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Title: Maternal effects on offspring consumption can stabilise fluctuating predator-prey systems.

Short title: A maternal effect that stabilises population dynamics

Jennie S. Garbutt^{a,1}, Tom J. Little^a, Andy Hoyle^b

- a. Institute of Evolutionary Biology, School of Biological Sciences, Ashworth Laboratories, University of Edinburgh, Edinburgh, UK, EH9 3JT.
 - b. Computing Science and Mathematics, University of Stirling, Stirling, FK9 4LA , UK
1. To whom correspondence should be addressed: Tel: +44 131 650 8678, Email: J.Garbutt@ed.ac.uk

Key words: Maternal effect, consumer-resource, predator-prey, mathematical model, dynamics, consumption rate

23 **Abstract**

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

38 **Introduction**

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

56 These maternal effects on offspring feeding rate represent a feedback mechanism by which
57 predators may respond to their prey. They could represent specific adaptations that allow
58 mothers to produce offspring with a rate of feeding most suited to the prevailing conditions,
59 an example of optimal foraging [13] across generations. However, such maternal effects
60 might also exist because starved mothers are only capable of producing inferior offspring
61 with a low feeding capability. Whatever their adaptive value, we expect that these maternal
62 effects will considerably affect the behaviour of predator-prey dynamics, perhaps exerting a

63 stabilising influence by reducing prey consumption at times of low prey population size and
64 vice versa. However, this verbal reasoning requires mathematical support as the dynamical
65 consequences are difficult to predict.

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

80 **The model**

81 *The baseline model*

82 First, we review the model dynamics of a predator-prey system without the maternal effect.
83 We took a minimal approach to modelling predator and prey populations, so we could
84 capture the key characteristics of their interactions. Our model was based on features of the
85 freshwater crustacean, *Daphnia magna*, and its algal prey, a particularly well-studied
86 predator-prey system. As *Daphnia* predators are limited by their capacity to process prey, but
87 do not need to learn to capture prey, the most appropriate functional response for this system
88 is a Hollings type II response. We used a Hollings type II model from [19] (and well-used in
89 the literature) in which the algae (prey, x) grows at rate r with carrying capacity K and is
90 consumed by the *Daphnia* predator (P) at rate C , converted to new predators with efficiency
91 e , and with handling time h . Predators die at rate μ . The differential equations underlying the
92 model are given in Equations 1 and 2.

93

94 Eq. 1 (prey):
$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - \frac{PCx}{(1+xh)}$$

95

96 Eq. 2 (predator):
$$\frac{dP}{dt} = \frac{ePCx}{(1+xh)} - \mu P$$

97

98 *The maternal effects model*

99 We incorporated a maternal effect on feeding rate into this baseline model by adding
100 compartments containing predators with different feeding rates. Here, we assume that the
101 maternal effect lasts the lifetime of the offspring (predator), and that offspring fall into one of
102 two categories: those with a high consumption rate (high feeding rate predators: P_H) and
103 those with a low consumption rate (low feeding rate predators: P_L) (see Fig. 1 A for a

104 schematic of the model). The difference between the feeding rates of these predators was
 105 determined by the parameter B , which was added to and subtracted from a constant to
 106 calculate the feeding rates of high and low feeding predators respectively (C_H and C_L ; see
 107 Table 1). We assumed that the predators differ only in the rate at which they consume prey,
 108 and that their feeding efficiency (e), handling time (h) and mortality rate (μ) are identical
 109 (Table 1). The differential equations underlying the model are specified in Equations 3-5.

110

111 Eq. 3 (prey):
$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K} \right) - \frac{C_L x P_L}{(1+xh)} - \frac{C_H x P_H}{(1+xh)}$$

112

113 Eq. 4 (P_H):
$$\frac{dP_H}{dt} = \frac{qeC_H x P_H}{(1+xh)} + \frac{qeC_L x P_L}{(1+xh)} - \mu P_H$$

114

115 Eq. 5 (P_L):
$$\frac{dP_L}{dt} = \frac{(1-q)eC_L x P_L}{(1+xh)} + \frac{(1-q)eC_H x P_H}{(1+xh)} - \mu P_L$$

116 Predators in both feeding rate categories are able to give birth to both high and low feeding
 117 offspring (P_H and P_L respectively). Our maternal effect of interest links maternal prey levels
 118 with offspring feeding rate. We mimicked this effect in our model by linking the probability
 119 of a predator being born a high feeder (q) to prey population size (x) using the sigmoidal
 120 curve given in Equation 6 and depicted in Fig. 1 *B* and *C*. The probability of being born a low
 121 feeder was given by $1-q$.

122

123 Eq. 6:
$$q = \frac{1}{1+e^{-a(x-\hat{x})}}$$

124

125 The slope of the sigmoidal curve at the mid-point is determined by a : increasing a increases
126 the sensitivity of the maternal effect, with small changes in prey density (x) strongly affecting
127 the birth proportions of high and low feeding predators at high values of a (Fig. 1B). The
128 mid-point of the sigmoidal curve (i.e. the value of x for which $q = 0.5$) is determined by \hat{x} :
129 increasing \hat{x} shifts the sigmoidal curve to the right, increasing the threshold of prey (x) at
130 which predators switch from giving birth to predominantly low feeding predators to giving
131 birth to predominantly high feeding predators (Fig. 1C).

132

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

136 **Results**

137 *The maternal effect stabilises population dynamics*

138 As expected, without the maternal effect, enriching our system by increasing the carrying
139 capacity of prey (K) destabilised the dynamics, increasing the amplitude of cycling of both
140 prey and predators, and lowering their population sizes at troughs (Fig. 2 A and B). Thus, we
141 reproduced the expected “paradox of enrichment” [19]. Adding a maternal effect stabilised
142 the dynamics of an enriched system (when $K = 10$) (Fig. 2 C and D). A moderate maternal
143 effect (when $B = 0.3$) causes the frequency of cycling to increase, which reduces the time the
144 population is close to zero, and causes the amplitude of the cycles to slightly decrease (Fig. 2
145 C). A larger maternal effect (when $B = 0.5$) stabilises the populations entirely (Fig. 2 D).
146 Furthermore, by stabilising the system, and so minimising or eliminating population troughs,
147 the maternal effect has a strongly beneficial effect on the size of the predator population
148 through time, with the population settling at level usually attained at the peaks of the cycles
149 in this scenario.

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

158 To further investigate why the system stabilised, we carried out stability analysis on the co-
159 existence steady state (details of this analysis are given in the Supplementary Material.) This
160 gave us conditions when: (1) the predator cannot be sustained, (2) the predator is sustained

161 and the populations are stable, and (3) the predator is sustained and the populations cycle.
162 These conditions can all be put in terms of the average predation rate of new offspring,
163 $C_L + q(C_H - C_L)$. Specifically: for low average predation rates, the predator does not survive;
164 for moderate rates, there is a stable predator population; and for high average predation rates,
165 the predator population cycles (Fig. 4). Hence, to stabilise the predator population and allow
166 them to co-exist with the prey, the maternal effect must act in such a way that it lowers the
167 average predation rate sufficiently. (We also showed that was also true for any number of
168 classes of feeding rates – the thresholds between stability and cycling remain identical, and
169 behaviour depends on the average feeding rate of all classes.)

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

173 However, if we look at this more generally, the average predation rate of new offspring can
174 be re-arranged to $C + 2B(q - 0.5)$. Interestingly, whether the maternal effect lowers this
175 predation rate depends on whether q is above or below 0.5. If $q < 0.5$, i.e. offspring are more
176 likely to be low feeders when the system is at equilibrium, which is the case in our *Daphnia*
177 example, then an increase in the maternal effect B lowers the average predation rate and leads
178 to stability; in contrast, if $q > 0.5$, i.e. offspring are more likely to be high feeders when the
179 system is at equilibrium, then an decrease in the maternal effect B lowers the average
180 predation rate. The value of q however depends on both the maternal effect parameters and
181 the prey population, which in turn depends on several demographic parameters, as well as the
182 average predation rate. Hence there is a complex relation between the maternal effect and
183 non-maternal effect parameters that allows a completely generalised result to be made.

184 *The maternal effect influences the size of stable populations*

185 We also explored how, in the parameter space where dynamics are stable (for instance, when
186 $B > 0.2$, $\hat{x} > 8$ and $a > 2$), the equilibrium population sizes of predators and prey, and the
187 composition of the predator population, are affected by further increases in \hat{x} , a and B (Fig.
188 5). Initially the maternal effect has a positive effect on the predator population, with the
189 predator settling at a relatively high equilibrium (Fig. 2D). However, increasing the
190 difference in feeding rate between high and low feeding predators (B) increases the
191 equilibrium size of the prey population, decreases the equilibrium size of the predator
192 population, and decreases the proportion of low feeders in the predator population. Increasing
193 \hat{x} and a also increases the equilibrium size of the prey population and reduces the equilibrium
194 size of the predator population, but does not affect the composition of the predator
195 population. Again, the three parameters interact in their effect on the equilibrium population
196 sizes.

197 **Discussion**

198 By building and analysing a novel mathematical model, we have demonstrated that a
199 maternal effect linking maternal prey availability to offspring predation rate can stabilise
200 predator-prey dynamics by lowering the average predation rate. The widespread occurrence
201 of this stabilising maternal effect might explain why enrichment does not always cause
202 predator-prey populations to fluctuate in nature – the absence of “paradox of enrichment”
203 behaviour [16–18]. However, it should be noted that some question whether the paradox of
204 enrichment is truly a predication that needs explanation or instead simply a theoretical failure
205 – a result, perhaps, of the assumption that predator-prey relationships are prey-dependent
206 rather than predator-dependent (under extreme predator-dependence paradox of enrichment-
207 type effects are absent)[20].

208 By exerting a stabilising influence on populations, and thus eliminating periods of extreme
209 low population size, a moderate maternal effect exerts an overall beneficial effect on predator
210 population sizes over time. By eliminating these population troughs maternal effects might
211 also decrease a population’s risk of extinction and increase its ability to tolerate harvesting.
212 However, increasing the strength of the maternal effect further may eventually decrease the
213 size of the predator population.

214 These results agree with previous theoretical studies suggesting that phenotypic plasticity in
215 induced defences can stabilise population dynamics [21,22]. However, for these results to
216 occur is dependent on how the maternal effect affects the average predation rate of new
217 offspring. For our example, using *Daphnia* as a case study, it decreased the predation rate,
218 hence stabilising the system. However, we showed that theoretically the maternal effect can
219 also increase the predation rate if more predators are born high feeders, this in turn can
220 actually drive population cycles [23]. Clearly, the nature of the maternal effect itself is

221 important in determining whether it exerts a stabilising or destabilising influence on
222 population dynamics – there is no one-size-fits-all explanation for how a maternal effect will
223 affect dynamics.

224 In this study, we initially focused on a natural example where a maternal effect on feeding
225 rate had been observed (the *Daphnia*-algal system), with two distinct feeding classes, but we
226 also broadened our results analytically to describe how a maternal effect can stabilise a
227 predator-prey system with *any* number of feeding classes. This analysis revealed that the
228 maternal effect stabilises predator populations because it reduces the average predator growth
229 rate, thus allowing the prey (and hence the predator) to be stably maintained. The prevalence
230 of this maternal effect on feeding rate beyond *Daphnia* needs to be further explored in the
231 wild, but we expect that many taxa display undiscovered but similar effects, because many
232 traits influenced by feeding rate, like growth rate, are affected by maternal diet [1–4].

233 The relationship between maternal prey availability and offspring predation rate was crucial
234 in determining the stabilising influence of a maternal effect. We assumed this relationship to
235 be sigmoidal (Fig. 1 B and C), but an important next step would be to experimentally
236 determine the actual relationship using a wide range of food availability, which would allow
237 us to understand if maternal effects in nature are sufficiently strong to stabilise population
238 dynamics. We also made logistical assumptions that could be tested by empirical work. First,
239 we assumed that predators retained their maternally-determined feeding rate throughout their
240 lifetime. Experiments could determine if the maternal food-induced change in offspring
241 feeding rate abates with time, or with changes in the food available to offspring. Indeed,
242 many taxa, for example *Daphnia* [24–30], are known to alter their consumption rate within a
243 generation in response to changes in food availability. Second, we assumed that the predators
244 only differ in their feeding rates, but other traits, like longevity and fecundity, are likely to

245 also differ as a consequence of feeding. Empirical work collecting data on the life history of
246 offspring from mothers on different feeding regimes could explore these others effects.

247 Our results allow us to speculate about the likely evolutionarily stable maternal effect
248 strategy. We might expect, for instance, the evolution of an intermediate maternal effect
249 because initial increases in the maternal effect are stabilising, which benefits the predator
250 population, but beyond the stability threshold any further increase in the maternal effect
251 actually reduces the size of the predator population (Fig. 5). Evolutionary invasion models
252 are necessary to explore the optimal maternal effect strategy. Such models could also be used
253 to explore how evolution of the maternal effect to be affected by the degree of enrichment,
254 the presence of other stabilising factors like predation, and the presence of seasonal forcing.

255 **Ethics statement**

256 This manuscript does not contain any research on humans or animals.

257 **Data accessibility statement**

258 This manuscript is theoretical and does not contain any data.

259 **Competing interests statement**

260 We have no competing interests.

261 **Author contributions**

262 JG, AH & TL conceived study. JG and AH built and analysed models. JG wrote the paper.

263 AH and TL commented on the paper.

264 **Funding**

265 This work was supported by a NERC grant no. NE/I026405/1.

266

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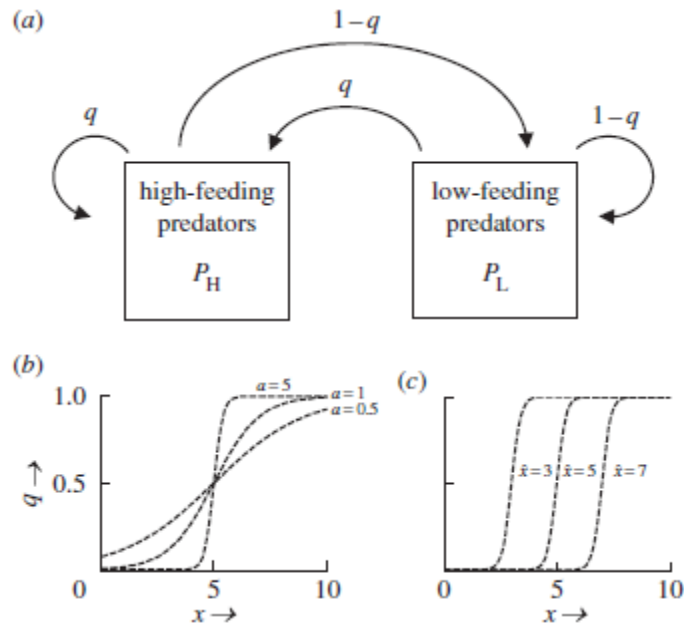
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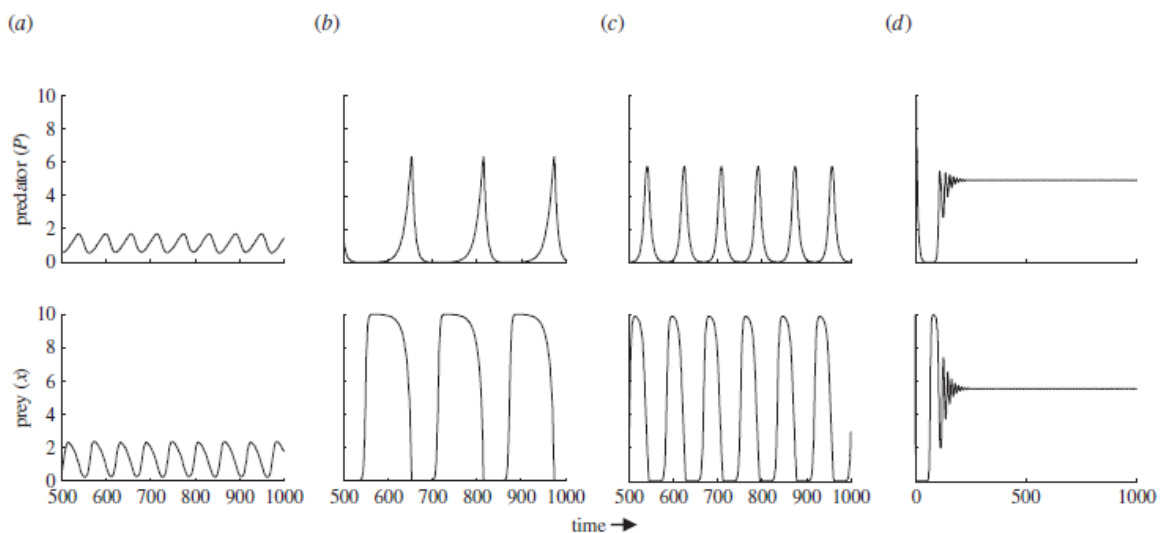
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346 **Figure legends**



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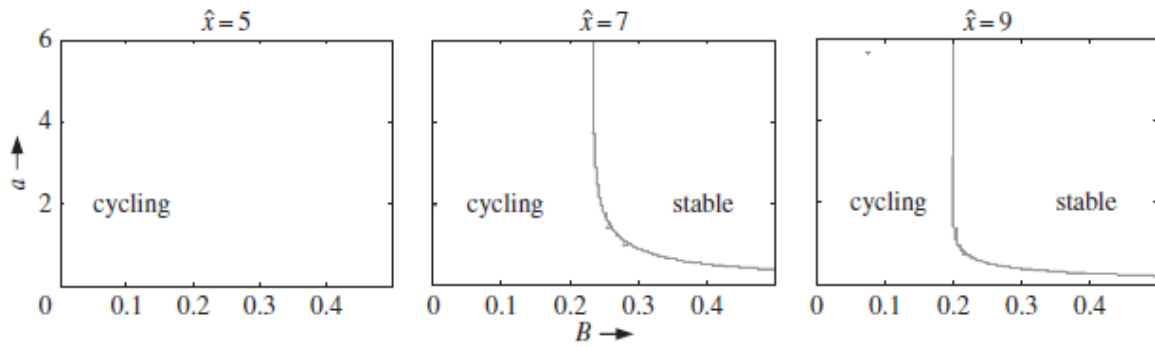
348 **Figure 1:** Maternal effects model. (A) Model schematic. Predators give birth to high-feeding
 349 (P_H) and low-feeding (P_L) predators with proportions q and $1 - q$. A sigmoidal curve describes
 350 how q changes with the density of the resource (x), as shown in (B) and (C). (B) Increasing a
 351 increases the slope of the curve and (C) increasing \hat{x} increases the midpoint of the curve. In
 352 (B) $\hat{x} = 5$ and in (C) $a = 5$.



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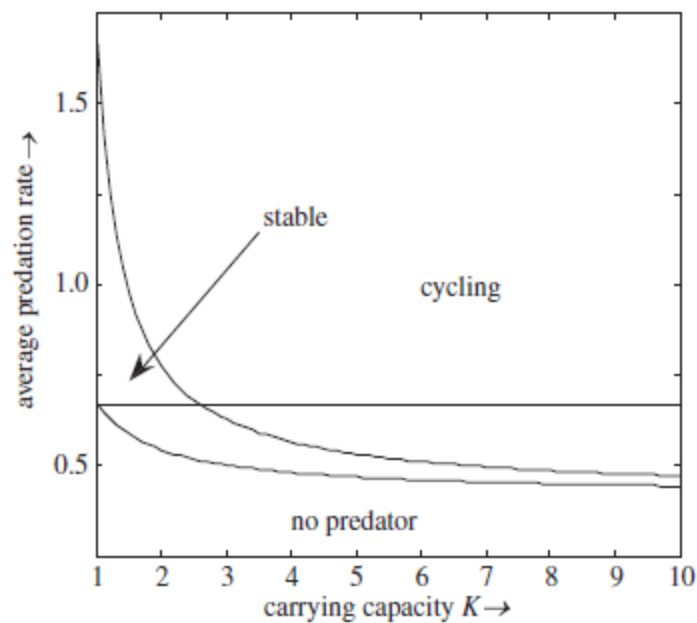
354 **Figure 2:** Population dynamics of predators and prey with and without the maternal effect:
 355 (A) $K = 3$ with no maternal effect, (B) $K = 10$ with no maternal effect, (C) $K=10$ with a

356 moderate ($B = 0.3$) maternal effect, (D) $K = 10$ with a large ($B = 0.5$) maternal effect. Plots
 357 are the last 500 days of a 1000 day simulation except for (D) in which the entire 1000 day
 358 simulation is shown. In A-D $C = 0.67$, $e = 0.6$, $h = 1.67$ and $\mu = 0.15$. In C and D $a = 2$ and \hat{x}
 359 $= 6$.



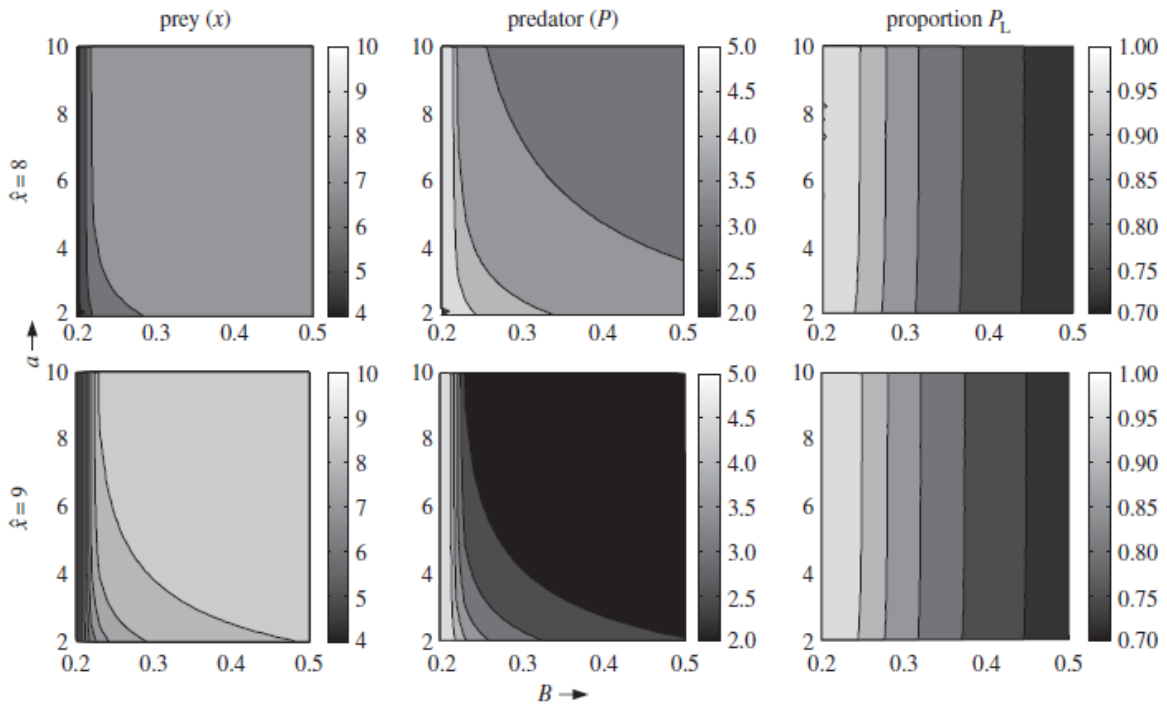
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361 **Figure 3:** Maternal effect and population stability. Combined effect of three maternal effect
 362 parameters (\hat{x} , a , and B) on population dynamics. Graphs show the parameter space in which
 363 cyclical dynamics occur (“Cycling”), or where populations reach a stable equilibrium
 364 (“Stable”).



365

366 **Figure 4:** Thresholds for where the predator population cannot survive (“No predator”),
 367 survive stably (“Stable”) and cycle (“Cycling”), and the average predation rate required for
 368 each to occur, plotted against varying capacity K . The dashed line is the predation rate
 369 without any maternal effect.



370

371 **Figure 5:** Maternal effect and stable equilibrium population sizes. Combined effect of three
 372 maternal effect parameters ($\hat{\chi}$, a , and B) on the population sizes of predators and prey and the
 373 proportion of low feeding predators (P_L) in the population.

374

375 **Table 1:** Parameterisation of the model. All parameter values were from [19].

376

Parameter	Symbol	Value
<i>Algae (x)</i>		
Maximal growth rate	r	0.5
Carrying capacity	K	10
<i>High feeding Daphnia (D_H)</i>		
Feeding rate	F_H	$0.67 + B$
Handling time	h	1.67
Death rate	μ	0.15
Conversion rate of algae into	e	0.6
<i>Daphnia</i>		
<i>Low feeding Daphnia (D_L)</i>		
Feeding rate	F_L	$0.67 - B$
Handling time	h	1.67
Death rate	μ	0.15
Conversion rate of algae into	e	0.6
<i>Daphnia</i>		

377