Unpalatable prey resolves the paradox of enrichment

Motomi Genkai-Kato[*] and Norio Yamamura

Center for Ecological Research, Kyoto University, Kyoto 606-8502, Japan

Enrichment is an increasingly serious trend in natural ecosystems. A theoretical model of a predator–prey system with a natural assumption of satiation in predation predicts that enrichment causes the populations to fluctuate to stochastic extinction. However, this 'paradox of enrichment' does not always occur in experimental and natural communities. Here we present a theoretical model that describes a novel mechanism for resolving the paradox in the case of a predator with optimal selective feeding. Specifically, a less profitable but edible (thus 'unpalatable') prey species sharply reduces the amplitude of population oscillations and firmly prevents the minimum abundances of species from falling below certain values. The presence of such an unpalatable prey thus guarantees the robustness of the system against enrichment.

Keywords: optimal foraging; paradox of enrichment; population oscillation; predator–prey system; unpalatable prey

1. INTRODUCTION

A predator–prey model incorporating a natural assumption of satiation in predation has led to a paradoxical prediction (Rosenzweig 1971; Gilpin 1972; May 1972): a sufficient enrichment of the prey leads to the risk of destruction of the system. Such an enrichment first destabilizes a stable equilibrium point, resulting in a limit cycle. The amplitudes of the population oscillations will grow rapidly and, thus, the minimum population abundances will approach zero as enrichment is further increased, so that stochastic effects could lead to extinction (smaller populations are more prone to such an extinction). Thus, Rosenzweig (1971) warned against enriching natural ecosystems in order to increase their food yield. Enrichment (often referred to as eutrophication) is increasingly widespread and serious in natural ecosystems because of the increased level of human activities.

In spite of the astonishing prediction of this classic model, the paradox has seldom been tested empirically. In one-predator–one-prey systems, there have been several experiments in which enrichment caused population oscillations (Huffaker *et al.* 1963; Luckinbill 1974; Bohannan & Lenski 1997). In contrast to these examples, McCauley and Murdoch (1990) showed by using a *Daphnia*–algal system that enrichment did not change the amplitude of the population oscillation, neither in a field nor an experimental system. Furthermore, Kirk (1998) recently showed with laboratory microcosms containing planktonic rotifer predators and phytoplankton prey that enrichment can stabilize the population oscillations through autotoxins produced by the predator.

These empirical studies imply that it is necessary to apply additional assumptions to the theoretical model.

For the empirical work by McCauley and Murdoch (1990), the presence of inedible prey is proposed as a plausible mechanism to resolve the discrepancy between theory and observation, in which the prey acts as a nutrient 'sponge' (Kretzschmar *et al.* 1993; Murdoch *et al.* 1998). The experiment by Kirk (1998) can be explained by the addition of density-dependent predator mortality to the classic model (Gilpin 1975), because this factor results in stabilizing an unstable system. Other models incorporating an assumption that the attack rate of the predator depends on the ratio of prey to predator abundances, claim that enrichment is not predicted to be destabilizing (Arditi & Ginzburg 1989). These 'ratio-dependent' models, however, are less widely accepted than 'prey-dependent' models in which the attack rate depends on the instantaneous density of prey (Oksanen *et al.* 1992; Diehl *et al.* 1993; Abrams 1994; Gleeson 1994).

In this paper, we theoretically propose a new mechanism that resolves the paradox of enrichment, using a one-predator–two-prey model in which the predator shows optimal selective feeding, which is a well-known behaviour of many predators (Werner & Hall 1974; Krebs *et al.* 1977; DeMott 1989). Several studies have shown that switching between prey by predators can stabilize predator–prey systems (Murdoch 1969; Murdoch & Oaten 1975; Tansky 1978; Teramoto *et al.* 1979). However, none of these studies considered cases in which the equilibrium was unstable and the system followed a limit cycle. The model applied here is different from the previous models with switching predators in that (i) we deal with non-equilibrium dynamics of limit cycles, and (ii) the predator displays the optimal selective feeding strategy which maximizes energy input, dependent on the profitabilities and the abundances of its prey (Charnov 1976). We assume that enrichment of a system increases only the prey carrying capacity, following the original model in which

the paradox of enrichment was discussed (Rosenzweig 1971). It is well-known that the stability of an equilibrium point depends on the carrying capacity, but not on the intrinsic growth rate which may affect the equilibrium abundance.

2. MODEL

Consider a system consisting of two prey species populations (X_1 and X_2) and one predator population (Y), the dynamics of which is defined by the following set of equations:

$$\frac{dX_1}{dt} = \left\{ \varepsilon_1 \left(1 - \frac{X_1}{K_1} - \alpha \frac{X_2}{K_1} \right) - r_1 Y \right\} X_1, \qquad (1a)$$

$$\frac{dX_2}{dt} = \left\{ \varepsilon_2 \left(1 - \beta \frac{X_1}{K_2} - \frac{X_2}{K_2} \right) - r_2 Y \right\} X_2, \qquad (1b)$$

$$\frac{dY}{dt} = \left\{ -\varepsilon_3 + k(g_1 r_1 X_1 + g_2 r_2 X_2) \right\} Y, \qquad (1c)$$

where $r_i = p_i a_i / (1 + \sum_j p_j h_j a_j X_j)$.

The ε and K parameters are the rates of growth of the two prey when scarce (ε_3 is the predator death rate) and the carrying capacities of the prey in the environment, respectively. The two prey species compete with each other, as described by a Lotka–Volterra competitive system with interspecific competition coefficients α and β. The energy value of an individual of prey species i is g_i. The conversion efficiency of consumed prey into the predator's reproduction rate is k. The term r_i corresponds to predation, in which the encounter efficiency with prey species i is a_i; the handling time for prey species i is h_i; p_i is the probability that the predator captures an individual of prey species i when encountered. We assume here that the predation is basically described by a type 2 functional response (concave downwards), because we are interested in the dynamics of an unstable system and the type 2 is the simplest functional response that produces a population oscillation.

Assume that the predator is an optimal forager that chooses the value for each of the probabilities p_i ($0 \leqslant p_i \leqslant 1; i = 1, 2$) in order to maximize the energy input by predation $g_1 r_1 X_1 + g_2 r_2 X_2$. The two prey species are assumed to be ranked in their profitability as $g_1/h_1 > g_2/h_2$ (i.e. prey X_1 is more profitable for the predator than prey X_2) so that p_1 should always be 1 (Charnov 1976). We also assume that the more profitable prey X_1 is superior in competition to the less profitable prey ($\alpha < \beta$), because otherwise the two prey species cannot coexist (Takeuchi 1996). We further assume that the more profitable prey X_1 yields enough nutrition to support a persisting predator population in the absence of the less profitable prey, or mathematically, that

$$\frac{g_1}{h_1} > \frac{\varepsilon_3}{k}. \qquad (2)$$

This inequality is derived from the condition that there exists a positive range of X_1 such that $dY/dt > 0$ when $X_2 = 0$ and $Y > 0$ in equation (1c).

It is known (Charnov 1976) that the predation rate $g_1 r_1 X_1 + g_2 r_2 X_2$ is maximized when $p_2 = 0$ (or $p_2 = 1$) if the abundance of the more profitable prey X_1 is greater (or smaller) than a critical abundance $\hat{X}_1$, where $\hat{X}_1 = g_2 / [a_1 h_1 h_2 (g_1/h_1 - g_2/h_2)]$.

Noting that $\hat{X}_1$ is an increasing function of the profitability g_2/h_2 of the less profitable prey X_2, let the prey be classified according to the range of its profitability g_2/h_2, i.e. let the value of $\hat{X}_1$ be classified into three categories: inedible prey ($\hat{X}_1 < X_1^{\min}$), unpalatable prey ($X_1^{\min} < \hat{X}_1 < X_1^*$), and palatable prey ($X_1^* < \hat{X}_1$), where $X_1^{\min}$ is the minimum abundance of X_1 in its oscillation when $X_2 = 0$, and $X_1^* (\equiv \varepsilon_3/[a_1(kg_1 - \varepsilon_3 h_1)])$ is the equilibrium value of X_1 when $X_2 = 0$, obtained from $dY/dt = 0$ in equation (1c) with $Y > 0$. Note that $X_1^{\min}$ and X_1^* do not depend on g_2 or h_2.

Setting $\hat{X}_1 = X_1^*$, we obtain the critical profitability of X_2, ε_3/k, below which (i.e. when $g_2/h_2 < \varepsilon_3/k$) the less profitable prey is classified as unpalatable and above which (when $g_2/h_2 > \varepsilon_3/k$) it is classified as palatable. Note from inequality (2) that an unpalatable or inedible prey cannot, while a palatable prey can, yield enough nutrition to support the predator population in the absence of the alternative prey.

3. RESULTS

We numerically calculated the dynamics of three species for different profitability of the less profitable prey and summarize the results in figure 1. We first observe that in the absence of the less profitable prey X_2, population oscillations occur with sufficient enrichment, i.e. for large values of K (the left-most panels in figure 1a,b). The presence of X_2 always reduces the amplitude of oscillation (the other panels in figure 1a,b). The degree of this stabilizing effect depends on the profitability g_2/h_2 of the less profitable prey X_2 (figure 1a,b,d). The stabilizing effect is the strongest when the less profitable prey is unpalatable. Within the range of unpalatable prey, the stabilizing effect becomes stronger as the profitability g_2/h_2 of the less profitable prey X_2 increases, and the oscillation is sharply suppressed (almost to a negligible level) at the critical profitability of the prey (ε_3/k), beyond which the amplitude of the oscillation discontinuously increases (figure 1d).

In the presence of inedible prey X_2, the effective carrying capacity of X_1 is reduced by competition (Kretzschmar *et al.* 1993), resulting in reduction in the amplitude of the oscillation. In the presence of unpalatable prey X_2, observe a vertical drop of the orbit in the X_1–Y space (figure 1b). A close-up view of the drop (figure 1c) indicates the following: an expanded population Y causes the reduction of X_1, but when X_1 falls below $\hat{X}_1$, the predator begins to eat not only X_1 but also X_2, which causes an immediate recovery of X_1, while decreasing Y itself (because $\hat{X}_1 < X_1^*$, where $dY/dt < 0$, as is clear from equation (1c)). As the profitability g_2/h_2 of the unpalatable prey X_2 increases, the $\hat{X}_1$ value and thus the realized minimum X_1 value increase, which causes the minimum Y to increase, resulting in the reduction in the amplitude of the oscillation (figure 1d).

In the case of palatable prey X_2, its population level is more heavily suppressed both by predation because of its
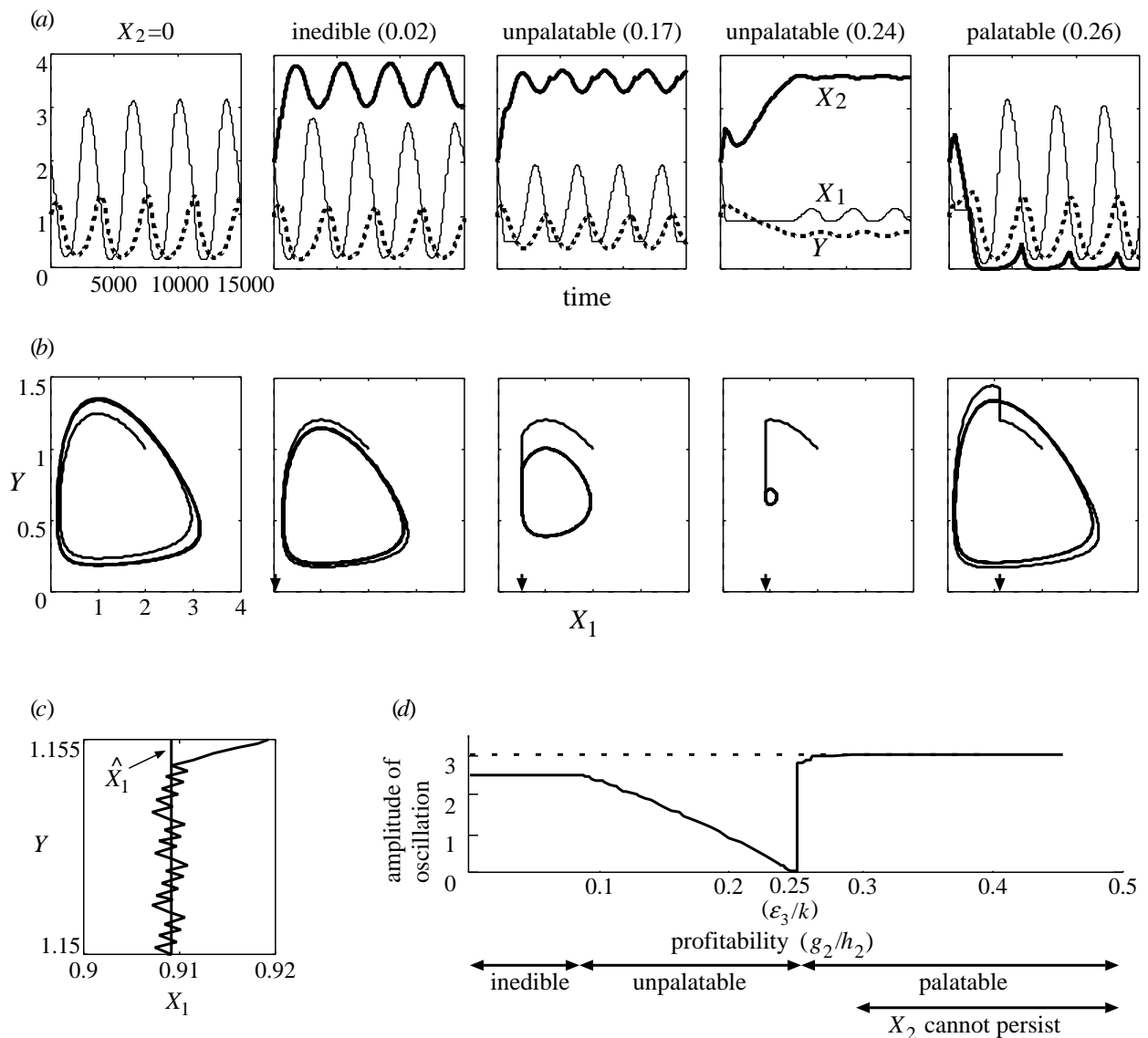
Figure 1. Dynamics of the predator–prey system described by equations (1) with the less profitable prey of different degrees of profitability. We solved this numerically by the Runge–Kutta method using the following values: $\varepsilon_1 = 0.5, \varepsilon_2 = 0.25, \varepsilon_3 = 0.25$, $\alpha = 0.1, \beta = 0.4, a_1 = a_2 = 1, k = 1, g_1 = g_2 = 0.5, h_1 = 1, K_1 = K_2 = 4$. We change the profitability g_2/h_2 of the less profitable prey X_2 by changing the h_2 value. (a) The temporal change in abundances of the more profitable prey (X_1, thin line), less profitable prey (X_2, thick line) and predator (Y, dotted line), and (b) the dynamics in the X_1–Y space of the system. Panels in (a) and (b) in the same column depict the same case. Numbers in parentheses in (a) express the profitability of the less profitable prey. Arrows in (b) express the values of $\hat{X}_1$. In the left-most panels of (a) and (b) the less profitable prey X_2 is absent, the initial values are $(X_1, X_2, Y) = (2, 0, 1)$ and the equilibrium point in the X_1–Y space is $(1, 0.75)$. In the other panels, the initial values are $(2, 2, 1)$ and the equilibrium point is $(1, 0.66)$. (c) A close-up view of the vertical drop in the X_1–Y space in the case of the unpalatable prey X_2 with profitability $g_2/h_2 = 0.24$. (d) Relationship between the profitability g_2/h_2 of the less profitable prey X_2 and the amplitude of the oscillation, defined by the difference between the maximum and minimum abundances of the more profitable prey X_1. The broken line represents the amplitude of the oscillation in the absence of the less profitable prey X_2. The profitability g_1/h_1 of the more profitable prey X_1 is 0.5.

relatively high profitability and by competition with the superior competitor X_1. The competitive influence of X_2 on X_1 is thus reduced, resulting in a larger value of the maximum X_1 as shown in figure 1a. The maximum Y is enhanced, not only by the large value of the maximum X_1, but also by a relatively high profitability of X_2, which subsequently causes the small values of the minimum X_1 and Y. Thus, the amplitude of the oscillation in the case of palatable prey is larger than that in the case of inedible prey (figure 1d).

Next, we examined the effects of increasing enrichment, or the carrying capacity K, on the oscillation

amplitude and the minimum abundance of prey X_1 under the presence of different categories of prey X_2. In the case of unpalatable prey, the minimum abundances of all the species populations are kept considerably higher than zero in the face of increasing enrichment, while they approach zero in the other cases (figure 2a). This means that an unpalatable prey prevents the abundances of all the species populations from becoming so low that stochastic fluctuation may cause them to go extinct. Although the amplitude of the population oscillation increases with an increasing enrichment in the case of any category of the less profitable prey, the increase is much
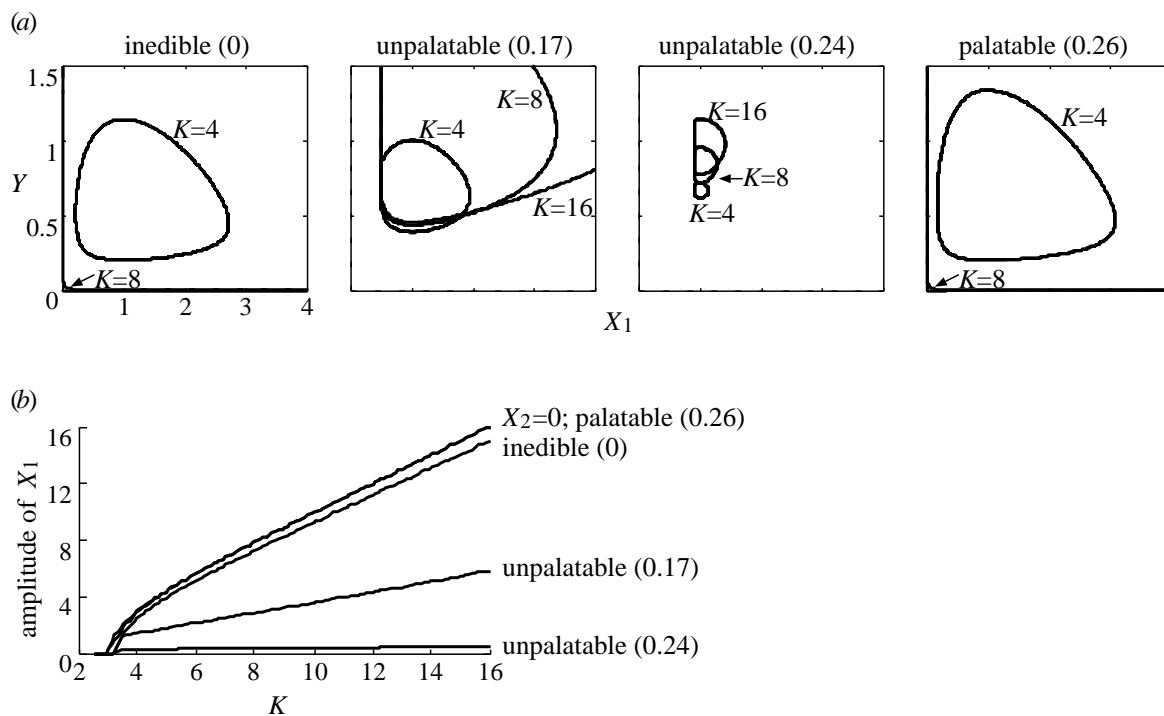
(a)

(b)

Figure 2. Effects of enrichment in the presence of the less profitable prey with different profitability values. Numbers in parentheses express the profitability g_2/h_2 of the less profitable prey X_2. The degree of enrichment is represented by the magnitude of the prey carrying capacity, $K\ (=K_1=K_2)$. The other parameters are the same as in figure 1. (*a*) Minimum abundances on the limit cycles in the X_1–Y space. In the case of inedible and palatable prey, the orbits with $K=16$ almost cling to the axes. (*b*) Relationship between enrichment and the amplitude of the oscillation, defined as in figure 1*d*.

slower in the case of unpalatable prey (figure 2*b*). Thus, unpalatable prey most effectively prevents the system from oscillating to population extinction in the face of increasing enrichment, resolving the puzzle over the paradox of enrichment.

4. DISCUSSION

Regarding the effect of enrichment on the parameters, we followed a historical theory that enrichment of the prey caused only a change in the carrying capacity, however, one might imagine that enrichment can cause an increase in the intrinsic growth rate (ε_1 and ε_2), or, further, both in the intrinsic growth rate and the carrying capacity. First, we confirmed by numerical simulation that an increase in the intrinsic growth rate had little effect on the amplitude of the population oscillation, in contrast to an increase in the carrying capacity, and caused the cycle to move upward in the X_1–Y space (which corresponded to an increase in the predator equilibrium abundance). Therefore, if enrichment increased only the intrinsic growth rate, the problem of the 'paradox of enrichment' would not exist in the first place. This is the reason why we confined our study to effects of the carrying capacity on the dynamics of the system.

Our model with an optimally foraging predator which maximized its energy intake, revealed that the stabilizing effect of the alternative (less profitable) prey species was strongest when it yielded insufficient nutrients on its own to maintain the predator population but its profitability was relatively high (i.e. unpalatable prey). The relationship between the profitability of the less profitable prey

and the amplitude of the population oscillation in figure 1*d* showed a discontinuous change between the categories of unpalatable and palatable prey, which is a new result in the stability analyses of communities. This discontinuous change implies the possibility that a population oscillation with small amplitude can explosively increase because of a small change in the profitability of the less profitable prey; for example, in the handling time in response to a change in temperature or in the energy value of individual prey in response to enrichment of the system. The reverse scenario that the amplitude is suddenly reduced is also possible. These possibilities could occur when the profitability of the less profitable prey takes a value near the critical profitability ε_3/k.

Our assumption of optimal behaviour by the predator was shown to prevent the paradoxical prediction regarding enrichment: in the presence of unpalatable prey, although the amplitude of the population oscillation increased somewhat with enrichment, the minimum abundance of the more profitable prey species was kept well above zero. Thus, the minimum abundance of the predator was subsequently kept considerably higher than zero, so that the predator–prey system was robust against any magnitude of enrichment. There have been theoretical works with other assumptions of adaptive behaviour by predators and prey which can stabilize population oscillations, although most of these works dealt with only the stability of the equilibrium points. Selective feeding by predators, in which they fed more intensively on the more abundant prey species, was shown to broaden the condition under which the equilibrium point was stable (Murdoch 1969; Murdoch & Oaten 1975; Tansky 1978;

Teramoto *et al*. 1979). Antipredator behaviours of prey can also stabilize population oscillations in a system with heterogeneity, such as refuges in which the predation risk is low but the prey has some disadvantage (Ruxton 1995; Křivan 1998). In conclusion, adaptive behaviours of predator and prey have a general tendency to make it harder for predators to overexploit a specific prey and so can have stabilizing effects.

Most real communities are more complex than the community analysed here. McCann *et al*. (1998) recently showed with communities of up to four species that interactions of weak to intermediate strength between species were important in promoting community persistence and stability. The presence of unpalatable prey in our model can be regarded as a cause of such a link, because the unpalatable prey is not always eaten by the predator. Although it will be difficult to analyse communities incorporating many (i.e. more than three) species and more realistic links, such as with adaptive behaviours of all species, it is an important and open problem to be solved step by step.

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