*A*) or the extent of metamorphosis (*B*), whereas in the green areas, evolution increases the degree of specialization or 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.

Appendix E from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Generality of the Results

We find that metamorphosis can evolve as a way to break up the trade-off between foraging success early in life and that late in life. Metamorphosis can evolve only when the supply rate of the secondary food source is high. Once evolved, it is a robust strategy that does not disappear easily when the environmental conditions change, leading to evolutionary bistability. In this appendix, we show that this result is robust to substantial differences in model structure and parameters.

Evolution of Metamorphosis in the Kooijman-Metz Model

We first study the evolution of metamorphosis in the Kooijman-Metz model (Kooijman and Metz 1984; de Roos et al. 1990), which assumes an energy allocation rule different from that of the model in the main text. We extend the Kooijman-Metz model with a second food source and metamorphosis. The model with one food source has been described before (Kooijman and Metz 1984; de Roos et al. 1990), and we therefore describe the model only briefly below.

The primary and secondary food sources, with biomass densities X_1 and X_2 , respectively, occur in two distinct habitats. The resources follow semichemostat dynamics, with turnover rate δ , and reach densities of $X_{1,\max}$ and $X_{2,\max}$ in the absence of the consumer population.

Larvae (L) are born with length ℓ_b , get access to the secondary food source at length ℓ_v , become juveniles (J) and undergo metamorphosis at length ℓ_w , and mature into adults (A) at length ℓ_j . Individual body mass w is proportional to cubed length with a proportionality constant β .

Resource ingestion by consumers is proportional to the squared length of an individual, with a proportionality constant I_m , and follows a Holling type 2 functional response. The size-dependent resource ingestion for consumers foraging on the primary food source is then given by

$$I_1(X_1, \ell) = \frac{I_m \xi X_1}{1 + \xi X_1} \ell^2, \quad (\text{E1})$$

where ξ is the shape parameter of the functional response. Ingested food is assimilated with a conversion efficiency ε . A fixed fraction κ is used for maintenance and growth in body mass. Maintenance, which is proportional to the cubed length of an individual, with a proportionality constant χ , takes precedence over growth. Adults channel a fraction $1 - \kappa$ of the assimilated food to reproduction, while nonmature individuals invest this fraction in maturation. The growth rate in the length of individuals feeding solely on the primary food source ($\ell < \ell_v$) is, after some rewriting (see de Roos et al. 1990), described as

$$g(X_1, \ell) = \gamma \left(\frac{\ell_m \xi X_1}{1 + \xi X_1} - \ell \right). \quad (\text{E2})$$

The parameter $\ell_m = \kappa \varepsilon I_m / \chi$ is the maximum size individuals can reach under unlimited food abundance, and the parameter $\gamma = \chi / 3\beta$ is the growth rate.

To facilitate the extension to a secondary food source and to be able to use the same trade-off between the two attack rates as in the main text, we reformulate the Holling type 2 functional response such that

$$I_1(X_1, \ell) = \frac{a_{1,L} X_1}{1 + h a_{1,L} X_1} \ell^2, \quad (\text{E3})$$

where $h = 1/I_m$ is the handling time and $a_{1,L} = I_m \xi$ is the attack rate of an individual in the larval life stage. Equation (E2) is now reformulated as

$$g(X_1, \ell) = \gamma \left(\ell_m h \frac{a_{1,L} X_1}{1 + h a_{1,L} X_1} - \ell \right). \quad (\text{E4})$$

The food intake of individuals feeding on two food sources ($\ell \geq \ell_v$) then equals

$$I_2(X_1, X_2, \ell) = \frac{\phi a_{1,i} X_1 + (1 - \phi) a_{2,i} X_2}{1 + h[\phi a_{1,i} X_1 + (1 - \phi) a_{2,i} X_2]} \ell^2, \quad (\text{E5})$$

where $a_{1,i}$ and $a_{2,i}$ are the attack rates of individuals in life stage i ($i = \text{L, J, A}$) on the primary and secondary food sources, respectively. The growth of these large individuals can be described by

$$g(X_1, X_2, \ell) = \gamma \left\{ \ell_m h \frac{\phi a_{1,i} X_1 + (1 - \phi) a_{2,i} X_2}{1 + h[\phi a_{1,i} X_1 + (1 - \phi) a_{2,i} X_2]} - \ell \right\}. \quad (\text{E6})$$

In equations (E5) and (E6), the parameter ϕ equals the relative preference of large individuals ($\ell \geq \ell_v$) for the primary food source (eq. [3]). Adults ($\ell \geq \ell_j$) produce offspring at a rate

$$b(X_1, X_2, \ell) = r_m h \frac{\phi a_{1,A} X_1 + (1 - \phi) a_{2,A} X_2}{1 + h[\phi a_{1,A} X_1 + (1 - \phi) a_{2,A} X_2]} \ell^2. \quad (\text{E7})$$

In this equation, the parameter $r_m = (1 - \kappa)\varepsilon I_m / \beta \ell^3$ represents the proportionality constant that relates fecundity to the squared length of an individual. All individuals experience a background mortality of μ . For the chosen parameter values, the model always approaches a stable ecological equilibrium; starvation conditions can therefore be ignored.

The total biomass B of individuals with a length between ℓ_1 and ℓ_2 can be computed as an integral over the consumer size distribution $c(t, \ell)$, weighted by proportionality constant β ,

$$B = \int_{\ell_1}^{\ell_2} \beta \ell^3 c(t, \ell) d\ell. \quad (\text{E8})$$

We assume a trade-off between the two attack rates such that, in the absence of metamorphosis, the two attack rates within a certain life stage (larvae, juveniles, or adults: $i = \text{L, J, A}$) are

$$\begin{aligned} a_{1,i} &= (1 - \psi_i)(A_{\max} - A_{\min}) + A_{\min}, \\ a_{2,i} &= \psi_i(A_{\max} - A_{\min}) + A_{\min}. \end{aligned} \quad (\text{E9})$$

The parameter ψ_i is, as in the main text, the relative degree of specialization of a certain life stage on the secondary food source. Metamorphosis is modeled in the same way as in the main text (eq. [10]). Individuals undergo metamorphosis at a body mass of $w_u = \beta \ell_u^3$ and die with a probability of $\rho\theta$, where the parameter θ equals the extent of metamorphosis. During metamorphosis, individuals furthermore lose $\theta(1 - q_s)w_u$ of their total body mass, which implies a reduction in length from ℓ_u to $[1 - \theta(1 - q_s)]^{1/3} \ell_u$.

Note that it is possible that individuals become, after metamorphosis, smaller than ℓ_v , the minimum length needed to feed on the secondary food source. For simplicity, however, we assume that individuals can always feed on the secondary food source after metamorphosis, independent of their body mass.

Parameter values are listed in table E1 and are based on roach (*Rutilus rutilus*) feeding on two unstructured zooplankton populations as food sources (de Roos and Persson 2002). The model-specific file needed for the analysis with the PSPManalysis package can be found in the online supplementary information together with an R script that executes all calculations made in our analyses.

Table E1: Parameters of the Kooijman-Metz model

Parameter	Description	Unit	Default value
δ	Food source turnover rate	day ⁻¹	.1
$X_{1,\max}$	Maximum biomass density of primary food source	mg L ⁻¹	.05
$X_{2,\max}$	Maximum biomass density of secondary food source	mg L ⁻¹	Variable
ℓ_b	Length at birth	mm	7
ℓ_v	Length at which the secondary food source becomes available	mm	50
ℓ_j	Length at maturation	mm	110
ℓ_m	Maximum length	mm	300
σ	Constant in habitat-switching rate	days mm ² mg ⁻¹	30
h	Handling time	days mm ² mg ⁻¹	10

Table E1 (Continued)

Parameter	Description	Unit	Default value
A_{\max}	Maximum value of the attack rate	$L \text{ mm}^{-2} \text{ day}^{-1}$	6.6667
A_{\min}	Minimum value of the attack rate	$L \text{ mm}^{-2} \text{ day}^{-1}$.66667
κ	Proportion invested in maintenance and growth7
γ	Growth rate parameter	day^{-1}	.006
r_m	Proportionality constant of reproduction	$\text{day}^{-1} \text{ mm}^{-2}$.003
μ	Mortality rate	day^{-1}	.05
β	Length-to-weight proportionality constant	mg mm^{-3}	9×10^{-3}
ρ	Probability of dying during full metamorphosis ($\theta = 1$)5
q_s	Fraction of original body mass that is left after full metamorphosis ($\theta = 1$)7
ψ_L^a	Degree of specialization of larvae on the secondary food source	...	0–1
θ^a	Extent of metamorphosis	...	0–1
ℓ_u^a	Length at metamorphosis	mm	>7

^a These parameters can change because of evolution.

Figure E1A shows that evolutionary bistability for the extent of metamorphosis arises also in the Kooijman-Metz model. For low supply rates of the secondary food source, metamorphosis cannot evolve. When the supply rate of the secondary food source becomes sufficiently high, metamorphosis originates abruptly. Once metamorphosis has evolved, it does not disappear when the supply rate of the secondary food source diminishes. Instead, metamorphosis initially becomes more pronounced, leading to adults that are highly specialized on the secondary food source. For very low supply rates of the secondary food source, the degree of metamorphosis lessens (fig. E1A). At the same time, the specialization parameter ψ_L increases (fig. E1B), such that large individuals remain fully specialized on the secondary food source (gray line in fig. E1B). Small individuals, however, slightly specialize on the secondary food source (black line in fig. E1B), which is disadvantageous for them, since they can feed only on the primary food source. Ultimately, the population becomes extinct when the supply rate of the secondary food source becomes too low (black dot in fig. E1A).

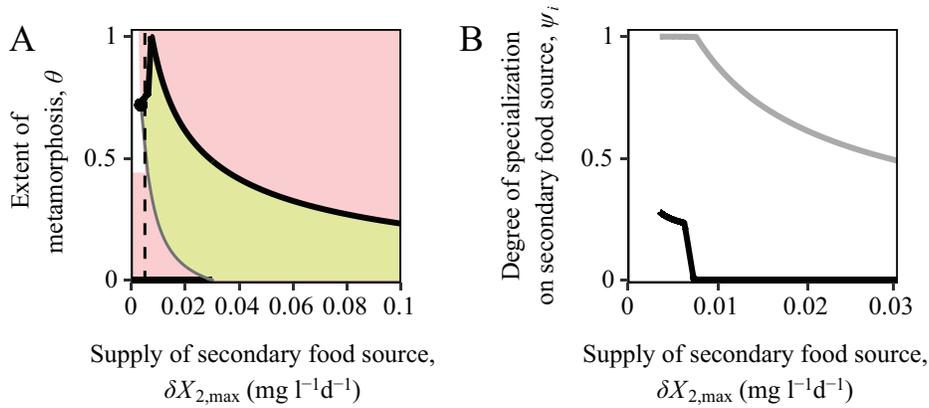


Figure E1: *A*, Evolution of the extent of metamorphosis as a function of the supply rate of the secondary food source ($\text{mg L}^{-1} \text{day}^{-1}$). Thick black lines indicate continuously stable strategies, and the thin gray line indicates evolutionary repellers. The population cannot persist in the white area; therefore, a metamorphosing population becomes extinct for low supply rates (dot). In the green area the extent of metamorphosis increases. In the red areas the extent of metamorphosis decreases. The dashed line indicates the supply rate of the primary food source. *B*, Degree of specialization on the secondary food source at the equilibrium with metamorphosis. The black line shows the degree of specialization of individuals before metamorphosis (ψ_L). The gray line shows the degree of specialization of individuals after metamorphosis ($\psi_A = \psi_L + \theta$). Parameter values are as shown in table 1.

The length at metamorphosis, ℓ_u , evolves to the length at which the secondary food source becomes available, ℓ_v , as soon as there is some degree of metamorphosis ($\theta > 0$). For decreasing values of the supply rate of the secondary food source, the length at metamorphosis does not change.

These results differ in two minor aspects from those in the main text. First, the length at metamorphosis does not increase with decreasing supply rate of the secondary food source. Second, the degree of metamorphosis decreases for

very low supply rates of the secondary food source, while at the same time the specialization parameter ψ_L slightly increases. In this way, large individuals are still fully specialized on the secondary food source but do not pay the costs of a full metamorphosis. Instead, small individuals become slightly less effective in feeding on the primary food source.

Evolution of Metamorphosis in a General Size-Structured Consumer-Resource Model

To further test the generality of our results with regard to major changes in the model structure, model parameters, and trade-off function, here we study the evolution of metamorphosis in a general size-structured population model. The model is an extension of the model described by de Roos et al. (2008). We extend the model by introducing a second food source that is available only for large individuals. It has been shown, using a stage-structured analog of this model, that specialization on such a food source is not possible when there is a trade-off between foraging efficiency early in life and that late in life (ten Brink and de Roos 2017).

In contrast to the main text, we do not distinguish between irreversible and reversible body mass of consumers; individuals are characterized only by their total body mass s . Larvae (L) are born with a body mass of s_b , get access to the secondary food source at a body mass of s_{\min} , possibly undergo metamorphosis and become juveniles (J) at a body mass of s_j , and become mature adults (A) when reaching a body mass of s_m . In contrast to the main text, we assume that the rates of food intake are linearly related to the body size of individual consumers. The dynamics of the two food sources are as in the Kooijman-Metz model analyzed in the preceding subsection.

We assume a Holling type 2 functional response; therefore, the mass-specific food intake of individuals with body mass s can be written as

$$I(s, X_1, X_2) = \begin{cases} \frac{a_{1,L}X_1}{1 + ha_{1,L}X_1} & \text{if } s < s_{\min}, \\ \frac{\phi a_{1,i}X_1 + (1 - \phi)a_{2,i}X_2}{1 + h[\phi a_{1,i}X_1 + (1 - \phi)a_{2,i}X_2]} & \text{otherwise.} \end{cases} \quad (\text{E10})$$

In this equation, the parameters $a_{1,i}$ and $a_{2,i}$ are the mass-specific attack rates of individuals in a certain life stage ($i = L, J, A$) on the primary and secondary food sources, respectively. The parameter h is the mass-specific handling time, and the parameter ϕ is again the relative preference of large individuals ($s \geq s_j$) for the primary food source (eq. [3]).

Ingested food is assimilated with efficiency ε and first used to cover maintenance costs. Maintenance requirements are assumed to scale linearly with body size, with proportionality constant T . The mass-specific net biomass production of individuals is determined by the difference between food intake $I(s, X_1, X_2)$ and maintenance costs. The net biomass production per unit body mass as a function of the resource densities then equals

$$\nu(s, X_1, X_2) = \varepsilon I(s, X_1, X_2) - T. \quad (\text{E11})$$

Immature individuals use their net biomass production to grow in body size, while mature individuals ($s = s_m$) do not grow and convert the net energy production in new offspring. The growth rate of juveniles ($s < s_m$) equals

$$g(s, X_1, X_2) = (\varepsilon I(s, X_1, X_2) - T)s, \quad (\text{E12})$$

and the reproduction rate of adults ($s = s_m$) equals

$$b(s, X_1, X_2) = \frac{(\varepsilon I(s, X_1, X_2) - T)s_m}{s_b}. \quad (\text{E13})$$

All individuals experience a constant background mortality rate of μ . The model always approaches a stable ecological equilibrium for the chosen parameters. Therefore, the right-hand sides of equations (E11)–(E13) are always positive, and possible starvation conditions of the consumers can be ignored.

We assume a trade-off between foraging on the primary food source and foraging on the secondary food source such that, in the absence of metamorphosis, the two attack rates in a certain life stage (larvae, juveniles, or adults [$i = L, J, A$]) are

$$\begin{aligned} a_{1,i} &= \psi_{1,i}(A_{\max} - A_{\min}) + A_{\min}, \\ a_{2,i} &= \psi_{2,i}(A_{\max} - A_{\min}) + A_{\min}. \end{aligned} \quad (\text{E14})$$

The parameters $\psi_{1,i}$ and $\psi_{2,i}$ indicate the relative degree of specialization of a life stage ($i = L, J, A$) on the primary and secondary food sources, respectively. The trade-off constraining the levels of specialization on the two food sources within a certain life stage is given by

$$\psi_{1,i}^{1/\zeta} + \psi_{2,i}^{1/\zeta} = 1, \quad (\text{E15})$$

where the parameter ζ determines the strength of the trade-off. For values of ζ larger (smaller) than 1, the trade-off is called strong (weak). In both the Kooijman-Metz model and the model in the main text, we assume a trade-off strength of 1, which translates to a linear trade-off between the two attack rates. We assume again that metamorphosis decouples the different life stages as follows:

$$\psi_{2,A} = \psi_{2,J} = \min(1, \psi_{2,L} + \theta), \quad (\text{E16})$$

where θ is the extent of the metamorphosis. When individuals reach the body mass at which they undergo metamorphosis ($s = s_j$), they lose $\theta(1 - q_s)s_j$ of their body mass, where the parameter q_s represents the fraction of the original body mass remaining after full metamorphosis and $1 - q_s$ is hence a measure of the relative cost of metamorphosis. Furthermore, individuals die during metamorphosis with a probability $\rho\theta$.

We assume that the maintenance rate, attack rate, and maximum ingestion rate (which is the inverse of the handling time), are all mass specific. Default values for these parameters are listed in table E2 and are derived from the scaling relations of these constants with the adult body weight s_m as presented by de Roos and Persson (2013). For the adult body mass, a value of 0.1 mg is chosen, and newborns are born with a body mass of 0.001 mg. The body mass at which the secondary food source becomes available is 0.01 mg, which implies that newborn individuals need to achieve a tenfold increase in their weight before the secondary food source becomes available to them. We assume that the probability of dying during full metamorphosis (ρ) equals 0.5. The parameter q_s equals 0.7. For the parameter ζ , the strength of the trade-off function, we examine three different values ($\zeta = 0.5, 1, \text{ or } 2$), representing a weak, linear, or strong trade-off between the two foraging efficiencies. Changing the parameters does not qualitatively change the results. The model-specific file needed for the analysis with the PSPManalysis package can be found in the online supplementary information, together with an R script that executes all calculations made in our analyses.

Table E2: Parameters of the size-structured model

Parameter	Description	Unit	Default value
δ	Food source turnover rate	day ⁻¹	.1
$X_{1,\max}$	Maximum biomass density of primary food source	mg L ⁻¹	4
$X_{2,\max}$	Maximum biomass density of secondary food source	mg L ⁻¹	Variable
σ	Constant in habitat-switching rate	days	30
A_{\max}	Maximum mass-specific attack rate	L mg ⁻¹ day ⁻¹	.6
A_{\min}	Minimum mass-specific attack rate	L mg ⁻¹ day ⁻¹	.06
ε	Conversion efficiency5
h	Mass-specific handling time	d	1
T	Mass-specific maintenance rate	day ⁻¹	.1
s_m	Adult weight	mg	.1
s_b	Newborn weight	mg	.001
s_{\min}	Body mass at which secondary food source becomes available	mg	.01
μ	Mortality rate	day ⁻¹	.02
ρ	Probability of dying during full metamorphosis ($\theta = 1$)5
q_s	Fraction of original body mass that is left after full metamorphosis ($\theta = 1$)	q_s	.7
ζ	Strength of trade-off function5, 1, or 2
$\psi_{2,L}^a$	Degree of specialization of larvae on the secondary food source	...	0–1
θ^a	Extent of metamorphosis	...	0–1
s_j^a	Weight at metamorphosis	mg	>.001

^a These parameters can change because of evolution.

Figure E2 shows that evolutionary bistability for the extent of metamorphosis arises also in the general size-structured model. As above, metamorphosis evolves abruptly as soon as the supply rate of the secondary food source reaches a high threshold. Again, metamorphosis becomes more pronounced when this supply rate diminishes. These results do not depend on the strength of the trade-off function. In contrast to the model in the main text, the population does not become

extinct for low supply rates of the secondary food source after metamorphosis has evolved. Instead, when this supply rate reaches a low threshold, the weight at metamorphosis s_j suddenly evolves to such high values that metamorphosis would take place only at a weight that not a single individual reaches. For low values of the supply rate of the secondary food source, all individuals are specialized in feeding on the primary food source and are not very efficient in feeding on the secondary food source.

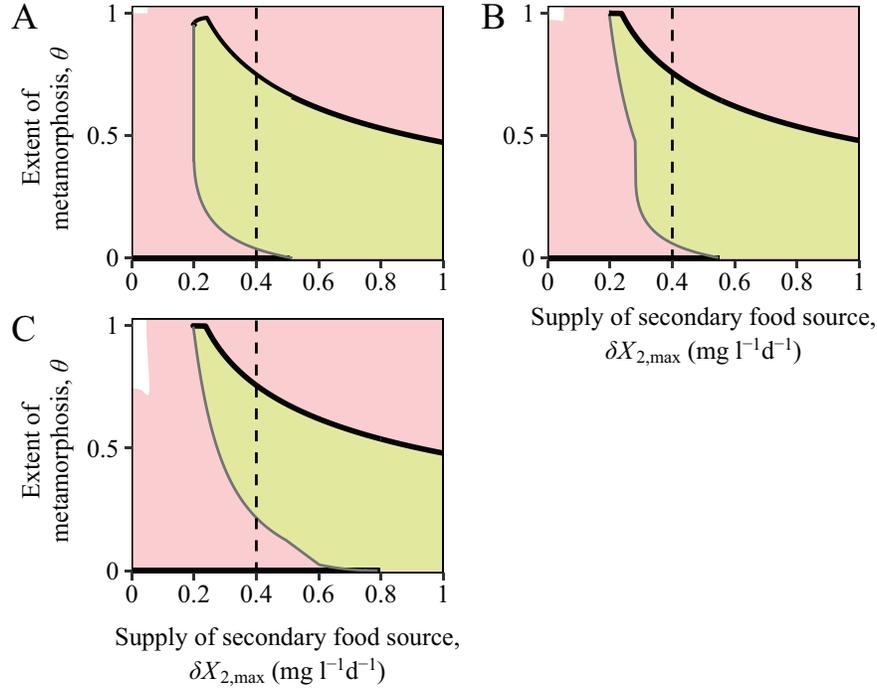


Figure E2: Evolution of the extent of metamorphosis as a function of the supply rate of the secondary food source ($\text{mg L}^{-1} \text{day}^{-1}$) for different trade-off functions. Thick black lines indicate continuously stable strategies, and thin gray lines indicate evolutionary repellers. The population cannot persist in the white areas. In the green areas the extent of metamorphosis increases. In the red areas the extent of metamorphosis decreases. The dashed line indicates the supply rate of the primary food source. Parameter values are as shown in table E2. *A*, Weak trade-off ($\zeta = 0.5$); *B*, linear trade-off ($\zeta = 1$); *C*, strong trade-off ($\zeta = 2$).

Appendix F from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Evolutionary Rescue Is Hardly Possible

In this appendix, we demonstrate that the evolutionary rescue of a metamorphosing population is hardly possible when environmental conditions change.

Figure 4A shows that metamorphosis does not disappear when the supply rate of the secondary food source decreases. Ultimately, the population will become extinct for very low supply rates (fig. 5B). This evolutionary trap occurs for parameter values for which also a viable evolutionary attractor exists, characterized by the absence of metamorphosis (fig. 4A). It would therefore be possible, in principle, that the population escapes extinction by evolving back to a nonmetamorphosing life history. Examination of the pairwise invasibility plots shows that this is rather unlikely (fig. F1). For most values of the supply rate $\delta X_{2,\max}$ of the secondary food source, a population with metamorphosis cannot be invaded by a variant (mutant, recombinant, or immigrant) without metamorphosis (fig. F1B, F1C). Only for a small range of values of $\delta X_{2,\max}$ close to the extinction boundary can a population with full metamorphosis be invaded by a variant that has a smaller degree of metamorphosis, provided that the variant strategy is sufficiently different from the resident strategy (fig. F1A). In this case, evolutionary rescue is possible; however, the population’s size for these values of the supply rate is very small (fig. 5B), which makes it highly susceptible to extinction through demographic or environmental stochasticity before a suitable variant strategy appears.

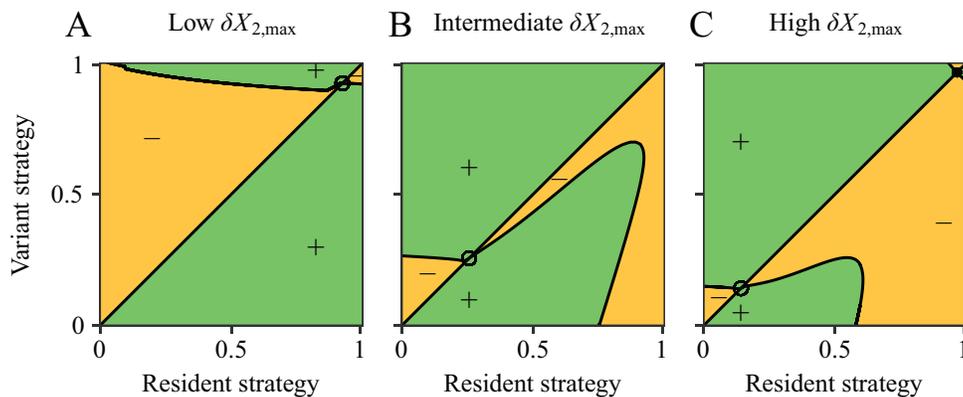


Figure F1: Evolutionary rescue is hardly possible for a metamorphosing population on the brink of extinction. *A*, Pairwise invasibility plot for the extent of metamorphosis θ at a low supply rate of the secondary food source. Green areas indicate where the variant strategy can invade the resident strategy (positive invasion fitness), while orange areas indicate where this is not possible (negative invasion fitness). The open circle indicates the location of the evolutionary repeller. *B*, Pairwise invasibility plot at an intermediate supply rate. *C*, Pairwise invasibility plot at a high supply rate. The filled circle indicates the location of the continuously stable strategy (CSS). For simplicity, we assume that the other two evolving traits, ψ_L and w_j , have values at the CSS of the population with metamorphosis and do not evolve. Parameters: $\delta X_{2,\max} = 0.0011$ (*A*), 0.0031 (*B*), or 0.0044 (*C*) $\text{mg L}^{-1} \text{day}^{-1}$; $\psi_L = 0$; and $w_j = 4.82$ (*A*), 1.78 (*B*), or 1.76 (*C*) g. Other parameter values are as shown in tables 2 and 3.

Appendix G from H. ten Brink et al., “The Evolutionary Ecology of Metamorphosis” (Am. Nat., vol. 193, no. 5, p. E116)

Model Equations and Functions

In this appendix, we describe the model equations, defining the system at the population level. The functions of the model are listed in table G1.

Table G1: Functions of the model

Function	Equation
Maximum attainable reversible mass	$y_{\max} = q_2 x$
Standardized body mass	$w = x + y_{\max}$
Relation between morphology of larvae, juveniles, and adults	$\psi_A = \psi_J = \min(1, \psi_L + \theta)$
Maximum attack rate on primary food source	$A_{1i} = (1 - \psi_i)(A_{\max} - A_{\min}) + A_{\min}$
Maximum attack rate on secondary food source	$A_{2i} = \psi_i(A_{\max} - A_{\min}) + A_{\min}$
Attack rate on primary food source	$a_1(w) = A_{1i}[(w/w_0)\exp(1 - (w/w_0))]^\alpha$
Attack rate on secondary food source	$a_2(w) = \begin{cases} 0 & \text{if } w \leq w_{\min}, \\ A_{2i}(\frac{w-w_{\min}}{w_0})^\alpha \exp(1 - \frac{w-w_{\min}}{w_0}) & \text{otherwise} \end{cases}$
Handling time	$h(w) = \zeta_1 + \zeta_2 w^{-\xi_3} e^{\xi_4 w}$
Preference for primary food source	$\phi(w, X_1, X_2) = \frac{1}{1 + \exp(\sigma(a_2(w)X_2 - a_1(w)X_1))}$
Food intake	$I(w, X_1, X_2) = \frac{\phi(w, X_1, X_2)a_1(w)X_1 + (1 - \phi(w, X_1, X_2))a_2(w)X_2}{1 + h(w)[\phi(w, X_1, X_2)a_1(w)X_1 + (1 - \phi(w, X_1, X_2))a_2(w)X_2]}$
Maintenance requirements	$E_m(x, y) = p_1(x + y)^{p_2}$
Net energy production	$E_g(x, y, X_1, X_2) = k_e I(w, X_1, X_2) - E_m(x, y)$
Fraction of net production allocated to growth in irreversible mass	$\kappa_i(x, y) = \begin{cases} \kappa_J(x, y) = \frac{y}{(1+q_1)q_2 x} & \text{if } (1+q_1)x < w_A, \\ \kappa_A(x, y) = \frac{y}{(1+q_A)q_A x} & \text{otherwise} \end{cases}$
Fraction of net production allocated to growth in reversible mass	$\kappa_r(x, y) = \begin{cases} 1 - \kappa_J(x, y) & \text{if } (1+q_1)x < w_A, \\ 1 - \kappa_A(x, y) & \text{if } y < q_2 x \text{ and } (1+q_1)x \geq w_A, \\ (1 - \kappa_J(x, y))\frac{\kappa_A(x, y)}{\kappa_J(x, y)} & \text{otherwise} \end{cases}$
Fecundity of adults	$b(x, y, X_1, X_2) = \begin{cases} 0 & \text{if } y < q_2 x \text{ or } (1+q_1)x < w_A, \\ \left(1 - \frac{\kappa_A(x, y)}{\kappa_J(x, y)}\right) \frac{\eta E_g(x, y, X_1, X_2)}{(1+q_1)x_0} & \text{otherwise} \end{cases}$
Amount of reversible body mass lost during metamorphosis	$\theta x_1(q_1 - q_2)$
Probability of dying during metamorphosis	$\rho\theta$

Note: The index i indicates a life stage: larva (L), juvenile (J), or adult (A).

The model characterizes the state of an individual by its irreversible mass x and reversible mass y . In principle, the population state would then be described by a density function $n(t, x, y)$, representing the density of individuals with irreversible mass x and reversible mass y at time t (Metz and Diekmann 1986). However, formulating a partial differential equation (PDE) for the density function $n(t, x, y)$ leads to mathematical difficulties. The reason for this is that the individual state space is two-dimensional, spanned by irreversible mass x and reversible mass y , but that the support of the density function $n(t, x, y)$ is only one-dimensional. Because all individuals are born with the same state at birth, all individuals that are born at the same moment in time will have the same values of x and y throughout their life. In other words, for every value of x , there is only a single value of y occurring in the population. The two i -state variables are thus at any particular time uniquely related to each other, although this relationship may vary with time. As a consequence, the density function $n(t, x, y)$ adopts nonzero values only at the one-dimensional curve that represents the unique relationship between x and y and is 0 for all other values of x and y . This also implies that the density function $n(t, x, y)$ is nondifferentiable in its last two arguments, as it jumps discontinuously from its nonzero value at its one-dimensional support to 0 for all other values. For this reason, partial derivatives like $\partial n(t, x, y)/\partial x$ and $\partial n(t, x, y)/\partial y$ that would occur in a PDE for $n(t, x, y)$ are mathematically ill defined. To cope with this singularity, the model is instead formulated in terms of a set of three age-dependent PDEs for the population density, irreversible mass, and reversible mass.

We define $n_i(t, a)$ as the density of individuals with age a at time t , $x_i(t, a)$ as the irreversible mass of individuals with age a at time t , and $y_i(t, a)$ as the reversible mass of individuals with age a at time t before metamorphosis. These

density functions are defined only over the age interval $[0, A_J(t)]$, where $A_J(t)$ refers to the age at which the individual reaches the size of metamorphosis. This age is dynamically defined by the condition $(1 + q_J)x_1(t, A_J(t)) = w_J$. Similarly, we define $n_2(t, a)$ as the density of individuals with age a at time t , $x_2(t, a)$ as the irreversible mass of individuals with age a at time t and $y_2(t, a)$ as the reversible mass of individuals with age a at time t after metamorphosis. These density functions are defined only for the complementary age interval $[A_J(t), \infty)$.

The dynamics of the density of individuals with age a before metamorphosis ($a \leq A_J(t)$) is described by

$$\frac{\partial n_1(t, a)}{\partial t} + \frac{\partial n_1(t, a)}{\partial a} = -\mu n_1(t, a), \quad (\text{G1a})$$

$$n_1(t, 0) = \int_{A_A(t)}^{\infty} b(x_2(t, a), y_2(t, a), X_1, X_2) n_2(t, a) da, \quad (\text{G1b})$$

where $A_A(t)$ refers to the age at maturation, which is defined by the condition $(1 + q_J)x_2(t, A_A(t)) = w_A$. Note that the equation above assumes that the body size at metamorphosis is smaller than the size at maturation, $w_J < w_A$, which always occurs in the model analyzed in the main text. The equations would be slightly different if the case $w_J > w_A$ could occur. The dynamics of the irreversible and reversible mass before metamorphosis are described by

$$\frac{\partial x_1(t, a)}{\partial t} + \frac{\partial x_1(t, a)}{\partial a} = \kappa_I(x_1(t, a), y_1(t, a)) E_g(x_1(t, a), y_1(t, a), X_1, X_2), \quad (\text{G2a})$$

$$x_1(t, 0) = x_b, \quad (\text{G2b})$$

$$\frac{\partial y_1(t, a)}{\partial t} + \frac{\partial y_1(t, a)}{\partial a} = \kappa_R(x_1(t, a), y_1(t, a)) E_g(x_1(t, a), y_1(t, a), X_1, X_2), \quad (\text{G2c})$$

$$y_1(t, 0) = q_J x_b. \quad (\text{G2d})$$

The dynamics of the density of individuals with age a following metamorphosis ($a > A_J(t)$) are described by

$$\frac{\partial n_2(t, a)}{\partial t} + \frac{\partial n_2(t, a)}{\partial a} = -\mu n_2(t, a), \quad (\text{G3a})$$

$$n_2(t, A_J(t)) = (1 - \rho\theta) n_1(t, A_J(t)), \quad (\text{G3b})$$

where $1 - \rho\theta$ is the probability of surviving metamorphosis. The dynamics of the irreversible and reversible mass following metamorphosis are described by

$$\frac{\partial x_2(t, a)}{\partial t} + \frac{\partial x_2(t, a)}{\partial a} = \kappa_I(x_2(t, a), y_2(t, a)) E_g(x_2(t, a), y_2(t, a), X_1, X_2), \quad (\text{G4a})$$

$$x_2(t, A_J(t)) = x_1(t, A_J(t)), \quad (\text{G4b})$$

$$\frac{\partial y_2(t, a)}{\partial t} + \frac{\partial y_2(t, a)}{\partial a} = \kappa_R(x_2(t, a), y_2(t, a)) E_g(x_1(t, a), y_1(t, a), X_1, X_2), \quad (\text{G4c})$$

$$y_2(t, A_J(t)) = y_1(t, A_J(t)) - \theta x_J(q_J - q_S). \quad (\text{G4d})$$

Finally, the dynamics of the resources are given by

$$\begin{aligned} \frac{dX_1}{dt} = & \delta(X_{1, \max} - X_1) - \int_0^{A_J(t)} I((1 + q_J)x_1(t, a), X_1, X_2) n_1(t, a) da \\ & - \int_{A_J(t)}^{\infty} I((1 + q_J)x_2(t, a), X_1, X_2) n_2(t, a) da, \end{aligned} \quad (\text{G5a})$$

$$\begin{aligned} \frac{dX_2}{dt} = & \delta(X_{2, \max} - X_2) - \int_0^{A_J(t)} I((1 + q_J)x_1(t, a), X_1, X_2) n_1(t, a) da \\ & - \int_{A_J(t)}^{\infty} I((1 + q_J)x_2(t, a), X_1, X_2) n_2(t, a) da. \end{aligned} \quad (\text{G5b})$$