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Maternal effects on offspring consumption can stabilize fluctuating predator–prey systems

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Maternal effects, where the conditions experienced by mothers affect the phenotype of their offspring, are widespread in nature and have the potential to influence population dynamics. However, they are very rarely included in models of population dynamics. Here, we investigate a recently discovered maternal effect, where maternal food availability affects the feeding rate of offspring so that well-fed mothers produce fast-feeding offspring. To understand how this maternal effect influences population dynamics, we explore novel predator–prey models where the consumption rate of predators is modified by changes in maternal prey availability. We address the ‘paradox of enrichment’, a theoretical prediction that nutrient enrichment destabilizes populations, leading to cycling behaviour and an increased risk of extinction, which has proved difficult to confirm in the wild. Our models show that enriched populations can be stabilized by maternal effects on feeding rate, thus presenting an intriguing potential explanation for the general absence of ‘paradox of enrichment’ behaviour in natural populations. This stabilizing influence should also reduce a population’s risk of extinction and vulnerability to harvesting.

1. Introduction

The environment experienced by a mother, for example the amount of food she consumes, may substantially alter the phenotype of her offspring [1–4], and empirical studies have begun to directly demonstrate that such maternal food effects can impact population dynamics [5,6]. However, very few theoretical models have explored the impact of maternal effects on population dynamics, with the few available studies focusing on effects of maternal age, maternal body size and maternal population density on offspring performance [7–9]. One neglected area of theoretical research concerns effects of maternal food consumption on offspring feeding rate. Yet we know that the quantity or quality of food available to mothers can profoundly affect the feeding behaviour or resource utilization traits of their offspring. For instance, mothers gestating during periods of famine (e.g. during the 1944 ‘Hunger winter’ in German-occupied parts of the Netherlands) gave birth to children with an elevated risk of obesity and with reduced glucose tolerance [10,11]. Recent experimental work has shown that maternal food availability can also affect the rate of offspring feeding: food-restricted freshwater crustacean (*Daphnia magna*) mothers produce offspring with a low feeding rate [12]. We expect that similar maternal effects are present in a wide range of taxa, perhaps underpinning the many effects of maternal nutrition on offspring growth rate and performance [1–4].

These maternal effects on offspring feeding rate represent a feedback mechanism by which predators may respond to their prey. They could represent specific adaptations that allow mothers to produce offspring with a rate of feeding most suited to the prevailing conditions, an example of optimal foraging [13] across generations. However, such maternal effects might also exist because starved mothers are only capable of producing inferior offspring with a low

feeding capability. Whatever their adaptive value, we expect that these maternal effects will considerably affect the behaviour of predator–prey dynamics, perhaps exerting a stabilizing influence by reducing prey consumption at times of low prey population size and vice versa. However, this verbal reasoning requires mathematical support as the dynamical consequences are difficult to predict.

In this study, we developed a simple predator–prey model that incorporates a maternal effect on feeding rate. We use this study to explore the stabilizing potential of the maternal effect. We also ask whether this maternal effect can resolve a major incongruity between theory and observation in ecology—the absence of the much-predicted ‘paradox of enrichment’—and also whether the maternal effect alters the size of populations of predators and their prey. Theoretical predator–prey models predict that increases in productivity destabilize consumer–resource dynamics, exacerbating the risk of extinction by increasing the amplitude and decreasing the minimum density of population oscillations. This is known as the ‘paradox of enrichment’ [14,15]. Yet increases in productivity (i.e. under eutrophic conditions) do not always lead to destabilization in natural systems, including populations of *Daphnia* [16–18]. Ecologists have thus struggled to bridge this gap between the predictions of simple mathematical models and the behaviour of natural systems. Here, we take a ‘proof of concept’ approach to exploring the potential for a maternal effect on offspring feeding rate to stabilize population dynamics.

2. The model

(a) The baseline model

First, we review the model dynamics of a predator–prey system without the maternal effect. We took a minimal approach to modelling predator and prey populations, so we could capture the key characteristics of their interactions. Our model was based on features of the freshwater crustacean *D. magna* and its algal prey, a particularly well-studied predator–prey system. As *Daphnia* predators are limited by their capacity to process prey, but do not need to learn to capture prey, the most appropriate functional response for this system is a Hollings type II response. We used a Hollings type II model from [19] (and well used in the literature) in which the algae (prey, x) grows at rate r with carrying capacity K and is consumed by the *Daphnia* predator (P) at rate C , converted to new predators with efficiency e and with handling time h . Predators die at rate μ . The differential equations underlying the model are given in equations (2.1) and (2.2):

$$\text{prey: } \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{PCx}{(1 + xh)} \quad (2.1)$$

and

$$\text{predator: } \frac{dP}{dt} = \frac{ePCx}{(1 + xh)} - \mu P. \quad (2.2)$$

(b) The maternal effects model

We incorporated a maternal effect on feeding rate into this baseline model by adding compartments containing predators with different feeding rates. Here, we assume that the

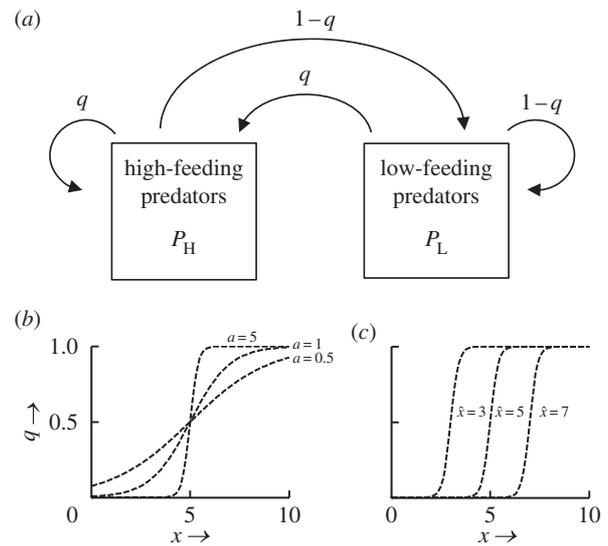


Figure 1. Maternal effects model. (a) Model schematic. Predators give birth to high-feeding (P_H) and low-feeding (P_L) predators with proportions q and $1 - q$. A sigmoidal curve describes how q changes with the density of the resource (x), as shown in (b,c). (b) Increasing a increases the slope of the curve and (c) increasing \hat{x} increases the mid-point of the curve. In (b) $\hat{x} = 5$ and in (c) $a = 5$.

Table 1. Parametrization of the model. All parameter values were from [19].

parameter	symbol	value
algae (x)		
maximal growth rate	r	0.5
carrying capacity	K	10
high-feeding <i>Daphnia</i> (P_H)		
feeding rate	C_H	$0.67 + B$
handling time	h	1.67
death rate	μ	0.15
conversion rate of algae into <i>Daphnia</i>	e	0.6
low-feeding <i>Daphnia</i> (P_L)		
feeding rate	C_L	$0.67 - B$
handling time	h	1.67
death rate	μ	0.15
conversion rate of algae into <i>Daphnia</i>	e	0.6

maternal effect lasts the lifetime of the offspring (predator), and that offspring fall into one of two categories: those with a high consumption rate (high-feeding predators: P_H) and those with a low consumption rate (low-feeding predators: P_L ; see figure 1a for a schematic of the model). The difference between the feeding rates of these predators was determined by the parameter B , which was added to and subtracted from a constant to calculate the feeding rates of high- and low-feeding predators, respectively (C_H and C_L ; table 1). We assumed that the predators differ only in the rate at which they consume prey and that their feeding efficiency (e), handling time (h) and mortality rate (μ) are

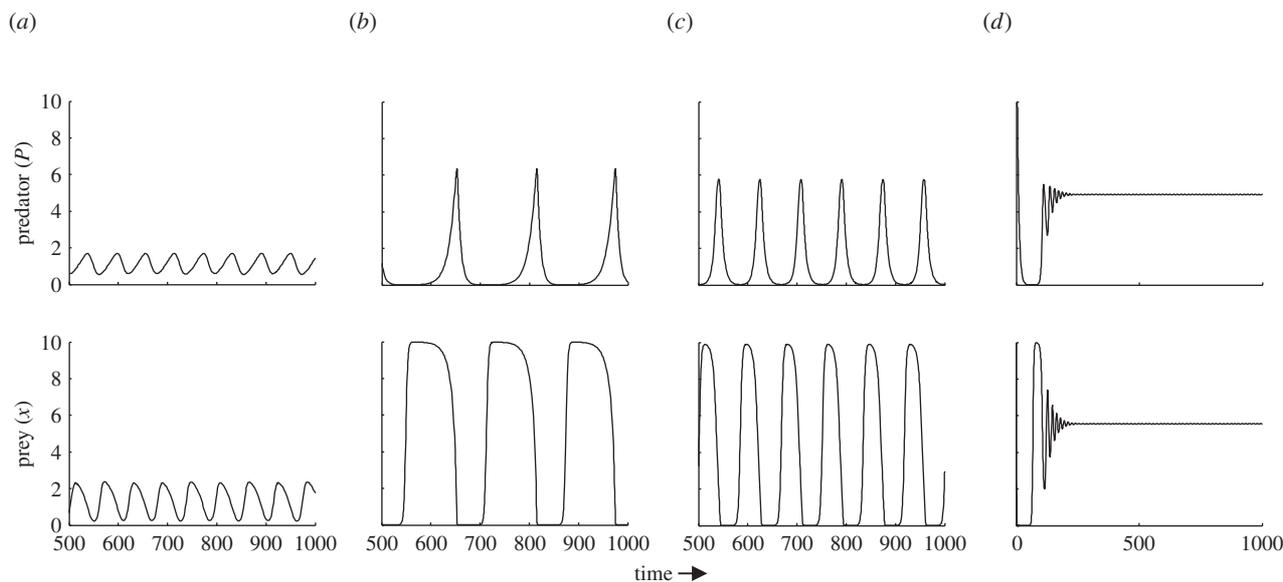


Figure 2. Population dynamics of predators and prey with and without the maternal effect: (a) $K = 3$ with no maternal effect, (b) $K = 10$ with no maternal effect, (c) $K = 10$ with a moderate ($B = 0.3$) maternal effect and (d) $K = 10$ with a large ($B = 0.5$) maternal effect. Plots are the last 500 days of a 1000-day simulation except for (d) in which the entire 1000-day simulation is shown. In (a–d), $C = 0.67$, $e = 0.6$, $h = 1.67$ and $\mu = 0.15$. In (c,d), $a = 2$ and $\hat{x} = 6$.

identical (table 1). The differential equations underlying the model are specified in equations (2.3)–(2.5):

$$\text{prey: } \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{C_L x P_L}{(1 + xh)} - \frac{C_H x P_H}{(1 + xh)}, \quad (2.3)$$

$$P_H: \frac{dP_H}{dt} = \frac{qeC_H x P_H}{(1 + xh)} + \frac{qeC_L x P_L}{(1 + xh)} - \mu P_H \quad (2.4)$$

and

$$P_L: \frac{dP_L}{dt} = \frac{(1 - q)eC_L x P_L}{(1 + xh)} + \frac{(1 - q)eC_H x P_H}{(1 + xh)} - \mu P_L. \quad (2.5)$$

Predators in both feeding rate categories are able to give birth to both high- and low-feeding offspring (P_H and P_L , respectively). Our maternal effect of interest links maternal prey levels with offspring feeding rate. We mimicked this effect in our model by linking the probability of a predator being born a high feeder (q) to prey population size (x) using the sigmoidal curve given by

$$q = \frac{1}{1 + e^{-a(x - \hat{x})}} \quad (2.6)$$

and depicted in figure 1*b,c*. The probability of being born a low feeder was given by $1 - q$. The slope of the sigmoidal curve at the mid-point is determined by a : increasing a increases the sensitivity of the maternal effect, with small changes in prey density (x) strongly affecting the birth proportions of high- and low-feeding predators at high values of a (figure 1*b*). The mid-point of the sigmoidal curve (i.e. the value of x for which $q = 0.5$) is determined by \hat{x} : increasing \hat{x} shifts the sigmoidal curve to the right, increasing the threshold of prey (x) at which predators switch from giving birth to predominantly low-feeding predators to giving birth to predominantly high-feeding predators (figure 1*c*).

The parameter values used are taken from a previous study exploring the seasonal dynamics of a *Daphnia*–algal system [19] and are provided in table 1. All simulations were performed in MATLAB (R2013b).

3. Results

(a) The maternal effect stabilizes population dynamics

As expected, without the maternal effect, enriching our system by increasing the carrying capacity of prey (K) destabilized the dynamics, increasing the amplitude of cycling of both prey and predators, and lowering their population sizes at troughs (figure 2*a,b*). Thus, we reproduced the expected ‘paradox of enrichment’ [19]. Adding a maternal effect stabilized the dynamics of an enriched system (when $K = 10$; figure 2*c,d*). A moderate maternal effect (when $B = 0.3$) causes the frequency of cycling to increase, which reduces the time the population is close to zero, and causes the amplitude of the cycles to slightly decrease (figure 2*c*). A larger maternal effect (when $B = 0.5$) stabilizes the populations entirely (figure 2*d*). Furthermore, by stabilizing the system, and so minimizing or eliminating population troughs, the maternal effect has a strongly beneficial effect on the size of the predator population through time, with the population settling at a level usually attained at the peaks of the cycles in this scenario.

Carrying out further sensitivity analysis, we explored the strength of the maternal effect necessary to cause stabilization. We varied the parameters linking prey population size with the birth rate of high- and low-feeding predators (a and \hat{x} ; figure 1*b,c*), along with the maternal effect parameter B , to explore the parameter values that promote stability (figure 3). Stable systems were defined as those in which, after approximately 3 years (1000 days), fluctuations in prey levels were less than 0.05 in amplitude. We found that stability occurred when $B > 0.2$ and was promoted by higher values of \hat{x} and a , with all three parameters interacting in their effect on stability.

To further investigate why the system stabilized, we carried out stability analysis on the coexistence steady state (details of this analysis are given in the electronic supplementary material). This gave us conditions when (i) the predator cannot be sustained, (ii) the predator is sustained and the populations are stable, and (iii) the predator is sustained

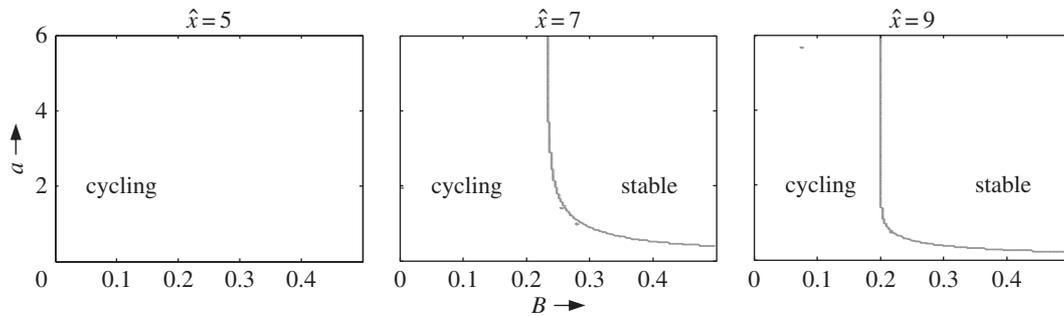


Figure 3. Maternal effect and population stability. Combined effect of three maternal effect parameters (\hat{x} , a and B) on population dynamics. Graphs show the parameter space in which cyclical dynamics occur ('cycling'), or where populations reach a stable equilibrium ('stable').

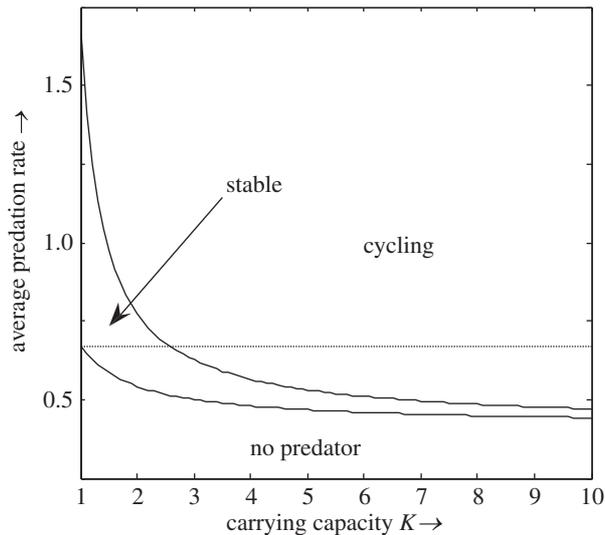


Figure 4. Thresholds for where the predator population cannot survive ('no predator'), survive stably ('stable') and cycle ('cycling'), and the average predation rate required for each to occur, plotted against varying capacity K . The dashed line is the predation rate without any maternal effect.

and the populations cycle. These conditions can all be put in terms of the average predation rate of new offspring, $C_L + q(C_H - C_L)$. Specifically: for low average predation rates, the predator does not survive; for moderate rates, there is a stable predator population; and for high average predation rates, the predator population cycles (figure 4). Hence, to stabilize the predator population and allow them to coexist with the prey, the maternal effect must act in such a way that it lowers the average predation rate sufficiently. (We also showed that was true for any number of classes of feeding rates—the thresholds between stability and cycling remain identical, and behaviour depends on the average feeding rate of all classes.)

In the *Daphnia* example, these conditions show that, when $K = 10$, the maternal effect needs to be sufficiently large to bring the average predation rate below 0.4707 for predator population to be stable.

However, if we look at this more generally, the average predation rate of new offspring can be re-arranged to $C + 2B(q - 0.5)$. Interestingly, whether the maternal effect lowers this predation rate depends on whether q is above or below 0.5. If $q < 0.5$ (i.e. offspring are more likely to be low feeders when the system is at equilibrium), which is the case in our *Daphnia* example, then an increase in the maternal

effect B lowers the average predation rate and leads to stability; in contrast, if $q > 0.5$ (i.e. offspring are more likely to be high feeders when the system is at equilibrium) then an decrease in the maternal effect B lowers the average predation rate. The value of q however depends on both the maternal effect parameters and the prey population, which in turn depend on several demographic parameters, as well as the average predation rate. Hence, there is a complex relation between the maternal effect and non-maternal effect parameters that allows a completely generalized result to be made.

(b) The maternal effect influences the size of stable populations

We also explored how, in the parameter space where dynamics are stable (for instance, when $B > 0.2$, $\hat{x} > 8$ and $a > 2$), the equilibrium population sizes of predators and prey, and the composition of the predator population, are affected by further increases in \hat{x} , a and B (figure 5). Initially, the maternal effect has a positive effect on the predator population, with the predator settling at a relatively high equilibrium (figure 2d). However, increasing the difference in feeding rate between high- and low-feeding predators (B) increases the equilibrium size of the prey population, decreases the equilibrium size of the predator population and decreases the proportion of low feeders in the predator population. Increasing \hat{x} and a also increases the equilibrium size of the prey population and reduces the equilibrium size of the predator population, but does not affect the composition of the predator population. Again, the three parameters interact in their effect on the equilibrium population sizes.

4. Discussion

By building and analysing a novel mathematical model, we have demonstrated that a maternal effect linking maternal prey availability to offspring predation rate can stabilize predator–prey dynamics by lowering the average predation rate. The widespread occurrence of this stabilizing maternal effect might explain why enrichment does not always cause predator–prey populations to fluctuate in nature—the absence of 'paradox of enrichment' behaviour [16–18].

By exerting a stabilizing influence on populations, and thus eliminating periods of extreme low population size, a moderate maternal effect exerts an overall beneficial effect on predator population sizes over time. By eliminating these population troughs, maternal effects might also decrease a population's risk of extinction and increase its ability to

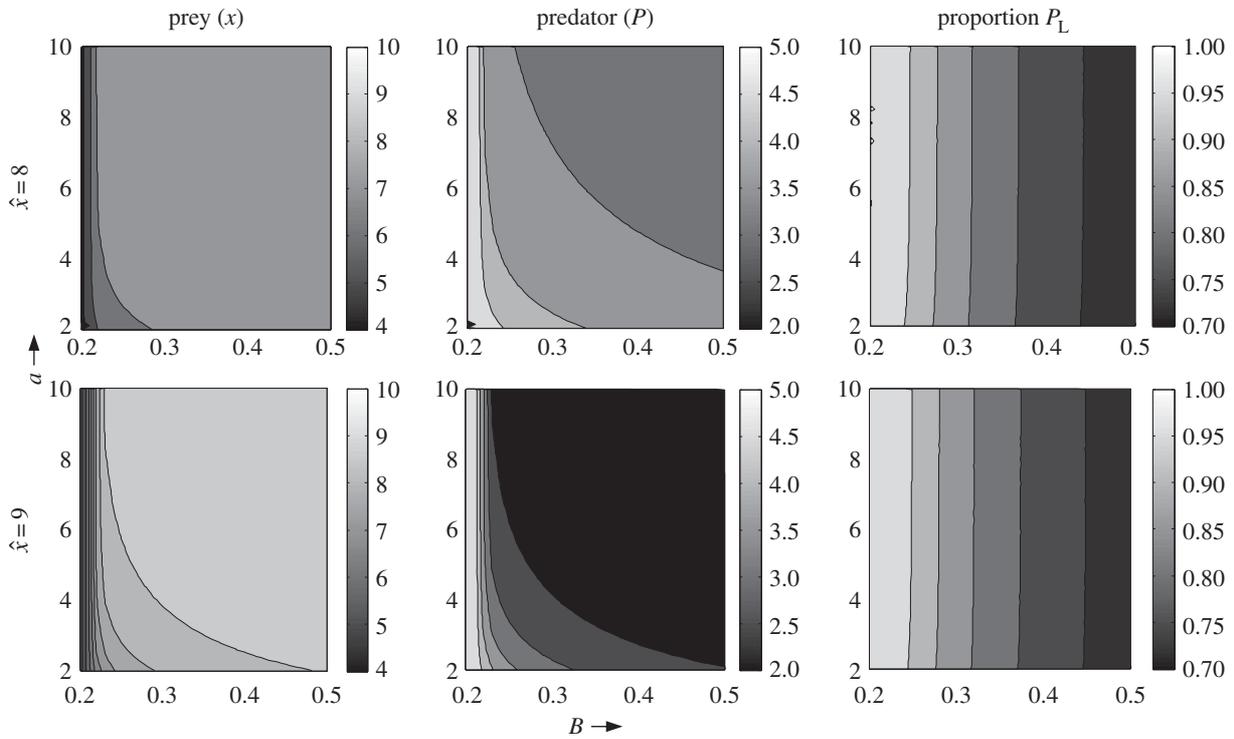


Figure 5. Maternal effect and stable equilibrium population sizes. Combined effect of three maternal effect parameters (\hat{x} , a and B) on the population sizes of predators and prey and the proportion of low-feeding predators (P_L) in the population.

tolerate harvesting. However, increasing the strength of the maternal effect further may eventually decrease the size of the predator population.

These results agree with previous theoretical studies suggesting that phenotypic plasticity in induced defences can stabilize population dynamics [20,21]. However, for these results to occur is dependent on how the maternal effect affects the average predation rate of new offspring. For our example, using *Daphnia* as a case study, it decreased the predation rate, hence stabilizing the system. However, we showed that theoretically the maternal effect can also increase the predation rate if more predators are born high feeders, and this in turn can actually drive population cycles [22]. Clearly, the nature of the maternal effect itself is important in determining whether it exerts a stabilizing or destabilizing influence on population dynamics—there is no one-size-fits-all explanation for how a maternal effect will affect dynamics.

It should also be noted that there is reason to question whether the paradox of enrichment is truly a prediction that needs explanation or is instead simply a theoretical failure—a result, perhaps, of the assumption that predator–prey relationships are prey-dependent rather than predator-dependent (under extreme predator dependence, paradox of enrichment-type effects are absent) [23].

In our study of maternal effects, we initially focused on a natural example where a maternal effect on feeding rate had been observed (the *Daphnia*–algal system), with two distinct feeding classes, but we also broadened our results analytically to describe how a maternal effect can stabilize a predator–prey system with *any* number of feeding classes. This analysis revealed that the maternal effect stabilizes predator populations because it reduces the average predator growth rate, thus allowing the prey (and hence the predator) to be stably maintained. The prevalence of this maternal

effect on feeding rate beyond *Daphnia* needs to be further explored in the wild, but we expect that many taxa display undiscovered but similar effects, because many traits influenced by feeding rate, like growth rate, are affected by maternal diet [1–4].

The relationship between maternal prey availability and offspring predation rate was crucial in determining the stabilizing influence of a maternal effect. We assumed this relationship to be sigmoidal (figure 1*b,c*), but an important next step would be to experimentally determine the actual relationship using a wide range of food availability, which would allow us to understand if maternal effects in nature are sufficiently strong to stabilize population dynamics. We also made logistical assumptions that could be tested by empirical work. First, we assumed that predators retained their maternally determined feeding rate throughout their lifetime. Experiments could determine if the maternal food-induced change in offspring feeding rate abates with time, or with changes in the food available to offspring. Indeed, many taxa, for example *Daphnia* [24–30], are known to alter their consumption rate within a generation in response to changes in food availability. Second, we assumed that the predators only differ in their feeding rates, but other traits, like longevity and fecundity, are likely to also differ as a consequence of feeding. Empirical work collecting data on the life history of offspring from mothers on different feeding regimes could explore these other effects.

The present results allow us to speculate about the likely evolutionarily stable maternal effect strategy. We might expect, for instance, the evolution of an intermediate maternal effect because initial increases in the maternal effect are stabilizing, which benefits the predator population, but beyond the stability threshold any further increase in the maternal effect actually reduces the size of the predator population (figure 5). Evolutionary invasion models are necessary

to explore the optimal maternal effect strategy. Such models could also be used to explore how evolution of the maternal effect to be affected by the degree of enrichment, the presence of other stabilizing factors like predation and the presence of seasonal forcing.

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