

Imperfect optimal foraging and the paradox of enrichment

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Abstract We show that the paradox of enrichment can be theoretically resolved in a flexible predator–prey system in which the predator practices imperfect optimal foraging. A previous study showed that perfect optimal foraging can mitigate increases in the amplitude of population oscillations associated with enrichment, but it did not show a stabilization pattern. Our results show that imperfect optimal foraging can stabilize the system and resolve the paradox of enrichment under nonequilibrium dynamics. Furthermore, the degree of stabilization with enrichment was stronger when the imperfection of optimal foraging was larger.

Keywords Paradox of enrichment · Optimal foraging · Flexibility · Stabilization · Predator–prey

Introduction

Ecologists have studied relationships between predator–prey interaction mechanisms and community stability (Murdoch et al. 2003). Classical theory predicted that basal resource enrichment would destabilize predator–prey systems (Rosenzweig 1971). Several field studies have suggested that the paradox of enrichment does not exist in

natural food webs (e.g., McCauley and Murdoch 1990). Thus, the paradox of enrichment is an unsolved problem among community ecology issues, and theoretical studies continue to attempt to resolve the paradox or explain the lack of the paradox in nature (Jensen and Ginzburg 2005).

Recently, Kondoh (2003, 2007) suggested that flexible web connections can stabilize the dynamics of a food-web structure. Flexibility represents a paradigm shift in studies on ecosystem stability because classical theoretical studies generally considered interaction links to be fixed (Kondoh 2005) despite widespread plasticity in predator–prey interactions (Tollrian and Harvell 1999; Agrawal 2001; Vos et al. 2005). Flexible web connections often can be achieved by adaptation, which is a universal property of organisms. Adaptive behaviors such as diet switching, habitat choice, ontogenetic niche shifts, and defense are examples of adaptations that lead to flexible interaction links (Kondoh 2003; Abrams et al. 2007; Takimoto 2003; Vos et al. 2004a, 2005; Kondoh 2007). Theoretical studies tackling classical ecological problems have demonstrated the importance of adaptive diet use to stability of interaction systems (Wilson and Yoshimura 1994; Kondoh 2003).

A one-predator–two-prey system is the minimum unit size for realizing flexible food-web connections through diet switching, which may be a consequence of optimal foraging by the predator species. Many theoretical studies have examined stability in a one-predator–two-prey system in which the predator practices optimal foraging. However, most of those studies did not focus on the relationship between food-web stability and basal resource enrichment (e.g., Fryxell and Lundberg 1994; Yamauchi and Yamamura 2005).

By considering a flexibility of food-web connections through optimal foraging of predator, Genkai-Kato and Yamamura (1999) did tackle the problem of the paradox of

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enrichment, and building on their study, Mougi and Nishimura (2007) presented one condition in which the paradox is theoretically resolved. Those studies analyzed nonequilibrium dynamics under higher enrichment, although most theoretical studies have analyzed convergence to an equilibrium in a linear approximating system despite the fact that the properties of behaviors of real food webs often exhibit nonequilibrium dynamics (McCann et al. 1998; Huismann and Weissing 1999; but see Kendall et al. 1998). Only a few studies analyzed the consequences of flexible links for both equilibrium and nonequilibrium dynamics (e.g., Vos et al. 2004b). A coupling of flexible behavior and nonequilibrium dynamics may stabilize the food webs and resolve the ecological paradoxes (Kondoh 2003; Mougi and Nishimura 2007).

Most previous studies assumed an adaptive forager practicing optimal foraging perfectly (Genkai-Kato and Yamamura 1999; Mougi and Nishimura 2007). In nature, however, it is difficult for predators to practice optimal foraging perfectly because of environmental, sensory, and physiological constraints (Fryxell and Lundberg 1994; Ma et al. 2003; Vos et al. 2006). In this paper, we show that if a predator's optimal foraging performance is imperfect, then the paradox of enrichment can be resolved in a simple one-predator–two-prey food-web structure in nonequilibrium dynamics. The major finding of our study is that imperfect diet switching can reduce or vanish the amplitude of population cycles in an enriched one-predator–two-prey system.

The model

Food-web dynamics

We use the familiar one-predator–two-prey system in which the predator practices optimal foraging (Fryxell and Lundberg 1994; Genkai-Kato and Yamamura 1999; Ma et al. 2003; Yamauchi and Yamamura 2005). The basic model formalism is based on our previous study (Mougi and Nishimura 2007). In this predator–prey system, the densities of the two prey species and the one predator species, denoted by X_i ($i=1$ or 2) and Y , respectively, are considered to show the following dynamics

$$\dot{X}_i = \left\{ r_i \left(1 - \frac{1}{K_i} \sum_{j \in \text{prey types}} \alpha_{ij} X_j \right) - \mu_i Y \right\} X_i \quad (1a)$$

$$\dot{Y} = \left(b \sum_{i \in \text{prey types}} g_i \mu_i X_i - d \right) Y \quad (1b)$$

where $\mu_i = p_i a_i / \left(1 + \sum_{i \in \text{preys}} p_i h_i a_i X_i \right)$. For the predator species, μ_i implies the instantaneous exploitation rate of

prey species i , defined by a type 2 functional response; a_i is the searching efficiency for prey i ; h_i is the handling time of prey i ; g_i is the energy value of an individual of prey i ; and p_i ($0 \leq p_i \leq 1$) is the capture probability of an individual of prey species i given an encounter; b is the conversion efficiency, which relates the predator's birth rate to prey consumption, and d is the death rate of the predator species. For prey i , α_{ij} are the intra- and interspecific competition coefficients ($\alpha_{ii}=1$); r_i is the per capita prey growth rate; and K_i is the carrying capacity of the prey, which traditionally (since Rosenzweig 1971) indicates the degree of enrichment.

Optimal diet use

We assume that the predators are optimal foragers and select their diet in accordance with optimal diet utilization theory (Stephens and Krebs 1986). Each predator determines whether to include or exclude a prey species in its diet on the basis of the prey's profitability in order to maximize its net rate of energy intake while foraging. Profitability of prey items is ranked according to the net energy gain, g , relative to handling time, h , upon an attack. The higher-ranked prey species is unconditionally included in the diet (i.e., $p_1=1$). Under perfect optimal foraging, the capture probability of an individual of the less profitable prey species 2 given an encounter, p_2 , equals zero or one, depending on whether the density of the more profitable prey X_1 is greater or less than the threshold density, $\bar{X}_1 (= g_2 / \{a_1 h_1 h_2 (g_1/h_1 - g_2/h_2)\})$. If the density of the more profitable prey drops below a critical threshold (the menu-change threshold), the less profitable prey is also included in the diet ($p_2=1$). Otherwise, the less profitable prey is excluded from the diet ($p_2=0$). Inclusion or exclusion of the less profitable prey (i.e., menu variety) depends on the difference in profitability between the prey items and the density of the more profitable prey (Stephens and Krebs 1986).

Imperfect optimal foraging

The above model is based on perfect optimal foraging. The diet expansion is often observed to be a sigmoid function of the densities of more profitable prey due to a number of biologically realistic uncertainties associated with predator assessment of prey encounter rates, prey profitabilities, or predator motivational state (Krebs and McCleery 1984; Stephens 1985), while patterns of diet choice are often qualitatively consistent with perfect optimality model (Stephens and Krebs 1986). Here, we extend the model, making it a general model that considers behavioral variation around expected step functions (Fryxell and Lundberg 1994; Ma et al. 2003). The general model is

one in which the capture probability of the less profitable prey is a continuous sigmoid function of X_1 , $p_2 = \widehat{X}_1^\varepsilon / (\widehat{X}_1^\varepsilon + X_1^\varepsilon)$, where ε is a parameter (>1) representing the accuracy of foraging. As ε increases, the continuous p_2 function approximates the step function of perfect optimal foraging; in other words, the smaller the value of ε , the greater the degree of inaccuracy, and vice versa. Because of this, the predator loses opportunity costs on both sides of a critical threshold.

The analysis of nonequilibrium dynamics

In the predator–prey systems, the equilibrium state changes from stable to unstable (oscillation) at a critical value of K through a Hopf bifurcation (Rosenzweig 1971). In our analysis, we focus on the nonequilibrium dynamics above the critical value of K (Genkai-Kato and Yamamura 1999). The density of each species in predator–prey communities potentially displays complex behavior at larger values of K . For evaluation of the stability of a system in a nonequilibrium state, we conducted a sufficiently long simulation run and obtained asymptotic behavior in which the amplitude (minimum density) of the population oscillation of all species does not change over time. We numerically calculated the amplitude of the population oscillation (difference between the maximum and minimum densities) and the minimum density, each of which is a stability index, and changes in the stability indices with an increase in K (in this model, the relationship between the amplitude and K is linear). Since the trends in the stability indices were identical for all species, we calculated stability for a single species (X_1). Although we chose arbitrary parameter values in our investigations, we confirmed that our main result was robust even when other parameter values were chosen. For

example, the result does not change within parameter ranges, $0.17 \leq d \leq 0.33$, $1 \leq b \leq 1.5$, $1 \leq a \leq 40$, $0.1 \leq r_i \leq 15$, and $0 \leq a_{ij} < 1$, if the parameters except for a focal parameter are fixed.

Results

We found that the effect of inaccuracy in optimal foraging resolves the paradox. Figure 1 shows the effect of inaccuracy in optimal foraging on stability. The amplitude of oscillation decreases as the inaccuracy of the predator's generalist–specialist switching policy increases (decreasing ε value) within a given inaccuracy region at a given value of the basal resource (see the range between the solid and dashed black lines in (b1), (b2), and (c) in Fig. 1, where $K=5$). In addition, the minimum density of each oscillation increases as the inaccuracy of optimal foraging increases (decreasing ε). As inaccuracy increases further, the oscillation disappears (Fig. 1a). These results indicate that stability increases as inaccuracy increases, as Fryxell and Lundberg (1994) implied.

When the accuracy of optimal foraging is high (Fig. 1c, i.e., high value of ε), the amplitude of oscillation around the equilibrium becomes large as K becomes large (see the solid gray line in Fig. 1c). When the inaccuracy of optimal foraging becomes high, the amplitude of oscillation around the equilibrium becomes small as K becomes large (see the solid gray line in Fig. 1b). Figure 2 schematically shows the changes in the equilibrium values and in the amplitude of the oscillations around the equilibria with increasing enrichment. Medium inaccuracy of optimal foraging (middle values of ε) can resolve the paradox under conditions of nonequilibrium dynamics (i.e., amplitudes decrease and

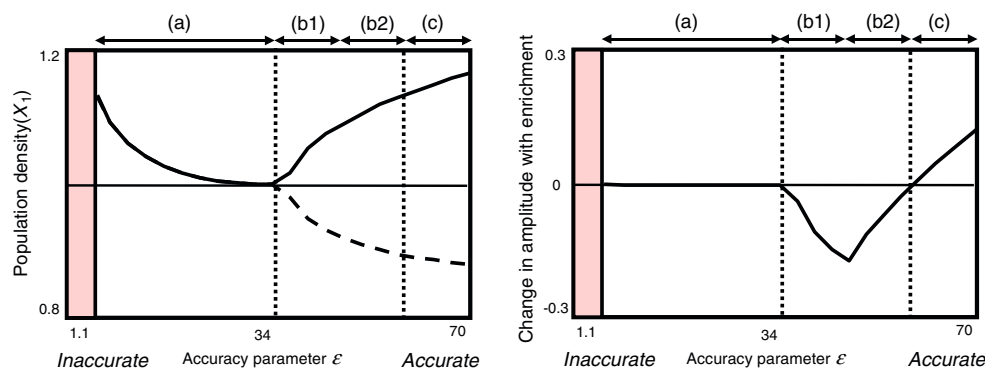


Fig. 1 Effect of inaccuracy on stability (*left panel*) and changes in stability with enrichment (*right panel*). The *black solid* and *dashed lines* indicate the maximum and minimum population density of prey species 1 ($K=5$). In region (a), the densities do not oscillate (equilibrium condition), and in regions (b) and (c), the densities oscillate (nonequilibrium condition). The *red region* is that in which the three species cannot coexist at higher values of K (i.e., the less profitable prey, X_2 ,

becomes extinct). The *gray line* indicates the degree of change in the amplitude of oscillation for species 1 as K increases from 5 to 50. *a–c* are regions showing different responses with enrichment. Parameter values used in these calculations were $\alpha_{12}=0.4$, $\alpha_{21}=0.1$, $b=1$, $d=0.25$, $r_1=0.5$, $r_2=0.25$, $a_1=a_2=1$, $g_1=g_2=0.5$, $h_1=1$, and $h_2=2.2$ (i.e., profitability of the more profitable prey is $g_1/h_1=0.5$ and that of the less profitable prey is $g_2/h_2=0.23$)

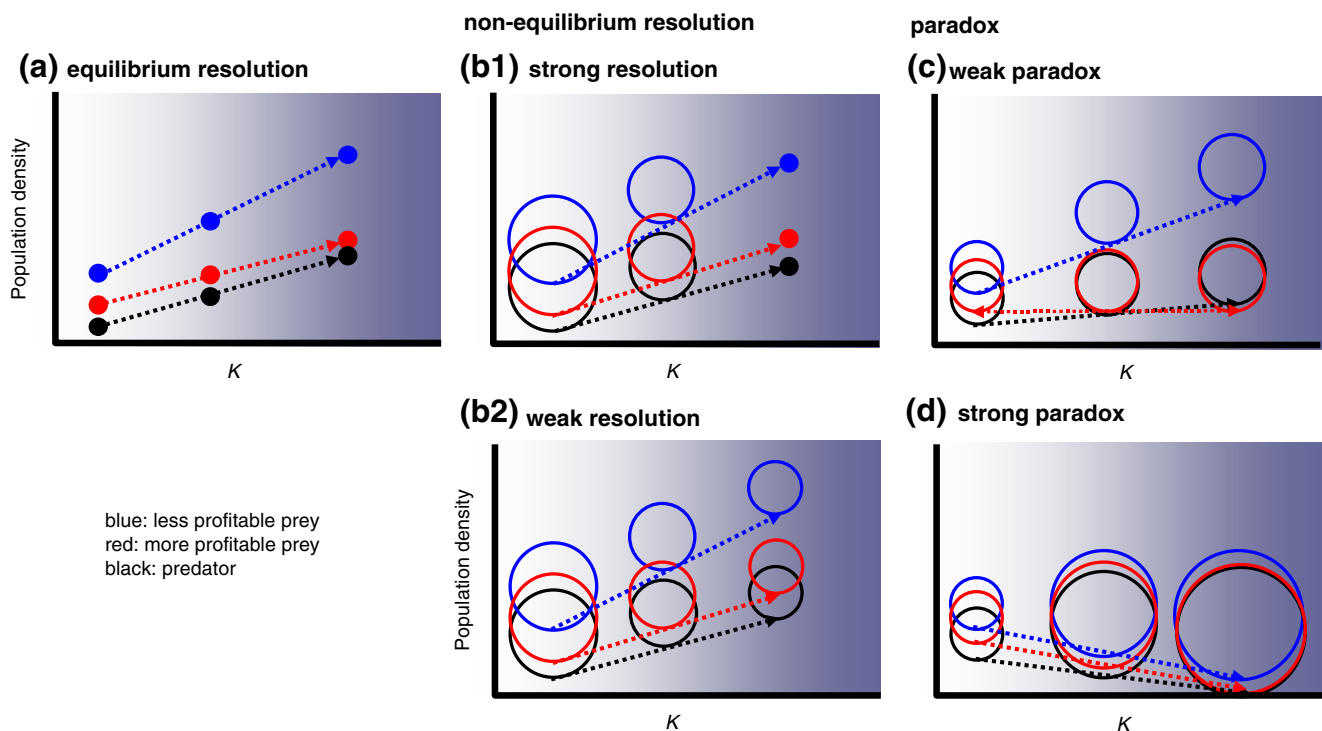


Fig. 2 Schematic diagram of the paradox of enrichment pattern and the pattern when the paradox is resolved in each region (**a**, **b1**, **b2**, and **c**) of inaccurate foraging indicated in Fig. 1. The panels are qualitative diagrams of the pattern of oscillation of population densities as the carrying capacity of the basal resource, K , increases (degree of enrichment). *Circles* qualitatively represent the amplitude of cycles of population density oscillation, and the position of the circles above the *horizontal baseline* reflects the minimum population density. *Points* represent that the amplitude is zero. *Arrows* represent the change in the minimum densities with enrichment. The *two-headed arrow* represent that the minimum density does not change with enrichment. In region (**a**), no paradox of enrichment exists because a stable equilibrium (no oscillation) exists and the equilibrium density of each species increases with increasing enrichment. In region **b**, under nonequilibrium conditions, resolution is achieved: the amplitude of

minimum densities increase with enrichment). Furthermore, it is also apparent that the paradox of enrichment is resolved for a wide range of ε values when the profitability value of the less profitable prey (g_2/h_2) is high and close to the boundary of the region of coexistence of all species (Fig. 3).

The imperfect foraging can also result from a perfect step function for p_2 but at the wrong (imperfect) threshold. We consider the following step function. When $X_1 > \hat{X}_1 + m$, $p_1=1$ and $p_2=0$, otherwise $p_1=1$ and $p_2=1$; m is the deviation from a perfect threshold. The case of $m=0$ implies the perfect step function. In this case, the paradox of enrichment always occurs (Fig. 3). However, we found that the paradox of enrichment can be resolved when values of m are positive and small under the condition that g_2/h_2 is slightly greater than or equal to 0.25 (note that under this parameter range, the paradox of enrichment is likely to be

resolved in case of a sigmoid function; see Fig. 3). Therefore, the essence for resolution of the paradox in our scenario is not a sigmoid function but imperfect optimal foraging.

oscillation of each species decreases with enrichment, and minimum densities increase with enrichment. In region **b1**, strong resolution is achieved because the amplitudes decrease to zero for larger values of K . In region **b2**, where the amplitudes decrease but do not reach zero at large values of K , the resolution is weak. In regions **c** and **d** (perfect optimal foraging), the paradox holds: the amplitudes of oscillation are never zero and they increase with enrichment. Where the minimum densities of the predator and the less profitable prey increase and that of the more profitable prey does not change with enrichment (region **c**), the paradox is weak (the pattern shown by Genkai-Kato and Yamamura 1999). Where minimum densities of all species decrease with enrichment (region **d**), the paradox is strong (this is the original pattern of the paradox of enrichment described by Rosenzweig 1971). Pattern **d**, which is distinguished from pattern **c** by the value of g_2/h_2 (Genkai-Kato and Yamamura 1999), is not shown in Figs. 1 or 3

Discussion

Efforts have been made to resolve the paradox of enrichment ever since Rosenzweig published his influential paper (Rosenzweig 1971) on ecosystem stability (Gilpin 1975; Arditi and Ginzburg 1989; Abrams and Walters 1996; Vos et al. 2004b). Most theoretical studies have used a local stability analysis to show resolution of the paradox. Although a local stability analysis is a handy and powerful tool for understanding the stability of a system, when we consider dynamical behavior per se as a reality, the

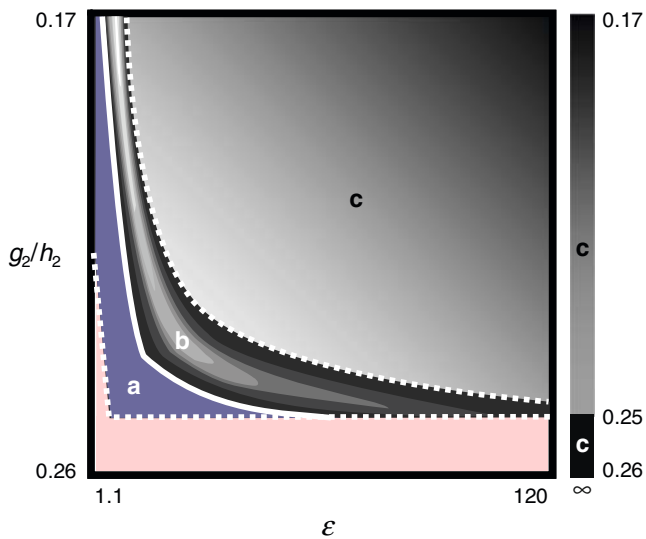


Fig. 3 Effect of changes in the profitability of the less profitable prey (g_2/h_2). Regions **a–c** in the panel correspond to those in Fig. 1 (i.e., **c** paradox region; **a** and **b** paradox-resolution regions). The red region is that where the three species cannot coexist at higher values of K (i.e., the less profitable prey, X_2 , becomes extinct). The bar on the right side of the right-hand figure shows the case of perfect optimal foraging. The lighter the shading in region **b**, the greater the decrease in the amplitude of oscillation with increasing enrichment. The darker the shading in region **c**, the greater the increase in the amplitude of oscillation with increasing enrichment. The parameter values are the same as those used in Fig. 1

amplitude of population oscillation and minimum population density are more useful indexes, particularly for investigating stability in nonequilibrium dynamics (McCann et al. 1998). The paradox of enrichment in a nonequilibrium dynamical system has not been solved (Abrams and Roth 1994; Jansen 1995; Genkai-Kato and Yamamura 1999; but see Mougi and Nishimura 2007).

Our results show that imperfect optimal foraging by the predator is likely to stabilize a flexible one-predator–two-prey system and that the paradox of enrichment can be resolved under nonequilibrium dynamics in a flexible predator–prey system in which the predator practices imperfect optimal foraging. Although perfect optimal foraging cannot result in stabilization with increasing enrichment or resolve the paradox of enrichment in a one-predator–two-prey system (Genkai-Kato and Yamamura 1999), the paradox can be resolved if the optimal foraging is not perfect.

Fryxell and Lundberg (1994) examined local stability in a one-predator–two-prey system with the imperfect foraging mechanism adopted in this paper. Their main result regarding system stability agrees with ours. Genkai-Kato and Yamamura (1999) investigated a one-predator–two-prey system with perfect optimal foraging by the predator and showed mitigation of the paradox of enrichment. We found that it is possible to resolve the paradox of

enrichment in a nonequilibrium dynamical system that integrates the systems of Fryxell and Lundberg (1994) and Genkai-Kato and Yamamura (1999). Previously, we showed that the paradox of enrichment can be resolved by a food-web structure involving multiple predator species (Mougi and Nishimura 2007; Mougi and Nishimura 2008a). In this study, however, we showed that resolution of the paradox under nonequilibrium dynamics is possible in one of the simplest flexible predator–prey systems.

A flexible food web represents a major paradigm shift in studies investigating the stability of ecosystems. Resolution of paradoxes in classical theories of ecology has been achieved in recent years by hypothesizing flexible food-web links made possible by adaptive behaviors (Wilson and Yoshimura 1994; Kondoh 2003; Mougi and Nishimura 2007, 2008a, b). Most studies on adaptive behavior assume an organism that practices a perfectly optimal behavior. The optimal behavior for one particular environmental condition is usually not a “flexible” one. There may for example be an optimal ratio (an ideal free distribution) of defended and undefended individuals in a system, and the community may get locked in such an IFD (DeAngelis et al. 2007). Such locked systems show different changes in their properties under enrichment than flexible, suboptimal ones (Vos et al. 2004a, b; DeAngelis et al. 2007). The predator–prey systems and food chains with inducible defenses modeled by Vos et al. (2004a, b) were flexible (not locked in an IFD) when parameterized in an ecologically realistic way. They may, thus, represent an example of a flexible but evolutionarily imperfect strategy (Vos et al. 2004a,b; DeAngelis et al. 2007). In our simple system, the flexible

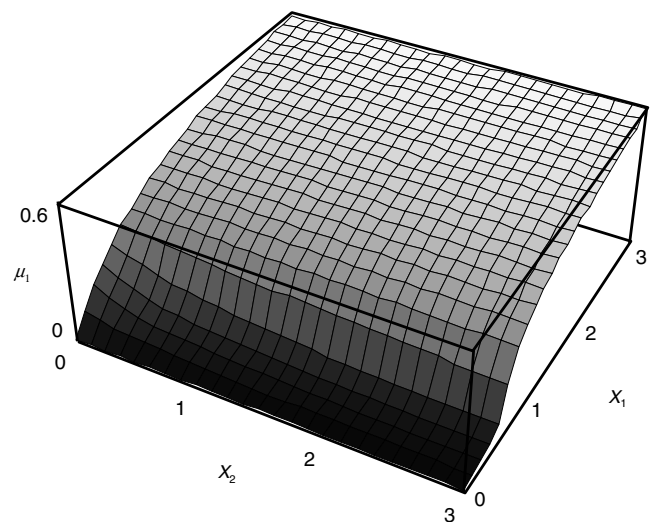


Fig. 4 Functional response on the more profitable prey in relation to population densities of two prey species when the paradox of enrichment is resolved. The parameter values are the same as those used in Fig. 1 except for $h_2=3$ and $\varepsilon=5$

food web made only by imperfect adaptation can be stable in the face of enrichment. In this context, consideration of imperfect behavior might change our understanding of the stability of the systems which assume a perfect organism not only quantitatively but also qualitatively.

The imperfect optimal foraging can relate to important ecological theories on food-web stability. First, the imperfect optimal foraging is essentially identical to weak interactions which stabilize food web modules (Yodzis 1981; McCann et al. 1998; McCann 2000). When optimal foraging is perfect, the system oscillate between one-predator–one-prey to one-predator–two-prey as discrete states. However, imperfect foraging implies a system dominated by a state of one-predator–two-prey. A key point in this context is that, when imperfect foraging is not strong, the link between the predator and the less profitable prey operate as a weak link.

The imperfect optimal foraging also relates to functional response that can stabilize predator–prey systems. When imperfect optimal foraging is not strong (Fig. 1b), the functional response on the more profitable prey relatively changes from Holling type II (which induces unstable system) to III (which induces stable system) with increase in the density of the less profitable prey (see Fig. 4 or Fryxell and Lundberg 1994). In fact, this is the essence of the mechanism for resolution of the paradox of enrichment. In our system, the density of the less profitable prey increases with enrichment compared with the more profitable prey (nutrient sponge; Murdoch et al. 1998). Thus, functional response on the more profitable prey relatively changes from types II to III with enrichment, and the system is stabilized.

Recently, Rall et al. (2008) showed that Holling type III functional response can contribute to stability of complex multispecies food webs. In this context, the imperfect optimal foraging may be a bridge between two long standing paradox of ecological theory, the paradox of enrichment and the prevalence of complex communities in spite that they are theoretically unstable (May 1972).

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References

- Abrams PA, Roth JD (1994) The effect of enrichment of three-species food chains with nonlinear functional responses. *Ecology* 75:1118–1130. doi:10.2307/1939435
- Abrams PA, Walters CJ (1996) Invulnerable prey and the paradox of enrichment. *Ecology* 77:1125–1133. doi:10.2307/2265581
- Abrams PA, Cressman R, Krivan V (2007) The role of behavioral dynamics in determining the patch distributions of interacting species. *Am Nat* 169:505–518. doi:10.1086/511963
- Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326. doi:10.1126/science.1060701
- Arditi R, Ginzburg LR (1989) Coupling in predator–prey dynamics: ratio-dependence. *J Theor Biol* 139:311–326. doi:10.1016/S0022-5193(89)80211-5
- DeAngelis DL, Vos M, Mooij WM, Abrams PA (2007) Feedback effects between the food chain and induced defense strategies. In: Rooney N, McCann KS, Noakes DLG (eds) From energetics to ecosystems: the dynamics and structure of ecological systems. The Peter Yodzis fundamental ecology series. Springer, New York, pp 213–236
- Fryxell JM, Lundberg P (1994) Diet choice and predator–prey dynamics. *Evol Ecol* 8:407–421. doi:10.1007/BF01238191
- Genkai-Kato M, Yamamura N (1999) Unpalatable prey resolves the paradox of enrichment. *Proc R Soc Lond B Biol Sci* 266:1215–1219. doi:10.1098/rspb.1999.0765
- Gilpin ME (1975) Group selection in predator–prey communities. Princeton University Press, Princeton
- Huisman J, Weissing FJ (1999) Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407–410. doi:10.1038/46540
- Jansen VAA (1995) Regulation of predator–prey systems through spatial interactions: a possible solution to the paradox of enrichment. *Oikos* 74:384–390. doi:10.2307/3545983
- Jensen CXJ, Ginzburg LR (2005) Paradoxes or theoretical failures? The jury is still out. *Ecol Modell* 188:3–14. doi:10.1016/j.ecolmodel.2005.05.001
- Kendall BE, Prendergast J, Bjørnstad ON (1998) The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecol Lett* 1:160–164. doi:10.1046/j.1461-0248.1998.00037.x
- Kondoh M (2003) Foraging adaptation and the relationship between food web complexity and stability. *Science* 299:1388–1391. doi:10.1126/science.1079154
- Kondoh M (2005) Linking flexible food-web structure to population stability: a theoretical consideration on adaptive food webs. In: De Ruiter PC, Wolters V, Moore JC (eds) Dynamic food webs: Multispecies assemblages, ecosystem development, and environmental change. Academic, Durham
- Kondoh M (2007) Anti-predator defence and the complexity–stability relationship of food webs. *Proc R Soc Lond B Biol Sci* 274:1617–1624. doi:10.1098/rspb.2007.0335
- Krebs JR, McCleery RH (1984) Optimization in behavioral ecology. In: Krebs JR, Davies NB (eds) Behavioral ecology. Blackwell, Oxford
- Ma BO, Abrams PA, Brassil CE (2003) Dynamic versus instantaneous models of diet choice. *Am Nat* 162:668–684. doi:10.1086/378783
- May RM (1972) Will a large complex system be stable? *Nature* 238:413–414. doi:10.1038/238413a0
- McCann KS (2000) The diversity–stability debate. *Nature* 405:228–233. doi:10.1038/35012234
- McCann KS, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. *Nature* 395:794–798. doi:10.1038/27427
- McCauley E, Murdoch WW (1990) Predator–prey dynamics in environments rich and poor in nutrients. *Nature* 343:455–457. doi:10.1038/343455a0
- Mougi A, Nishimura K (2007) A resolution of the paradox of enrichment. *J Theor Biol* 248:194–201. doi:10.1016/j.jtbi.2007.04.005
- Mougi A, Nishimura K (2008a) Enrichment can damp population cycles: a balance of inflexible and flexible interactions. *Oikos*. doi:10.1111/j.2008.0030-1299.16688.x

- Mougi A, Nishimura K (2008b) The paradox of enrichment in an adaptive world. *Proc R Soc Lond B Biol Sci* 275:2563–2568. doi:10.1098/rspb.2008.0889
- Murdoch WW, Nisbet RM, McCauley E, deRoos AM, Gurney WSC (1998) Plankton abundance and dynamics across nutrient levels: tests of hypotheses. *Ecology* 79:1339–1356
- Murdoch WW, Briggs CJ, Nisbet RM (2003) Resource-consumer dynamics. Princeton University Press, Princeton
- Rall BC, Guill C, Brose U (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos* 117:202–213. doi:10.1111/j.2007.0030-1299.15491.x
- Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387. doi:10.1126/science.171.3969.385
- Stephens DW (1985) How important are partial preferences. *Anim Behav* 33:667–669. doi:10.1016/S0003-3472(85)80092-0
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton
- Takimoto G (2003) Adaptive plasticity in ontogenetic niche shifts stabilizes consumer-resource dynamics. *Am Nat* 162:93–109. doi:10.1086/375540
- Tollrian R, Harvell CD (1999) The ecology and evolution of inducible defenses. Princeton University Press, Princeton
- Vos M, Verschoor AM, Kooi BW, Wäckers FL, DeAngelis DL, Mooij WM (2004a) Inducible defences and trophic structure. *Ecology* 85:2783–2794. doi:10.1890/03-0670
- Vos M, Kooi BW, DeAngelis DL, Mooij WM (2004b) Inducible defences and the paradox of enrichment. *Oikos* 105:471–480. doi:10.1111/j.0030-1299.2004.12930.x
- Vos M, Kooi BW, DeAngelis DL, Mooij WM (2005) Inducible defenses in food webs. In: De Ruiter PC, Wolters V, Moore JC (eds) Dynamic food webs: Multispecies assemblages, ecosystem development, and environmental change. Academic, Durham, pp 114–127
- Vos M, Vet LEM, Wäckers FL, Middelburg JJ, van der Putten WH, Mooij WM, Heip CHP, van Donk E (2006) Infochemicals structure marine, terrestrial and freshwater food webs. *Ecol Inform* 1:23–32. doi:10.1016/j.ecoinf.2005.06.001
- Wilson DS, Yoshimura J (1994) On the coexistence of specialists and generalists. *Am Nat* 144:692–707. doi:10.1086/285702
- Yamauchi A, Yamamura N (2005) Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology* 86:2513–2524. doi:10.1890/04-1524
- Yodzis P (1981) The stability of real ecosystems. *Nature* 289:674–676. doi:10.1038/289674a0