EFFECTS OF DEFENSE EVOLUTION AND DIET CHOICE ON POPULATION DYNAMICS IN A ONE-PREDATOR–TWO-PREY SYSTEM

Atsushi Yamauchi[1] and Norio Yamamura

Center for Ecological Research, Kyoto University, Hirano 2-509-3, Otsu 520-2113, Japan

Abstract. The population dynamics of a one-predator–two-prey system were modeled. This model included the evolution of antipredator defense in the prey species and the optimal diet choice in the predator and was analyzed numerically using computer simulations. Results showed that defense evolution in the prey species tended to promote coexistence of the three species and, depending on parameters, reduced the amplitude of density fluctuations. Introducing optimal diet choice by the predator into the model also promoted coexistence and generally reduced density fluctuations. When the additive genetic variance for defense intensity was large (i.e., the evolutionary rate of defense was rapid), coexistence of the three species and stabilization of dynamics tended to be promoted. As a consequence, we concluded that (1) the evolution of antipredator defense can be an important factor in the persistence of a community, either with or without the optimal diet choice of predator; and (2) when population dynamics are combined with the evolutionary dynamics of trait development, the relative time scale of the two processes plays an important role in the stability of the system.

Key words: defense evolution; one-predator–two-prey system; optimal diet choice; population dynamics; theory.

Introduction

In predator–prey systems, the predator will vary its foraging behavior depending upon the conditions or characteristics of its prey. Such predator responses to prey conditions have been studied theoretically using two approaches. In one type of approach, the probability that a predator attacks a prey item was represented by a continuous "switching" function, which was dependent on the frequency of each prey type (Murdoch 1969). This assumes that, to some extent, there is a trade-off by the predator between searching times for two prey items. The theoretical effects of such switching on population dynamics have been well studied in a one-predator–two-prey system (Murdoch and Oaten 1975, Comins and Hassell 1976, Murdoch 1977, Tansky 1978, Teramoto et al. 1979, Vance 1978, Hutson 1984, van Baalen et al. 2001). Vance (1978) and Hutson (1984) showed that switching in predators leads to predation-mediated coexistence of the two prey items, while van Baalen et al. (2001) showed that switching to alternative food promotes persistence of the prey–predator system. Matsuda (1985), Mukherjee and Roy (1998), and Abrams (1999) analyzed the evolution of the switching strategy of predators in a one-predator–two-prey system. In the second type of approach, the predator's response was represented by a stepwise function, based on "optimal diet choice" theory (Charnov 1976, Stephens and Krebs 1986). This theory assumed

that there is no trade-off for the predator in the search times for two prey types. According to this theory, a predator determines the probability of attack based on the encounter rate, handling time and quality of each prey, where the optimal probability for a particular prey, depending on conditions, is either 0 or 1 (Charnov 1976).

In the prey–predator system, the qualities of the prey can affect population dynamics. This relationship has been investigated by several studies, some of which focused on the population dynamics, ignoring predator behaviors (Leibold 1989, 1996, Grover 1995, Genkai-Kato and Yamamura 2000). However, the prey quality is an important factor in determining the predator behaviors, especially within the optimal diet choice theory. Therefore, other authors have investigated the effects of prey quality (usually "profitability" or "palatability") on predator–prey population dynamics and incorporated the optimal diet choice of the predator (Holt 1983, Gleeson and Wilson 1986, Fryxell and Lundberg 1994, Křivan 1996, 1998, Genkai-Kato and Yamamura 1999, Křivan and Sikder 1999), with most of those studies suggesting that optimal diet choice contributes to the coexistence of species.

Prey quality is also an interesting issue from an evolutionary biological viewpoint. A reduction in the quality of a particular prey type might decrease predation pressure, i.e., it is an antipredator defense. For example, the presence of poisonous chemicals (e.g., alkaloids) and/or indigestible contents (e.g., lignin and hemicellulose) in plant tissues reduces their quality for predators and acts as an antipredator defense. Many studies

have analyzed such evolutionary processes (de Jong 1995, Yamamura and Tsuji 1995, Iwasa et al. 1996, Loreau and de Mazancourt 1999, de Jong and van der Meijden 2000), but few have considered defense evolution in the context of population dynamics. Matsuda et al. (1993), de Mazancourt and Loreau (2000), and de Mazancourt et al. (2001) have, however, addressed this issue from the viewpoint of the population dynamics or nutrient dynamics, although Matsuda et al. (1993) focused on a two-predator–one-prey system and de Mazancourt and Loreau (2000) and de Mazancourt et al. (2001) did not explicitly consider the relationship between the predator behavior response and the prey defense. Edelstein-Keshet and Rausher (1989) and Underwood (1999) analyzed the relationship between the population dynamics of herbivores and plants that, within a single generation, increased their defense level in response to the level of herbivory (induced defense), although they neither explicitly incorporated the population dynamics of plants, nor focused on the evolutionary aspects of defense.

In summary, there have been several types of theoretical studies analyzing the relationship between optimal foraging, defense evolution and population dynamics among predator–prey systems. These have mainly focused on the following aspects: (1) the effects of optimal foraging behavior of predators on population dynamics; (2) the effects of a constant level of antipredator defense on population dynamics, excluding optimal diet choice in the predator; (3) the effects of a constant level of antipredator defense on population dynamics, including optimal diet choice in the predator; and (4) the relationship between the evolution of antipredator defense strategies and population (or nutrient) dynamics. However, few studies to date have combined optimal foraging, defense evolution and population dynamics. Abrams and Matsuda (1993) analyzed the dynamics of a one-predator–two-prey system and included the evolution of both predator switching and antipredator defense of prey items. They analyzed indirect effects for the two prey types, but they did not determine the stability or persistence of the system.

In the present study, we construct a model of population dynamics for a one-predator–two-prey system that includes the evolution of prey defense and optimal diet choice of the predator. This enables examination of the influence of these multiple effects on population dynamics, e.g., stability and persistence. Due to its complexity, computer simulations were used to analyze the model.

MATHEMATICAL MODEL

Basic model

The present model incorporated a single species of predator and two prey species, the population sizes of which were denoted by x, y, and z, respectively. It assumed that no competition existed between the two

prey species and that a predator could search for both prey species simultaneously, i.e., that there was no trade-off between the search times for either prey. Each prey was characterized by five parameters: intrinsic growth rate (r), carrying capacity (K), encounter rate with the predator (α), handling time (h), and ''basic quality'' for the predator (g). To investigate the effects of defense evolution and optimal behavior on population dynamics, we assumed that all these parameters are the same for both prey species, except encounter rate with the predator, which was assumed to differ (α_x and α_y). The population dynamics of the predator were characterized by an exchange rate from the foraged prey biomass to its own growth (r_z) and death rate (d). These were calculated by

$$\frac{dx}{dt} = r\left(1 - \frac{x}{K}\right)x - f_x(x, y)z \tag{1a}$$

$$\frac{dy}{dt} = r\left(1 - \frac{y}{K}\right)y - f_y(x, y)z \tag{1b}$$

$$\frac{dz}{dt} = r_z[gf_x(x, y) + gf_y(x, y)]z - dz \tag{1c}$$

where

$$f_x(x, y) = \frac{p_x\alpha_x x}{1 + p_x\alpha_x xh + p_y\alpha_y yh} \tag{1d}$$

$$f_y(x, y) = \frac{p_y\alpha_y y}{1 + p_x\alpha_x xh + p_y\alpha_y yh}. \tag{1e}$$

Eqs. 1d and e describe the foraging rates of the predator on the two prey items, based on a type II functional response; p_x and p_y are the probability of attack by the predator on the two prey items. Here, the predators were considered to always attack the prey when they were encountered ($p_x = p_y = 1$). The first term of Eqs. 1a and b represents a logistic growth rate in prey populations, while the second term represents the reduction in population growth rate due to predation.

It should be noted that, in this model, an attack by the predator was not assumed to always result in the death of the prey. If it had been, then the evolution of antipredator defenses (see *Defense evolution in prey species*) would have been very difficult, as the mutant genotype with high defense ability would not realize any advantage due to the lethal effect of the predator's attack. This problem can be solved, but different considerations should be applied on animal and plant prey species. In animal prey–predator interactions, prey can avoid predation after encounters with a predator by either counterattacking and/or fleeing. We consider that the predator has to spend the same handling time (on battle or chase), even if the prey finally escape. Here, the defensive trait could increase the probability of successful avoidance of predation, thereby increasing prey survivorship. In this case, $f_x(x, y)/x$ and $f_y(x, y)/y$ in Eqs. 1a and b can be regarded as the probability of

a single prey individual being encountered, attacked, and killed by predators. In contrast, in plant–herbivore interactions, plants cannot avoid predation during encounters with predators. However, herbivores usually only forage on certain parts of the plant; this does not cause the death of the plant but reduces plant biomass, in turn reducing the plant's reproductive ability. In this case, a defensive trait will reduce the loss of reproductive ability in the foraged plant, with $f_x(x, y)/x$ and $f_y(x, y)/y$ considered to represent the loss of reproductive ability of a single plant, with plant death included only as a logistic term. The assumption that prey items that are attacked are not actually killed was needed to define prey fitness and model the evolution of antipredator defenses (see *Defense evolution in prey species*).

Defense evolution in prey species

Antipredation defense in prey species can reduce predation pressure, although it probably requires some investment of resources. This results in a trade-off between the level of defense and reproductive output. In the present model, it was assumed that when the reproduction rate of a prey species is reduced, the predation probability and the loss of reproductive ability are concomitantly reduced. It is reasonable to assume that the predation probability and the loss in prey biomass decrease monotonically with the defense cost and that it approaches zero with infinite cost. One of the simplest functions representing such a relationship is an exponential function with a negative exponent: $\exp(-\beta u)$, where u is the defense level (and also the reduction in reproduction rate) and β represents the efficiency of the defense. Accordingly, even if the basic quality of the prey is g, the prey defense decreases the predator's reward, by which its overall quality becomes $g(\exp[-\beta u])$. In this analysis, the defense level was assumed not to influence the handling time, an assumption that is helpful to consider the optimal diet choice of predator between the two food items with the same basic handling time, h (see below). Therefore, if two prey species adopt the defense levels u_x and u_y, respectively, Eqs. (1a–e) could be rewritten as

$$\frac{dx}{dt} = r\left(1 - u_x - \frac{x}{K}\right)x - \frac{p_x\alpha_x e^{-\beta u_x}z}{1 + p_x\alpha_x xh + p_y\alpha_y yh}x \quad (2a)$$

$$\frac{dy}{dt} = r\left(1 - u_y - \frac{y}{K}\right)y - \frac{p_y\alpha_y e^{-\beta u_y}z}{1 + p_x\alpha_x xh + p_y\alpha_y yh}y \quad (2b)$$

$$\frac{dz}{dt} = r_z g\frac{p_x\alpha_x xe^{-\beta u_x} + p_y\alpha_y ye^{-\beta u_y}}{1 + p_x\alpha_x xh + p_y\alpha_y yh}z - dz. \quad (2c)$$

In this model, the predators always attack both prey independently of their defense levels, therefore, p_x and p_y are still 1. We considered that the defense levels u_x and u_y could evolve, with the dynamics of this based on the quantitative genetic model. According to Iwasa

et al. (1991), the evolutionary dynamics of a single genotype, for example, s, can be formulated by

$$\frac{d\bar{s}}{dt} = G_s\frac{\partial}{\partial s}\log\phi\bigg|_{s=\bar{s}} \quad (3)$$

which represents changes in the average genotype in the population, $\bar{s}$. In this equation, $\phi(s\,|\,\bar{s})$ is the fitness of an individual with genotype s in a population with average genotype $\bar{s}$. G_s is the additive genetic variance of s.

We formulated the evolutionary dynamics of the defense level based on the model of Iwasa et al. (1991). We assumed that generation times of two prey species are identical and they coincide with a unit time of the population dynamic. In addition, the additive genetic variance of u_x and u_y was assumed to be identical between the two prey species and was denoted by G. According to these assumptions, changes in genotypes u_x and u_y during a unit time interval can be represented by

$$\frac{du_x}{dt} = G\frac{\partial}{\partial u_x}\left(\frac{1}{x}\frac{dx}{dt}\right) \quad (4a)$$

$$\frac{du_y}{dt} = G\frac{\partial}{\partial u_y}\left(\frac{1}{y}\frac{dy}{dt}\right). \quad (4b)$$

See the Appendix for the derivation. In these equations, $(dx/dt)/x$ and $(dy/dt)/y$ represent logarithms of individual fitness of two prey species (see also Eq. 3). These calculations of evolutionary dynamics accord with those of Abrams (1992a, b).

Optimal diet choice

In the present model, it was assumed that predators could search for two prey species simultaneously. If there is no trade-off in the search times for the two prey species, the optimal foraging strategy can be considered to be based on optimal diet choice theory (Charnov 1976, Stephens and Krebs 1986). Although the basic quality of prey was represented by g, the prey defense reduces the predator's reward, with the corrected quality calculated as $g(\exp[-\beta u])$. From the corrected qualities, handling times and encounter rate of both prey items, the probability of the predator attacking the two prey species can be determined as

$$(p_x, p_y) = \begin{cases} (1, 0) & \text{if } \dfrac{\alpha_x xge^{-\beta u_x}}{1 + \alpha_x xh} > \dfrac{ge^{-\beta u_y}}{h} \\[3mm] (0, 1) & \text{if } \dfrac{\alpha_y yge^{-\beta u_y}}{1 + \alpha_y yh} > \dfrac{ge^{-\beta u_x}}{h} \\[3mm] (1, 1) & \text{otherwise.} \end{cases} \quad (5)$$

Since the defense levels of the prey species (u_x and u_y) evolve and change, the probability of attack by the predator (p_x and p_y) is dynamic. The avoidance of predation as a result of the prey defense may decrease predator-handling time by reducing the probability of

a successful attack or shortening the length of the foraging activity. If the handling time is proportional to prey quality (see the assumption about "vulnerability" by Abrams and Matsuda [1997]), the handling times of x and y should be $h(\exp[-\beta u_x])$ and $h(\exp[-\beta u_y])$, respectively. According to Eq. 5, in this case, both p_x and p_y are always 1, implying that when the basic handling time was identical for both prey species, the predator would always include both prey species in its diet, independent of the prey defense intensities. To avoid such a scenario in this model, in analyzing the interaction between the prey defense and the predator diet choice, we assumed that defense level does not influence handling time.

Changes in variables and parameters

We calculated population dynamics including both evolution of defense in the prey and optimal diet choice in the predator, Eqs. 2–5, although we simplified calculations by transforming variables and parameters, which decreased the number of parameters. Variables x, y, and z were transformed as $X = \alpha_x gr_z x$, $Y = \alpha_y gr_z y$, $Z = \alpha_x z$, and parameters were replaced by $\kappa = \alpha_x gr_z K$, $\eta = h/(gr_z)$, and $A = \alpha_y/\alpha_x$. Following these changes in variables and parameters, Eqs. 2–5 could be rewritten as

$$\frac{dX}{dt} = r\left(1 - u_x - \frac{X}{\kappa}\right)X - \frac{p_x e^{-\beta u_x} Z}{1 + p_x X \eta + p_y Y \eta}X \quad (6a)$$

$$\frac{dY}{dt} = r\left(1 - u_y - \frac{Y}{A\kappa}\right)Y - \frac{p_y e^{-\beta u_y} AZ}{1 + p_x X \eta + p_y Y \eta}Y \quad (6b)$$

$$\frac{dZ}{dt} = \frac{p_x X e^{-\beta u_x} + p_y Y e^{-\beta u_y}}{1 + p_x X \eta + p_y Y \eta}Z - dZ \quad (6c)$$

$$\frac{du_x}{dt} = G\frac{\partial}{\partial u_x}\left(\frac{1}{X}\frac{dX}{dt}\right) \quad (6d)$$

$$\frac{du_y}{dt} = G\frac{\partial}{\partial u_y}\left(\frac{1}{Y}\frac{dY}{dt}\right) \quad (6e)$$

$$(p_x, p_y) = \begin{cases} (1, 0) & \text{if } \dfrac{Xe^{-\beta u_x}}{1 + X\eta} > \dfrac{e^{-\beta u_y}}{\eta} \\[2ex] (0, 1) & \text{if } \dfrac{Ye^{-\beta u_y}}{1 + Y\eta} > \dfrac{e^{-\beta u_x}}{\eta} \\[2ex] (1, 1) & \text{otherwise.} \end{cases} \quad (6f)$$

Consequently, the 10 parameters (r, K, r_z, d, β, h, g, α_x, α_y, G) were reduced to seven parameters (r, κ, d, β, η, A, G), although the dynamics of this system were still too complicated to be analyzed theoretically, as they included two different time scales: the evolution of prey defenses and predator diet optimization through behavioral changes. Accordingly, we analyzed properties of the system numerically, using computer simulations.

RESULTS

Persistence and stability of the system

Among parameters, the intrinsic growth rate of prey species, r, and the death rate of the predator, d, may be particularly important as they determine the basic population dynamics. In addition, G is a determinant factor of the evolutionary rate of prey defense traits. As such, in the numerical analysis, we focused on the effects of r, d and G on the population dynamics of the study system. The parameter A ($= \alpha_y/\alpha_x$) was set at five, which meant that prey species y encountered the predator five times more frequently than did prey species x. In the simulations, a small density of predators ($Z = 0.1$) were introduced into a system where the densities of the two prey species were at the carrying capacity without antipredator defenses. The dynamics of the population were simulated using the Runge-Kutta method. For each given parameter set, the simulation was run for 1×10^5 time steps, with a single time step being 0.05. If any variable fell below 1×10^{-16} during the calculation, the value was replaced by 0, which avoided an underflow error.

In Fig. 1, an example of the consequences on population dynamics is presented at different predator death rates (d) and where population dynamics were combined with both defense evolution and optimal diet choice. The population dynamics converged to equilibrium under some parameter values, but continuously fluctuated under other values. If the analysis reached equilibrium during 1×10^5 time steps, we plotted the equilibrium value of each variable in Fig. 1. If an equilibrium was not achieved in this period, the mean value for the last 5000 time steps was plotted with error bar (SD) for that period. The upper panel of Fig. 1 shows the scaled population densities of three species, X, Y, and Z ($\alpha_x gr_z x$, $\alpha_y gr_z y$, and $\alpha_x z$). In the example, as d increased, the mean values of the prey tended to increase while the mean population density of the predator decreased. Prey species with a higher encounter rate (y) could not persist at low values of d, while the predator (z) became extinct at high values of d. The middle panel of Fig. 1 represents the defense levels of the two prey species, u_x and u_y. This panel indicates that when two prey species (x and y) coexisted, the prey species with the higher encounter rate with the predator evolved a higher level of defense; however, with increasing values of d, the defense levels decreased in both prey species. The lower panel shows the probability of the predator attacking the two prey species, p_x and p_y. Under the given parameter set, the prey species with the lower encounter rate (x) was always attacked by the predator ($p_x = 1$), while the species with the higher encounter rate (y) was frequently excluded from the diet of predator ($p_y = 0$ or 1) at intermediate values of d. In fluctuating cases, values of mean $\pm$ SD are shown. From the second and third
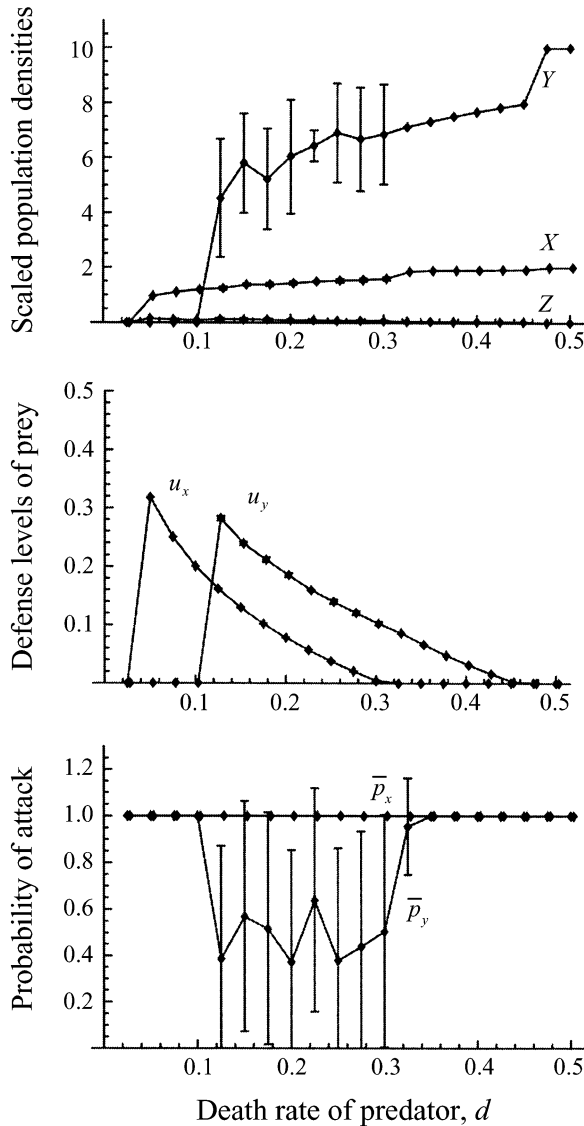
FIG. 1. An example of the consequences for population dynamics in the presence of both defense evolution and optimal diet choice, and variable values of d. In each panel, if the population dynamics reached equilibrium during 1×10^5 time steps, the population at equilibrium is plotted. If equilibrium was not achieved, then the mean value for the last 5000 time steps was plotted, with error bars representing one standard deviation. The upper panel represents the scaled population densities of the three species, X, Y, and Z. The middle panel represents the defense levels of the two prey species, u_x and u_y, while the lower panel shows the probability of attack for the predator against the two prey species, p_x and p_y. Intrinsic growth rate of prey (r) = 0.075, scaled carrying capacity of prey (κ) = 2, efficiency of defense (β) = 5, scaled handling time of prey (η) = 1, ratio of encounter rates of prey (A) = 5, additive genetic variance of defense (G) = 0.001.

panels of Fig. 1, it can be seen that the predator tended to attack a prey species with low defense more often.

The results are generalized in Figs. 2–4. These illustrate the effects on population dynamics for various

combinations of genetic variance of defense (G) and scaled handling time (η). The rate of evolutionary change has been considered to be generally much slower than the dynamics of population change; although recent studies have revealed that there are many cases where these two time scales are comparable (Stockwell et al. 2003, Yoshida et al. 2003). We investigated model performance under different relative time scales (by varying the value of G), and in addition, in order to examine the effects of the shape of the functional response on population dynamics, we analyzed the model with various values of η ($= h/(gr_z)$).

In all panels of all figures, the horizontal and vertical axes represent r and d, respectively. In each, the upper row indicates the consequences for population dynamics in the absence of defense evolution and optimal diet choice; the middle row models the consequences on population dynamics in the presence of defense evolution but absence of optimal diet choice; and the lower row models the consequences in the presence of both factors. The first column shows the combinations of species that remained until 1×10^5 time steps were completed and the second column illustrates whether population dynamics reached equilibria during 1×10^5 time steps. If it did not, we calculated an index of fluctuation that is the sum of the coefficients of variation (standard deviation/mean) of the three variables, X, Y and Z ($\alpha_x gr_z x$, $\alpha_y gr_z y$, and $\alpha_x z$) for the last 5000 time steps. In this column, the index is represented by a density plot, in which the index value was 0 in white areas, ≥ 3 in black areas, and intermediate in gray areas. The third column indicates which prey species evolved defense. When both species remained extant, defense had generally evolved in both prey species (x and y) or only in the prey with the higher encounter rate (y). The fourth column illustrates whether the diet of the predator temporally changed. In the absence of optimal diet choice, the predator always attacked the prey at every encounter ($p_x = p_y = 1$). In contrast, when optimal diet choice was included, the predator often temporally excluded from its diet the prey species with the higher encounter rate (y), but still always included the prey at the lower encounter rate (x). Consequently, there were two possible patterns in the probability of attack: the predator always attacked both prey species ($p_x = p_y = 1$); or it temporally ignored the prey with the higher encounter rate ($p_x = 1$, $p_y = 0$ or 1). This panel illustrates the patterns in the probability of attack for the last 5000 time steps, in which white and black areas represent $p_x = p_y = 1$ and $p_x = 1$, $p_y = 0$ or 1, respectively.

Fig. 2 illustrates the results when $G = 0.001$ and $\eta = 1$. From the first row of Fig. 2, it can be seen that in the absence of prey defense, the consequence for population dynamics significantly depended on the death rate of the predator, d. When d was very small the predator population rapidly increased and both prey species were overconsumed. This resulted in the ex-
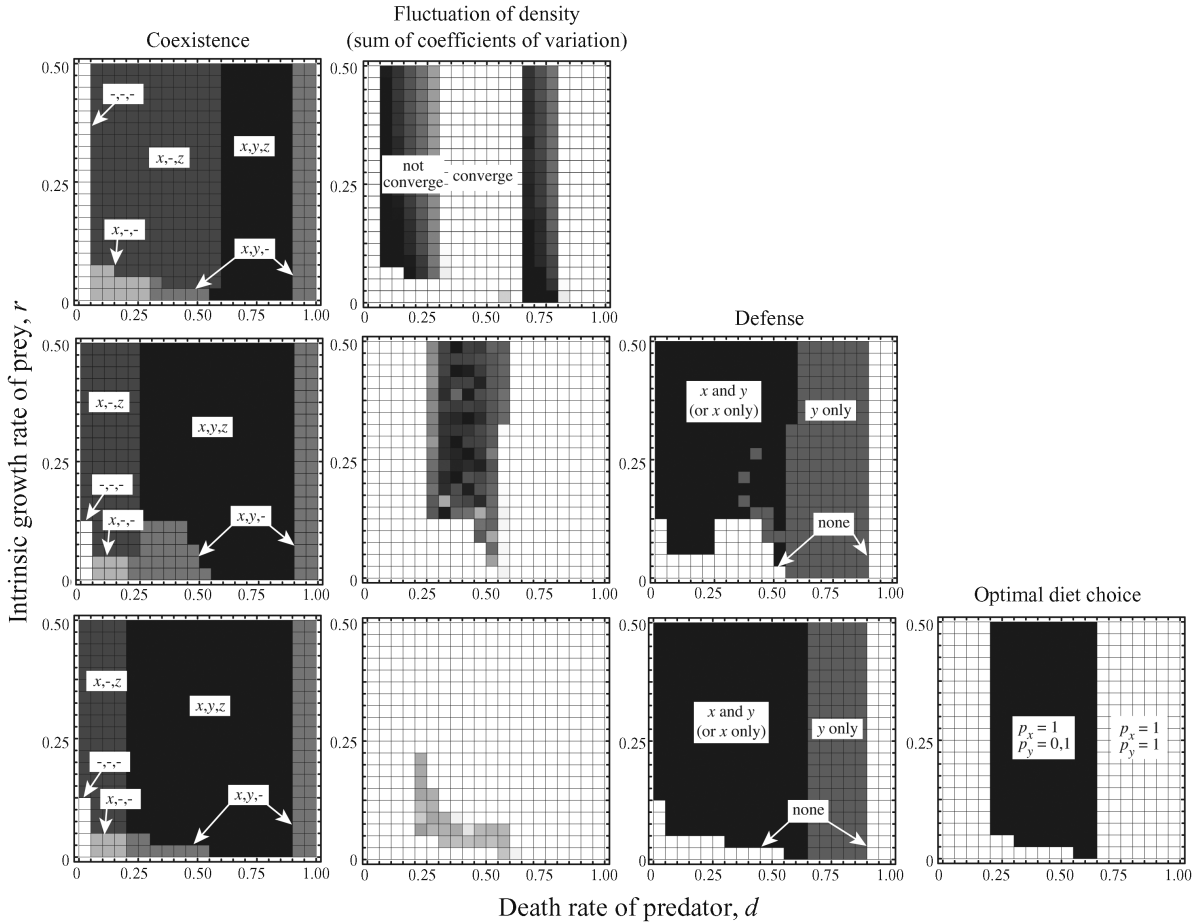
FIG. 2. The consequences for population dynamics at $G = 0.001$. The upper row shows population dynamics in the absence of both defense evolution and optimal diet choice, the middle row shows results in the presence of just defense evolution, and the lower row shows results in the presence of both defense evolution and optimal diet choice. In all panels, the horizontal and vertical axes are d and r, respectively. The first column indicates species that are extant for 1×10^5 time steps. The second column illustrates the fluctuation index of the last 5000 time steps using a density plot, where the value is 0 in white areas, ≥ 3 in black areas, and intermediate in gray areas. The third column indicates which prey species evolved defense. The fourth column illustrates temporally changing patterns in the probability of attacking a prey species during the last 5000 time steps, where white and black areas represent $p_x = p_y = 1$ and $p_x = 1$, $p_y = 0$ or 1, respectively. Parameters are $\kappa = 2$, $\beta = 5$, $\eta = 1$, and $A = 5$.

tinction of both prey species and the subsequent extinction of the predator. When d was slightly larger, a single prey species coexisted with the predator under large r values, or sometimes the two prey species remained without the predator under small r values. Furthermore, the two prey species and the predator could coexist at intermediate values of d, although the two prey species remained without the predator when d exceeded a critical value. In either case, where prey and predator coexisted, the population dynamics converged on an equilibrium over some parameter regions, but continuously oscillated in other regions (Fig. 2, first row, second column).

The dynamic properties of the model changed when the evolution of defense in prey species was introduced into the system. The evolution of defense tended to facilitate the coexistence of all species (Fig. 2, second

row, first column). At intermediate values of d, the evolution of defense rescued species y from extinction, and caused fluctuations in population densities (second column). However, at other values of d, the evolution of defense generally suppressed such fluctuations. The third column of the figure indicates that defense was likely to evolve simultaneously in both prey species under small values of d, but under higher values of d evolved only in the prey species with high encounter rate (y). The third row of Fig. 2 shows that the additional introduction of optimal diet choice in the predator also changed the dynamic consequence to some degree. The optimal diet choice expanded the parameter region where all species coexisted (first column) and reduced the magnitude of fluctuations in population densities (second column). In addition, the inclusion of optimal behavior in the predator tended to enhance
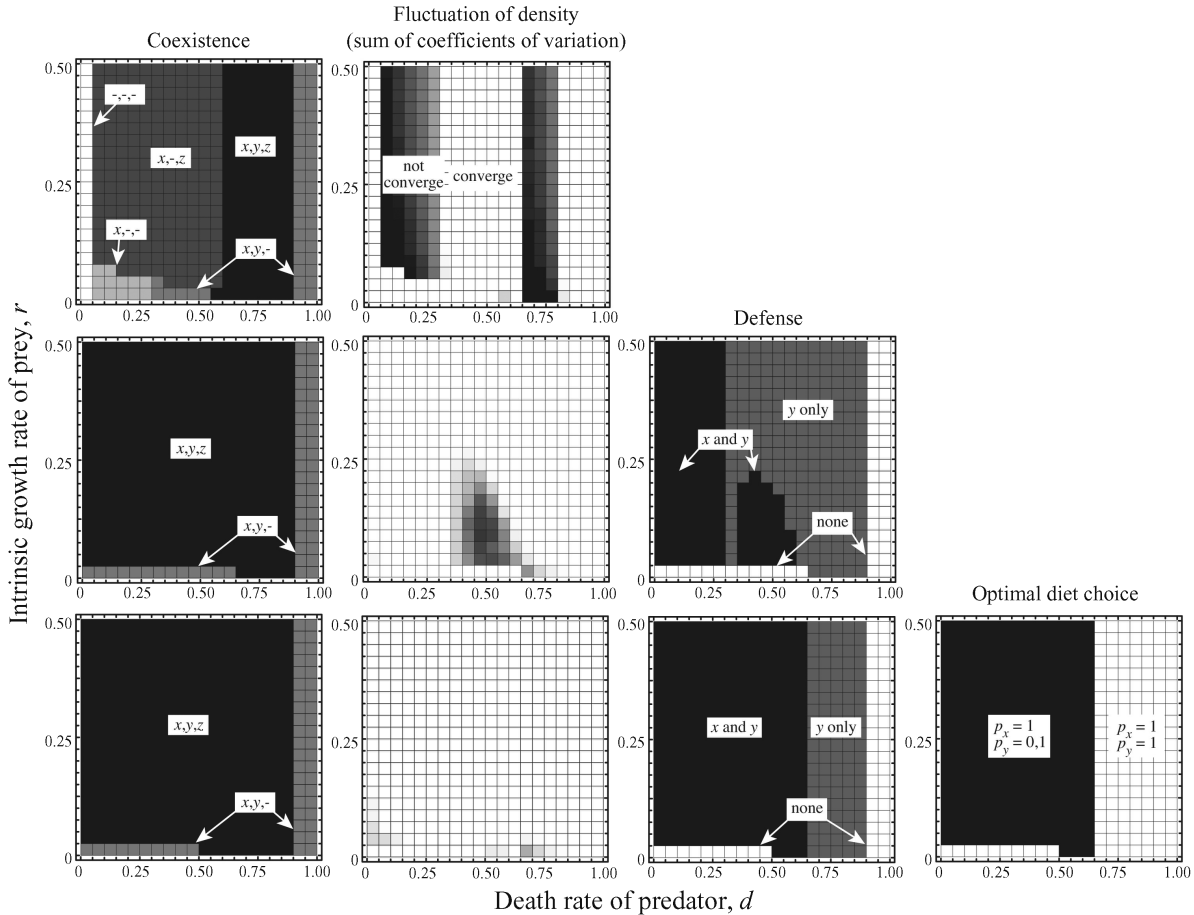
FIG. 3. The consequences for population dynamics at $G = 0.01$. Parameter values and conditions are identical to those of Fig. 2.

the evolution of defense in the prey species (third column). The fourth column illustrates the optimal foraging pattern of the predator. In some parameter regions (white areas) the predator always attacked both prey species ($p_x = p_y = 1$), although in other regions (black areas), the diet of predator varied, in accordance with optimal diet selection. In the latter cases, the prey with lower encounter rate was always attacked ($p_x = 1$), but the prey with higher encounter rate was often temporally excluded from the diet ($p_y = 0$ or 1). When just the evolution of prey defense was included, or when the evolution of prey defense and the optimal diet choice in the predator were both included, there also existed a critical value of d above which the two prey species coexisted in the absence of the predator, similarly to a case without both.

Fig. 3 illustrates the results when the additive genetic variance $G = 0.01$ (10 times greater than its value in Fig. 2). There are clear differences between Figs. 2 and 3. In Fig. 2, the evolution of prey defense promoted the coexistence of the three species, and increased population fluctuations within a certain parameter region. In Fig. 3, the coexistence of the three species was more

strongly promoted as a result of the evolution of prey defense (second row, first column), and the magnitudes and parameter area of population fluctuations were smaller (second row, second column). In Fig. 3, defensive traits were more likely to evolve only in the prey species with the higher encounter rate (y; second row, third column). However, the additional introduction of optimal diet choice in the predator significantly promoted the evolution of defense in the prey species with the lower encounter rate (x), which resulted in a similar pattern of defense evolution as found in with Fig. 2 (third row, third column). In the third row of Fig. 3, it appears that there were almost no fluctuations in population density. When the predator changed its diet to forage optimally, this resulted in fluctuations in population densities (Fig. 3, third row, fourth column). However, under the large values of genetic variance, these fluctuations were too small to be detected as seen in the third row of Fig. 3.

We also examined the consequences of varying the scaled handling time, η ($= h/(gr_z)$). In Fig. 4, $\eta = 2$, twice its value in Fig. 2. The similarity of this figure with Fig. 2, in which the values on the horizontal axis
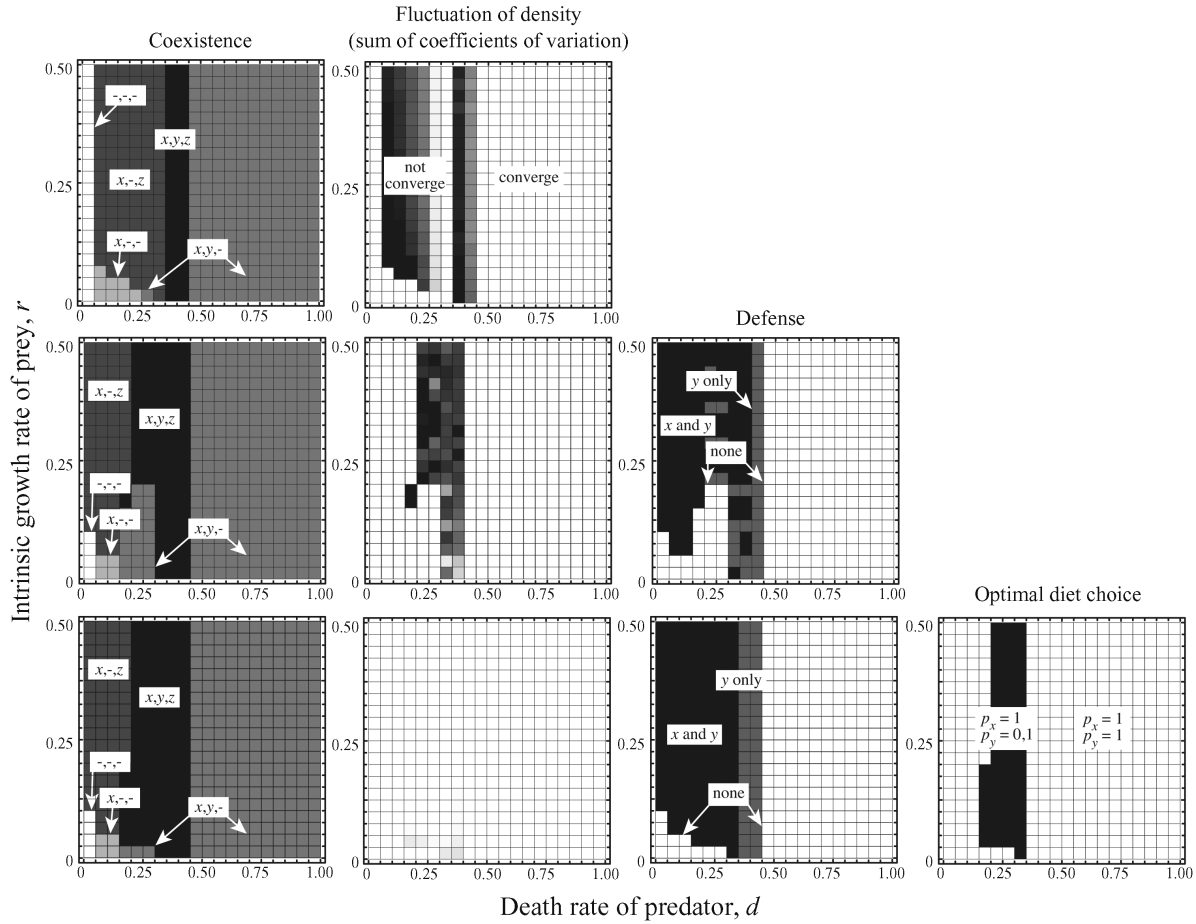
FIG. 4. The consequences for population dynamics at $G = 0.001$ and $\eta = 2$. Other parameter values and conditions are identical to those of Fig. 2.

are halved, implies that the change in handling time had an effect similar to changing the scale of the d axis. The change in handling time, however, may have had some qualitative consequences for population dynamics. When d was smaller than the critical value, it was possible for the predator to coexist with one or both of the prey species. Within such a parameter region, the parameter area where all three species coexisted appeared relatively smaller in Fig. 4 than in Fig. 2 (see the first columns of both figures), implying that an increase in handling time to some degree suppressed the coexistence of all three species.

Indirect effects between prey species

Multiple prey–predator systems generally result in "apparent competition" between the prey species (Holt 1977, see also a review by Holt and Lawton 1994). In order to investigate the indirect effects between the two prey species, we examined the responses of one prey species following a temporal change in biomass of the other prey species. We chose a parameter set in which population biomasses converged to an equilibrium in the absence of both defense evolution in the prey and

optimal diet choice in the predator ($r = 0.25$ and $d = 0.65$ in Fig. 2). We increased the biomass of one of the prey species to $1.5\times$ that of the value at an equilibrium. In Fig. 5, the responses of the predator and the other prey to the changes of one prey are presented, relative to their equilibrium values. In this figure, the left column indicates the response to an increase in the prey species with the lower encounter rate (x), while the right column indicates the response to an increase in the prey species with the higher encounter rate (y). In the upper row the effects on population dynamics in the absence of both defense evolution in the prey and the evolution of optimal diet choice in the predator are presented; the middle row presents the results including defense evolution but excluding optimal diet choice; and the lower row presents results including both factors.

In the absence of both defense evolution and optimal diet choice, we see that there is apparent competition between the two prey species (the upper row of Fig. 5). The species with the lower encounter rate had a greater effect through apparent competition on species with the higher encounter rate than vice versa. Since
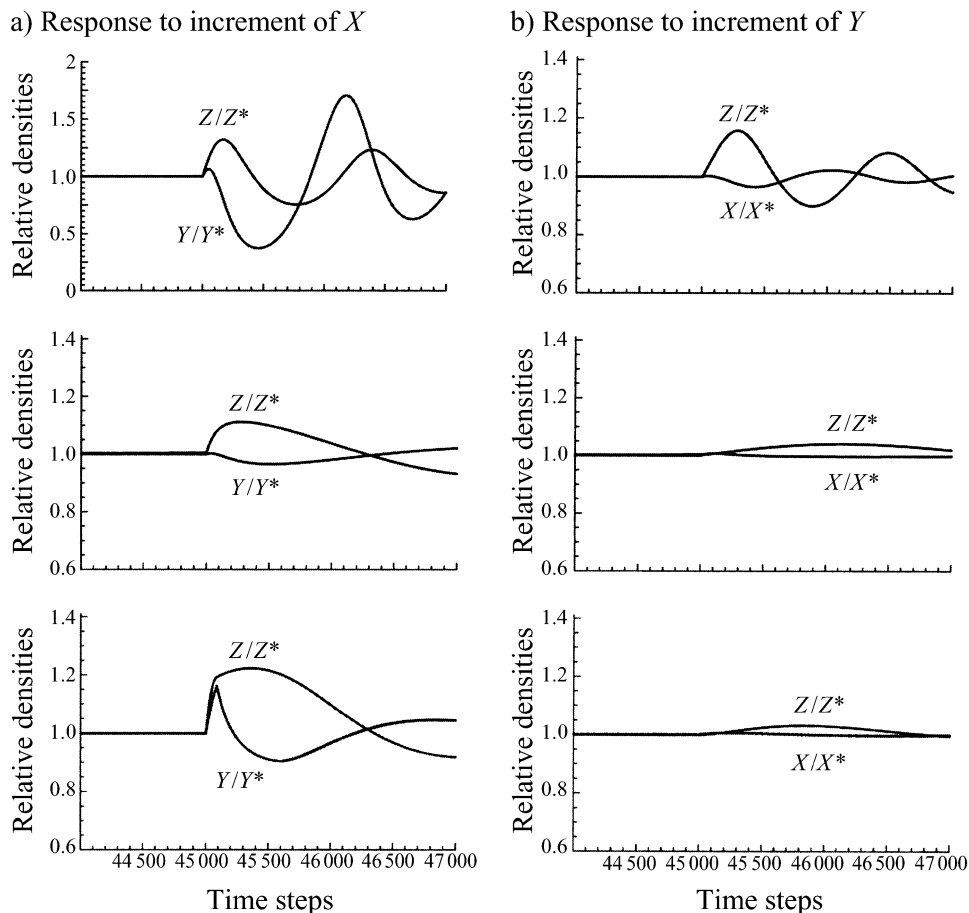
a) Response to increment of *X*   b) Response to increment of *Y*

FIG. 5. Indirect interactions between the two prey species. A parameter set under which population dynamics converged to equilibrium (X^*, Y^*, Z^*) was chosen ($r = 0.25$ and $d = 0.65$; other conditions were the same as Fig. 2). After reaching equilibrium (at 45 000 time steps), the biomass of both prey species increased to $1.5\times$ the equilibrium value. The left-hand column illustrates population responses to an increase in the prey species with the lower encounter rate (species *X*), while the right-hand column illustrates the responses to an increase in prey species *Y* at the higher encounter rate. In this figure, changes in the relative biomass toward equilibrium are shown for the predator and either prey. The upper row shows the population dynamics in the absence of defense evolution and optimal diet choice; the middle row, in the presence of defense evolution only; and the lower row, in the presence of both variables. It should be remarked that the *y*-axis of upper-left panel ranges from 0 to 2.0, although the *y*-axis of other panels ranges from 0.6 to 1.4.

the prey species with the lower encounter rate tended to achieve much higher biomass in the equilibrium, its increase in the biomass resulted in a notable increase in predator biomass, which had a significant negative effect on the prey species with the higher encounter rate. When defense evolution was introduced into this system (Fig. 5, middle panels), the apparent competition was weakened. This was because the prey species with the higher encounter (*y*) rate tended to evolve a higher level of defense, which tended to suppress the response of predator against biomass change of either prey, resulting in the weaker apparent competition between both prey species. It was also notable that when both defense evolution and diet choice existed (Fig. 5, lower panels), the prey species with the lower encounter rate (*x*) had significant short-term positive effects on the other prey species (*y*). When the predator adopt-

ed an optimal diet choice, an increase in the biomass of the prey species with the lower encounter rate (*x*), which had evolved lower levels of defense, led the predators to temporally exclude the prey species with the higher encounter rate (*y*) from their diet, which had evolved higher levels of defense. This caused a short-term positive effect of the former on the latter species. These results also indicates that both defense evolution of prey species and diet choice of predator were likely to stabilize the population dynamics in one-predator–two-prey systems.

Holt and Kotler (1987) analyzed short-term apparent competition, combining both optimal diet choice theory and patch use theory to the population dynamics of two prey species. They pointed out that apparent interaction varies with environmental conditions. On the other hand, in the present analysis, optimal diet

choice theory and defense evolution were introduced into the population dynamics of two prey and one predator species. In either study, it was suggested that the optimal foraging of predator must be an important factor in considering interaction between prey species.

DISCUSSION

To study the effects of defense evolution in prey species on the optimal foraging strategy of a predator, we assumed identical handling time for both prey species. In this situation, and in the absence of prey defenses, the predator always attacked both prey species (see Eq. 5) and optimal diet choice was not an effective strategy. The foraging strategy of the predator varied only when their prey species evolved defensive traits. We could not, however, analyze the role of optimal diet choice on population dynamics in the absence of evolution of defense in the prey. Previous studies have pointed out that optimal diet choice alone might result in both the suppression of density fluctuations and the promotion of coexistence in one-predator–two-prey systems (Gleeson and Wilson 1986, Genkai-Kato and Yamamura 1999). Despite the lack of information about the effects of optimal diet choice alone, in this study we successfully identified the joint effects of antipredator defense evolution in the prey and optimal foraging behavior in the predator.

The evolution of defense traits affected the conditions for species coexistence and the magnitude of fluctuations in population densities in a one-predator–two-prey system. In the absence of defense evolution, the prey species with the higher encounter rate tended to become extinct as a result of higher predation pressure. When defense evolution was introduced, the prey species with the higher encounter rate with the predator evolved a higher level of defense than that of the species with the lower encounter rate, which reduced the predation pressure for the former species. As a consequence, the prey species with the higher encounter rate avoided extinction, which promoted coexistence. When evolution of defense allowed all three species to coexist, it often caused population fluctuations, although this effect depended upon the relative rate of defense evolution in the prey species. Rapid defense evolution under high genetic variance tended to suppress the density fluctuations. In addition, the rate of evolution had consequences for the prey defense, with rapid evolution less likely to result in the evolution of defense traits in the prey species with the lower encounter rate (Figs. 2 and 3, second row and third column).

The optimal diet choice in the predator also affected population dynamics in one-predator–two-prey systems. When the predator foraged optimally, the defensive traits not only evolved in the prey species with the higher encounter rate but also in the species with the lower encounter rate. Optimal diet choice, in comparison with results that included only defense evo-

lution, also reduced the magnitude of population fluctuations in certain parameter regions, although populations nevertheless still fluctuated in such cases. At a smaller scale, the diet choice of the predator resulted in ''noisy'' changes in populations as a result of frequent changes in its diet. When the prey with the lower encounter rate evolved the defensive traits as an antipredator strategy, the predator excluded it from its diet, which reduced the selective pressure for defense. The defense levels in the prey subsequently fell, by which predator included the prey to its diet, again, and, as a consequence, the selective pressure for defense traits increased. This cycle was repeated over a short time interval and resulted in ''noisy'' population dynamics that did not reach any equilibrium.

Preliminary simulations also indicated that the evolution of both defense and optimal diet choice equalized the densities of the two prey species ($\bar{x}/\bar{y}$ ($= A(\bar{X}/\bar{Y})$) tended to approach 1). Even when optimal diet choice was absent, defense evolution notably equalized the densities of the two prey species. The prey species with the higher encounter rate tended to evolve a higher level of defense to avoid the correspondingly higher predation pressure. When optimal diet choice was introduced, the predator temporally ignored the prey with the higher encounter rate because of its low quality, acting to equalize the prey densities. The equalizing effect may positively influence coexistence through suppression of extinctions resulting from stochastic disturbances.

Despite these effects, optimal diet choice did not seem to significantly affect population dynamics because of the greater influence of defense evolution, which determines the conditions for coexistence with or without optimal foraging. Several studies have shown that when palatability differs between two prey species, the optimal diet choice of predator reduces the amplitude of oscillation of population density, which results in coexistence (Gleeson and Wilson 1986, Křivan 1996, 1998, Genkai-Kato and Yamamura 1999, Křivan and Sikder 1999). However, our analysis suggests that the evolution of defense can promote coexistence by stabilizing predation pressure across the two prey species, even in the absence of optimal diet choice. The optimal diet choice may have only supplemental effects in promoting species coexistence when defense has evolved in prey species.

Our analysis illustrates the consequences that the additive genetic variance of defense evolution has for population dynamics. We suggested that when defense trait evolution was included in analyses of population dynamics, the relative time scale of the evolution may influence overall population dynamics. In our analysis we focus on the evolutionary change in defense levels, which in some cases can change within a single generation in response to herbivory; i.e., induced defense (reviewed by Coleman and Jones 1991, Karban and Kuć 1999). The present study does not cover directly

such a plastic response of plants. However, if the level of induced defense rapidly changes toward a direction increasing own fitness over a few generations, it could have a similar effect with a rapid evolution of defense level with a large additive genetic variance. When the genetic variance was large, defense evolution (and also the optimal diet choice) tended to suppress fluctuations in population density, which stabilized population dynamics (see Fig. 3). This suggests that induced defense against herbivory could significantly stabilize the dynamics of a one-predator–two-prey system.

We included traditional diet choice theory in our analyses, in which the optimal probability of attack on a particular prey species is 0 or 1, depending on conditions, but never resulting in intermediate probabilities between 0 and 1 (Charnov 1976, Stephens and Krebs 1986). Recent theoretical studies have, however, shown that intermediate probabilities (termed partial preference) are possible when other factors are included in models. Berec and Křivan (2000) indicated that partial preference occurred when the predator has insufficient information only. Yearsley (2003) showed that partial preference results if the predator cannot change its tactics rapidly in response to prey population dynamics. The partial preference of predators may suppress the ''noisy'' behaviors of population dynamics as a result of a gradual response by the predator rather than a stepwise response. Or the partial preference might be difficult to realize a steady state in the system, since the partial preference tends to result from behavioral constraints or incomplete information. The effects of partial preference on population dynamics need to be studied further and in the context of the methods used in this study.

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APPENDIX

The derivation of evolutionary dynamics of defense evolution is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-133-A1.