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A Parent-Offspring Trade-Off Limits the Evolution of an Ontogenetic Niche Shift

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Appendix B from H. ten Brink and A. M. de Roos, "A Parent-Offspring Trade-Off Limits the Evolution of an Ontogenetic Niche Shift" (Am. Nat., vol. 190, no. 1, p. 45)

Robustness of the Results

We found that individuals can broaden or shift their diet when they grow larger. However, specialization on the new diet is not possible when this negatively affects the smallest individuals. To check the robustness of this outcome with regard to major changes in the model structure and model parameters, we studied the evolution of ontogenetic niche shifts with a fully size-structured population model, assuming that the food sources occur in the same habitat ($\beta = 1$). The model is an extension of the consumer-resource model described by Persson et al. (1998). In contrast to the model of Persson et al. (1998), we assume continuous reproduction and equilibrium conditions. We extend the model by introducing a second, unstructured, food source population.

The feeding, growth, reproduction, and mortality of an individual are assumed to be functions of two variables, irreversible and reversible mass, referred to as x and y, respectively. Irreversible mass is structural mass, such as bones and organs, and cannot be starved away. On the other hand, reversible mass (such as fat, muscle tissue, and, in the case of adults, gonads) can be used to cover basic metabolism during starvation. There is a maximum ratio of reversible mass to irreversible mass that equals q_j. Newborn individuals are born with irreversible mass x_b and the maximum amount of reversible mass ($q_j x_b$). Since we study only equilibrium dynamics, starvation does not occur and individuals always have the maximum amount of reversible mass ($q_j x$). When they reach size x_f, individuals become adults. Total body length, attack rates, and handling times are assumed to depend only on irreversible mass (Persson et al. 1998), through the quantity $w = x(1 + q_j)$. As in the main text, we assume that there are two resources, both following semichemostat dynamics. One food source, the original food source, is available for all individuals, while the alternative food source is available only after an individual has reached a certain size ($w > w_{min} = x_{min}(1 + q_j)$). We assume that the attack rates on both food sources are hump-shaped functions of the body mass of an individual:

$$a_1(w) = A_1\left(\frac{w}{w_0}\exp\left(1 - \frac{w}{w_0}\right)\right)^\alpha,$$ (B1)

$$a_2(w) = \begin{cases} 0 & w \leq w_{min}, \\ A_2\left(\frac{w - w_{min}}{w_0}\exp\left(1 - \frac{w - w_{min}}{w_0}\right)\right)^\alpha & \text{otherwise.} \end{cases}$$ (B2)

In these equations, A_1 and A_2 are the maximum attack rates that can be reached when the body size of an individual equals w_0 and $w_0 + w_{min}$ on the original and alternative food sources, respectively. The exponent α determines how rapidly the attack rates increase with body size for small individuals. To incorporate a trade-off between foraging skills on the two different food sources, we again assume a linear trade-off between the two maximum attack rates (A_1 and A_2). The same function as in the main text is used (eq. [5]) for the trade-off between A_1 and A_2:

$$A_1 = \psi A_{max},$$
$$A_2 = (1 - \psi)A_{max}.$$ (B3)

We assume a Holling type 2 functional response; therefore, the food ingestion of an individual can be written as

$$I(X_1, X_2, w) = \frac{a_1(w)X_1 + a_2(w)X_2}{1 + h(w)(a_1(w)X_1 + a_2(w)X_2)},$$ (B4)

whereby

$$h(w) = \zeta_1 + \zeta_2 w^{-\zeta_3} e^{\zeta_4 w}.$$ (B5)

The total energy intake of an individual equals the food intake rate multiplied by a conversion factor k_e. Assimilated energy is first used to cover maintenance costs. The metabolic demands per unit of time is a function of both irreversible and reversible mass and can be described by a power function,

$$E_m(x, y) = p_1(x + y)^{p_2}. \tag{B6}$$

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

$$\kappa_j(x, y) = \frac{y}{(1 + q_j)q_j x}. \tag{B7}$$

The remaining part is allocated to growth in reversible mass. Adults allocate a fraction $\kappa_a(x, y)$ to growth in irreversible mass, a fraction $q_j\kappa_a(x, y)$ to growth in reversible mass, and the remainder, $1 - (1 + q_j)\kappa_a$. to reproduction. The fraction $\kappa_a(x, y)$ allocated to reversible mass equals

$$\kappa_a(x, y) = \frac{y}{(1 + q_a)q_a x}. \tag{B8}$$

The number of eggs an individual adult produces per unit of time is

$$b(x, y, X_1, X_2) = \begin{cases} (1 - (1 + q_j)\kappa_a(x, y))E_g(x, y, X_1, X_2)\eta & x > x_f, \\ 0 & \text{otherwise,} \end{cases} \tag{B9}$$

where η is a conversion factor. A more detailed description of the model can be found in Persson et al. (1998).

Metabolic demands and handling time are parameterized for the interaction between a planktivorous fish population of roach *Rutilus rutilus* and two zooplankton populations as food sources, following Persson et al. (1998). Parameters are listed in table B1. Since we take into account only the situation where the two habitats completely overlap ($\beta = 1$), only specialization ψ evolves. Using the PSPManalysis software package (de Roos 2016), we calculated to which value ψ evolves for different combinations of $X_{1,max}$ and $X_{2,max}$. To test how the size at which the alternative food source becomes available influences the evolution of ontogenetic niche shifts, we did the calculations for two different values of x_{min}. The model-specific file and the R script used for the PSPManalysis can be found in this zip file.

All evolutionarily singular strategies found were evolutionarily stable attractors (CSSs). We found again that specialization on the alternative food source is not possible (fig. B1*A*). Even when individuals can feed on the alternative food source when they are relatively small ($x_{min} = 0.01$ while size at birth $x_b = 0.000804$), individuals specialize on the original food source (fig. B1*B*).

This analysis shows that our results are robust to substantial differences in model structure and parameters. In contrast to the stage-structured biomass model, adults can still grow, and their maximum size depends on the food source densities. For the stage-structured biomass model we assumed equal mass-specific handling times. We have now assumed mass-specific functions for both the attack rate and the handling time (Persson et al. 1998). While in the main text the model was parameterized for an invertebrate species, we have now parameterized the model for a vertebrate species (*R. rutilus*).
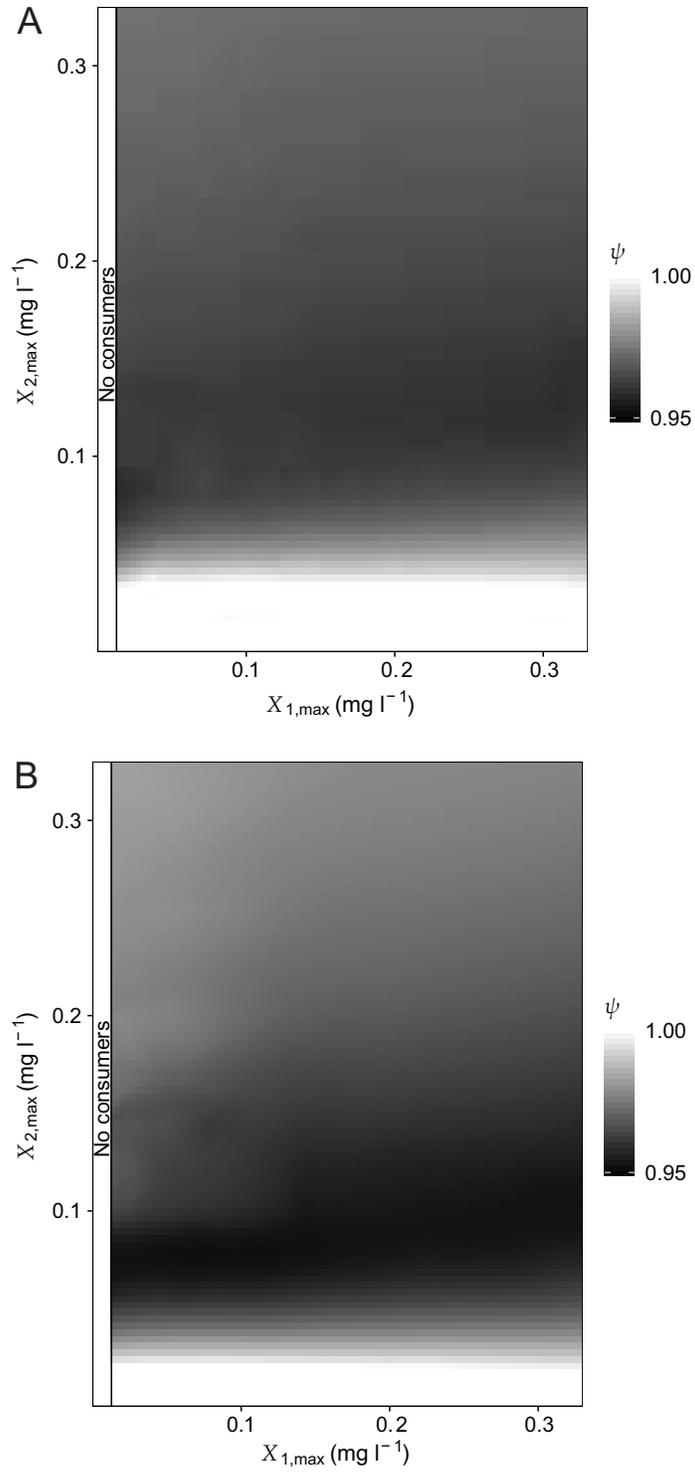
Figure B1: Evolutionary outcome for different combinations of $X_{1,\,max}$ and $X_{2,\,max}$ when the two habitats completely overlap for the fully size-structured model. We used two different values for x_{min}, the irreversible mass at which the alternative food source becomes available. A, $x_{min} = 1$; B, $x_{min} = 0.01$. Parameter ψ will always evolve to high values.

Table B1: Parameters of the model

Parameter	Default value	Unit	Description
δ	.5	day^{-1}	Food source turnover rate
$X_{1,\,max}$, $X_{2,\,max}$	Variable	$g\ L^{-1}$	Maximum biomass density of food sources 1 and 2
x_b	.000804	g	Irreversible mass of newborns
x_{min}	.01 or 1	g	Irreversible mass at which alternative food source becomes available
x_f	5	g	Irreversible mass at maturation
A_{max}	1×10^5	$L\ day^{-1}$	Maximum attack rate
w_0	17.42	g	Effective body mass at which maximum attack rate is attained
α	.93	. . .	Size scaling exponent of the attack functions
ζ_1[a]	.36	day	Constant used in the handling-time function
ζ_2[a]	7.45	$day\ g^{\zeta_3}$	Constant used in the handling-time function
ζ_3	.68	. . .	Slope of decline in handling time at small consumer sizes
ζ_4	1.15×10^{-3}	g^{-1}	Slope of increase in handling time at large consumer sizes
p_1	.033	$g^{1-p_2}\ day^{-1}$	Metabolic constant
p_2	.77	. . .	Metabolic constant
k_e[a]	.61	. . .	Conversion factor
q_j	.742	. . .	Constant determining maximum reversible mass
q_a	1	. . .	Constant used for the adult allocation function
η	.5	g	Gonad-offspring conversion
μ	.01	day^{-1}	Background mortality rate

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