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Effects of Nonspecific Adaptive Defense by Pests on Efficiency of Biological Control by Multiple Natural Enemies

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Whether introduction of multiple natural enemies is more effective to suppress agricultural pests than that of a single enemy is one of the important questions for biological control. Intra–guild predation (IGP) among natural enemies has often been considered as a candidate to explain failure of biological control by multiple enemies. Classical theoretical studies on IGP supported the view, whereas some empirical studies did not. Since the classical models were very simple, neglect of adaptive behavior of pests and natural enemies might be a reason for the partial discrepancy between the theory and observation. In a companion paper, we considered two kinds of predator–specific adaptive defenses by the pest in an IGP system and revealed their possible effects on biological control by multiple natural enemies. In the present paper, we examined the effects of predator–nonspecific adaptive defense on success or failure of biological control by multiple natural enemies. Although the predator–nonspecific defense enhanced three species coexistence as the predator–specific defense did, introduction of two natural enemies could rarely improve the efficiency of biological control. We found that the specificity of the defense against two predators and the trade–off between allocation of effort toward two kinds of defenses were key factors to realize more efficient suppression of the pest by multiple natural enemies. Our results suggest that considering plasticity in behavior of pests and natural enemies may be essential to evaluate and predict efficiencies of biological control.

Key words: adaptive defense, biological control, indirect effects, intra–guild predation, nonspecific defense

INTRODUCTION

Biological control to suppress agricultural pests by introducing their natural enemies is one of the key methods for efficient pest control. However, it is known that the efficiency of biological control largely depends on biotic (e.g. composition or densities of pests and natural enemies) or abiotic (e.g. temperature, humidity etc.) conditions (Rosenheim, 1998; Stiling and Cornelissen, 2005; Janssen *et al.*, 2006). When a single natural enemy is not sufficiently effective to suppress pests, multiple natural enemy species have often been introduced. However, whether multiple enemies are more effective than a single enemy has been debated for a long time (Rosenheim *et al.*, 1995; Lucas, 2005; Straub *et al.*, 2008). Some empirical studies showed more efficient pest control by multiple natural enemies (Heinz and Nelson, 1996; Sher *et al.*, 2000; Eubanks, 2001; Dinter, 2002; Snyder and Ives, 2003), while the others did not so (Rosenheim *et al.*, 1993; Rosenheim, 2001; Schausberger and Walzer, 2001; Snyder and Ives, 2001; Rosenheim *et al.*, 2004). Prey–predator interactions among natural enemies (i.e. intra–guild predation: IGP) has been considered to be one

of the reasons for this conflict (Müller and Brodeur, 2002; Janssen *et al.*, 2006).

Classical theoretical studies on IGP proved that the equilibrium population density of the shared prey attacked by two predators is always higher than that preyed upon by only the more efficient intermediate predator (Holt and Polis, 1997). In other words, multiple natural enemies cannot suppress the pest more effectively than a single natural enemy. Since this prediction does not match some empirical observations (Heinz and Nelson, 1996; Sher *et al.*, 2000; Eubanks, 2001; Dinter, 2002; Snyder and Ives, 2003), theoreticians have tried to fill the gap between the theoretical and empirical results by considering additional factors ignored in classical studies (Briggs and Borer, 2005; Daugherty *et al.*, 2007). It has been shown that multiple natural enemies can effectively suppress the pest in a short term if sufficiently abundant omnivores were introduced and IGP was relatively weak (Briggs and Borer, 2005), or in a long term if the intermediate predator had an alternative resource (Daugherty *et al.*, 2007)

In a companion paper, we focused on behavioral plasticity of pests and natural enemies to resolve the problem. We assumed that the shared prey (pest) could employ two kinds of predator–specific (effective against only one predator species) adaptive defenses and showed that introduction of multiple natural enemies could be more effective than that of a single one (Ikegawa *et al.*, in review). This was because the shared prey cannot successfully defend themselves against attacks from multiple enemies, due to a trade–off between two kinds of defenses. However, in natural fields, the defense by the

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prey is often predator–nonspecific. For example, reducing activity for mating or foraging to avoid encounters with predators may be a predator–nonspecific (effective against several predators) defense (Huang and Sih, 1991; Krupa and Sih, 1998). In this study, we consider the three species IGP module and assume that the shared prey can employ a single predator–nonspecific defense and dynamically allocate defensive effort toward the defense to increase its own fitness. We examine its effects on (1) persistence of each predator species and (2) suppression of the shared prey.

MODEL

In this article, we consider the three species IGP module and regard a pest species as a shared prey and two natural enemy species as an intermediate predator, and an omnivore which also consumes the intermediate predator. Population densities of the shared prey, intermediate predator, and omnivore are described as R, N, and P, respectively.

First, similarly as in previous theoretical studies considering predator–nonspecific defense by the shared prey (Matsuda *et al.*, 1994, 1996), we assume that the shared prey can adaptively allocate effort (e) toward a predator–nonspecific defense to decrease loss by predation from both the intermediate predator and omnivore, and that proportional reduction in predation rates from the intermediate predator and omnivore is described as follows:

$$D_i = 1 - f_i e \ (i \in \{N, P\}), \qquad (1)$$

where f_i represents the efficiency of the defense against the predator species i ($0 \le f_i \le 1$). For the benefit, the shared prey incurs defensive costs and proportional reduction in its own reproduction rate is described as follows:

$$C = 1 - ce \ (i \in \{N, P\}), \qquad (2)$$

where c represents the coefficient of the defensive costs. We assume that allocation of the defensive effort is constrained within $0 \le e \le 1$, and that the shared prey can adaptively vary the effort to increase its own instantaneous fitness W described by the per–capita growth rate of its own ($W = (dR/dt)/R$). The dynamics of the defensive effort is assumed to be expressed by the replicator–like equation (Matsuda *et al.*, 1994, 1996; Kondoh, 2007; Nakazawa *et al.*, 2010) and described as follows:

$$\frac{de}{dt} = ve\,(1 - e)\,\frac{\partial W}{\partial e} \ , \qquad (3)$$

where v is the rate of adaptation of the defensive effort. $\partial W/\partial e$ determines the direction and rate of variation in the defensive effort. The defensive effort (e) never exceeds 1 (resp. falls below 0) because the right hand side of eq. (3) asymptotes to 0 as e approaches 1 (resp. 0).

Population dynamics of three species are assumed

to be the same as those in classical theoretical studies on IGP (Polis and Holt, 1992; Holt and Polis, 1997), except for the benefits (D_N and D_P) and cost (C) of adaptive defense by the shared prey, and described as follows:

$$\frac{dR}{dt} = \left(r_R C - \frac{R}{k_R}\right) R - a_{RN} D_N RN - a_{RP} D_P RP \quad (4\text{–A})$$

$$\frac{dN}{dt} = b_{RN}\, a_{RN} D_N RN - m_N N - a_{NP} NP \qquad (4\text{–B})$$

$$\frac{dP}{dt} = b_{RP}\, a_{RP} D_P RP + b_{NP}\, a_{NP} NP - m_P P, \qquad (4\text{–C})$$

where r_R is the intrinsic growth rate of the shared prey; k_R is the inverse of density dependence of the shared prey and a measure of the carrying capacity; a_{ij} is the encounter rate between predator species j and prey species i ($i \in \{R, N\}$, $j \in \{N, P\}$), b_{ij} is the conversion efficiency of predator species j consuming prey species i ($i \in \{R, N\}$, $j \in \{N, P\}$); m_i is density–independent mortality of predator species i ($i \in \{N, P\}$).

We assume that the intermediate predator is superior to the omnivore in consuming the shared prey ($\frac{m_N}{b_{RN} a_{RN}} < \frac{m_P}{b_{RP} a_{RP}}$), which is one of the necessary conditions for coexistence of two predators in an IGP system in the absence of any defenses (Holt and Polis, 1997). We derive equilibrium population densities and defensive efforts by setting the right–hand sides of eqs. (3) and (4) to zero. Then, we evaluate their local asymptotic stability by the Routh–Hurwitz criterion. We numerically calculate mean population densities and defensive efforts over a period when the equilibria are unstable and the solutions are periodic. A predator species is considered to be persistent if a positive equilibrium or a steady state at which the species survives is stable or there exists a stable positive limit cycle.

To examine the effects of adaptive defense on efficiency of biological control by multiple natural enemies, we first assume symmetric efficiencies of the defense against two predators, and that they are three times larger than the defensive cost ($f_N = f_P = 0.75$, $c = 0.25$). Next, we vary either one of the efficiencies of defense with the other one fixed to examine the effects of asymmetric efficiencies of the defense on qualitative outcomes.

RESULTS

Effects of adaptive defense

First, we assumed that efficiencies of adaptive defense against two predators were symmetric ($f_N = f_P = 0.75$) and examined how the encounter rates between the omnivore and two prey (a_{NP} and a_{RP}) affect persistence of each predator species, use or nonuse of adaptive defense, and stability of the systems with and without adaptive defense (Fig. 1a and c, respectively). When we did not consider the adaptive defense by the shared prey, coexistence of two predators was stable (region *RNP* in Fig. 1c) if and only if the predation rate of the omnivore on the shared prey (a_{RP}) was small and that on
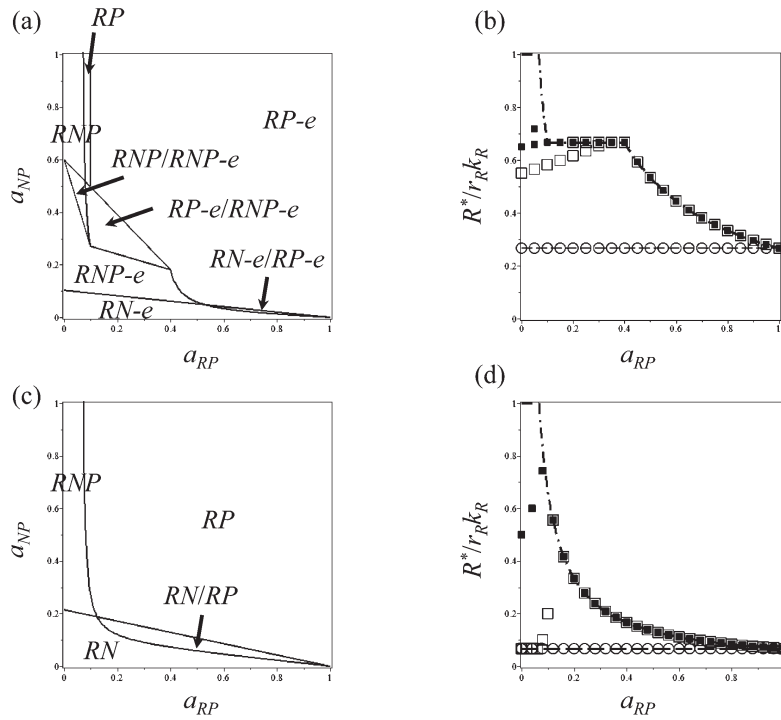
Fig. 1. (a)(c) Dependence of equilibrium states on the encounter rates between the omnivore and two prey species (a) in the presence of and (c) in the absence of adaptive defense. Horizontal and vertical axes indicate the encounter rate between the omnivore and the shared prey (a_{RP}), and that between the omnivore and the intermediate predator (a_{NP}), respectively. Equilibrium states are categorized by persistence of two predators: *RNP*: both predators persist, *RN*: only the intermediate predator persists, *RP*: only the omnivore persists. We use "/" to represent bistability. If the shared prey employs the defense, we add "*e*" as a suffix of each state. (b)(d) Dependence of the equilibrium population density of the shared prey on the encounter rate between the omnivore and the shared prey (a_{RP}: horizontal axes) (b) in the presence of and (d) in the absence of adaptive defense. Vertical axes indicate the relative equilibrium population density of the shared prey in the presence of either one or both predators (R^*) to that in the absence of both predators (carrying capacity of the shared prey; $r_R k_R$). Dashed lines indicate the equilibrium population density of the shared prey in the absence of the omnivore as a function of a_{RP} and chained lines indicate that in the absence of the intermediate predator. Each symbol represents different values of the encounter rate between the omnivore and the intermediate predator (circles: $a_{NP} = 0$, open boxes: $a_{NP} = 0.25$, closed boxes: $a_{NP} = 0.5$). Other parameter values are $r_R = 5$, $k_R = 3$, $b_{RN} = b_{RP} = b_{NP} = 0.5$, $a_{RN} = 1$, $m_N = m_P = 0.5$, $f_N = f_P = 0.75$, $c = 0.25$, $v = 1$.

the intermediate predator (a_{NP}) was large, which was the classical results on IGP (Polis and Holt, 1992; Holt and Polis, 1997). However, when adaptive defense was incorporated, two predators coexisted even if both a_{RP} and a_{NP} were intermediate (region *RNP–e* in Fig. 1a). In addition, bistability also arose (region *RP–e/RNP–e*, *RNP/RNP–e* and *RN–e/RP–e* in Fig. 1a). In region *RP–e/RNP–e*, three species could coexist or the intermediate predator went extinct and adaptive defense was employed at both steady states. In region *RNP/RNP–e*, three species could coexist and it depended on initial conditions whether adaptive defense was employed or not. In region *RN–e/RP–e*, either the omnivore or intermediate predator went extinct and the adaptive defense was employed at both steady states.

Next, we examined effects of adaptive defense by the shared prey on its own density by comparing cases

with and without defense (Fig. 1b and d, respectively). Vertical axes represents the relative equilibrium population density of the shared prey to the carrying capacity ($R^*/r_R k_R$). Hereafter, we call it the relative equilibrium density R_r^*. When we considered adaptive defense by the shared prey, R_r^* in the case of multiple natural enemies (open and closed boxes in Fig. 1b) never fell below that in the case of only the intermediate predator (a dashed line in Fig. 1b) regardless of the strength of IGP (encounter rate between the omnivore and intermediate predator, a_{NP}). In other words, even if the shared prey employed predator–nonspecific defense, introduction of multiple natural enemies was unfavorable for biological control, which was qualitatively the same as in the case of no adaptive defenses (Fig. 1d).

## Effects of differences in efficiencies of adaptive defense

In the previous subsection, we assumed that efficiencies of defense against two predators were symmetric. Here, we relaxed this assumption and examined effects of the asymmetric efficiencies of defense on equilibrium states and suppression of the shared prey. In Fig. 2, three panels differing in the efficiency of defense against the intermediate predator (f_N) were shown while fixing that against the omnivore ($f_P = 0.75$). When $f_N = 0$ (the defense was effective against only the omnivore), three species could coexist in a stable equilibrium by the adaptive defense even if a_{NP} was high and a_{RP} was intermediate (region RNP–e in Fig. 2a) and coexist in an oscillatory state if a_{NP} was low and a_{RP} was high (region oscil.–RNP–e in Fig. 2a). However, bistability appeared in the case of symmetric efficiencies disappeared. As the defense became efficient against the intermediate predator (f_N increased) and the efficiencies came closer to symmetry, the region of stable and unstable three species coexistence became narrower and the region of bistability appeared again (Fig. 2e).

Effects of the efficiency of defense against the intermediate predator (f_N) on suppression of the shared prey were weak (Fig. 2b, d and f). As f_N became lower (adaptive defense became less effective against the intermediate predator), the population density of the shared prey

in the presence of multiple predators became slightly lower (open and closed boxes in Fig. 2b, d, and f). However, it was still higher than that in the case of only the intermediate predator (dashed lines in Fig. 2b, d, and f) even if $f_N = 0$ and the defense against the intermediate predator had no effect. Consequently, even if the defense against the intermediate predator was inefficient, biological control introducing multiple natural enemies was unsuccessful.

Next, we varied the efficiency of defense against the omnivore (f_P) while fixing that against the intermediate predator ($f_N = 0.75$) (Fig. 3). As the defense became inefficient against the omnivore (f_P decreased), the region of bistability where either one of the predators went extinct (region RN–e/RP–e in Fig. 3e) disappeared. As in the case of inefficient defense against the intermediate predator, highly asymmetric efficiencies of defense seemed to make the system mono–stable. However, when f_P was low, three species could stably coexist by adaptive defense if a_{NP} was low and a_{RP} was high. This was because the defense was more effective against the intermediate predator and the omnivore which was less interfered by the defense was released from the competitive pressure (region RNP–e in Fig. 3c and e).

The degree of suppression of the shared prey also qualitatively changed if f_P became lower. When a_{RP} was sufficiently high, population densities of the shared prey
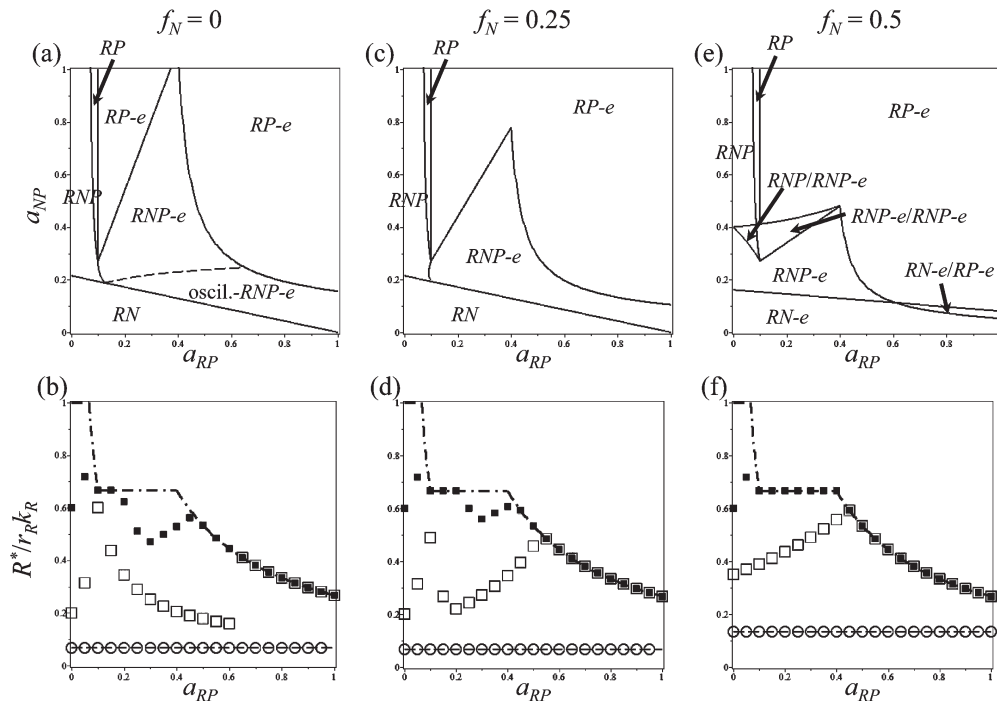
Fig. 2. (a)(c)(e) Dependence of equilibrium states on the encounter rates between the omnivore and two prey species. Axes and descriptions of equilibrium states are identical with those in Fig. 1a and c. If the system is unstable and population densities and defensive efforts oscillate, we add "oscil." as a prefix of each state. (b)(d)(f) Dependence of the equilibrium population density of the shared prey on the encounter rate between the omnivore and the shared prey (a_{RP}). Axes are identical with those in Fig. 1b and d. Each symbol represents different values of the encounter rate between the omnivore and the intermediate predator (circles: $a_{NP} = 0$, open boxes: $a_{NP} = 0.25$, closed boxes: $a_{NP} = 0.5$). We fix the efficiency of defense against the omnivore ($f_P = 0.75$) and vary that against the intermediate predator: $f_N = 0$ for (a) and (b), $f_N = 0.25$ for (c) and (d), and $f_N = 0.5$ for (e) and (f). Other parameter values are identical with those in Fig. 1.
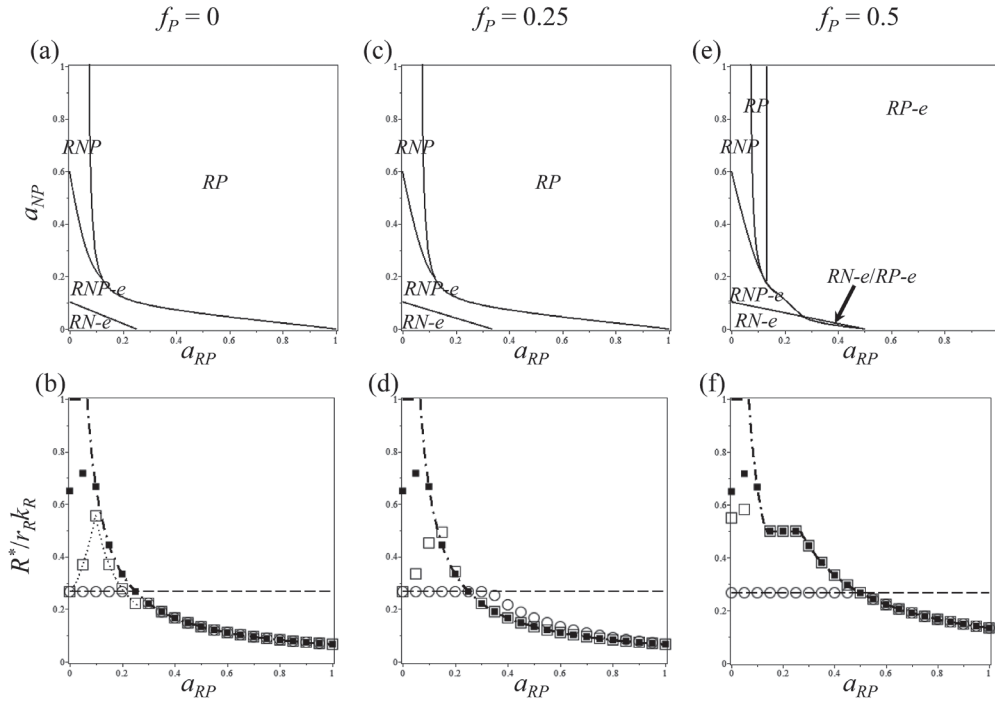
Fig. 3. (a)(c)(e) Dependence of equilibrium states on the encounter rates between the omnivore and two prey species. Axes and description of equilibrium states are identical with those in Fig. 1a and c. (b)(d)(f) Dependence of the equilibrium population density of the shared prey on the encounter rate between the omnivore and the shared prey (a_{RP}). Axes are identical with those in Fig. 1b and d. Each symbol represents different values of the encounter rate between the omnivore and the intermediate predator (circles: $a_{NP} = 0$, open boxes: $a_{NP} = 0.1$, closed boxes: $a_{NP} = 0.5$). A dotted line in (b) indicates variation in R_r^* as a continuous function of a_{RP} to show that introduction of two predators is effective over an interval when $a_{NP} = 0.1$. We fix the efficiency of defense against the intermediate predator ($f_N = 0.75$) and vary that against the omnivore: $f_P = 0$ for (a) and (b), $f_P = 0.25$ for (c) and (d), and $f_P = 0.5$ for (e) and (f). Other parameter values are identical with those in Fig. 1.

when only the omnivore was introduced (chained lines in Fig. 3b, d, and f) was lower than that when only the intermediate predator was introduced (dashed lines in Fig. 3b, d, and f). This was because adaptive defense was not so effective against the omnivore (low f_P) and the omnivore was superior to the intermediate predator as a single natural enemy when the pest employed the adaptive defense. It should be noted that introduction of multiple natural enemies could be more effective to suppress the shared prey than that of either one of the predators only in very limited conditions; f_P was sufficiently low and both a_{RP} and a_{NP} were intermediate (an open box below the dashed and chained lines in Fig. 3b).

DISCUSSION

In this study, we considered predator–nonspecific adaptive defense by the shared prey (pest) rather than the predator–specific adaptive defense assumed in the companion paper and examined its effect on persistence of each predator species and suppression of the shared prey. As a result, it was found that two natural enemies scarcely enhanced suppression of the shared prey which employed predator–nonspecific adaptive defense, although the defense promoted stable three species coexistence.

The region of stable three species coexistence (including bistability) in the case of adaptive defense with symmetric efficiencies was broader than that in the case of no defenses (Fig. 1a and c). However, the coexistence region was narrower than that in the case of two kinds of predator–specific adaptive defenses in our companion paper (Ikegawa *et al.*, in review). While the predator–specific defenses against a competitively superior predator might indirectly benefit the inferior one and enhance coexistence because of the trade–off between two kinds of specific defenses (Nakazawa *et al.*, 2010), the predator–nonspecific defense do not so because the shared prey could not allocate different efforts against different predators, as shown in some previous studies on adaptive defense (Matsuda *et al.*, 1994, 1996). As the efficiency of the defense against the intermediate predator (f_N) decreased while the other one kept constant, the intermediate predator could persist even if IGP was strong (a_{NP} was high) (Fig. 2a, c, e). This was because the defense more effective against the omnivore indirectly benefited the intermediate predator. By the similar mechanism, as efficiency of the defense against the omnivore (f_P) decreased, the omnivore could persist even if the encounter rates with both prey (a_{RP} and a_{NP}) were low. After all, the predator–nonspecific defense seems to enhance three species coexistence yet the degree of

enhancement is weaker than that by the predator–specific defenses, which is qualitatively the same as the results of previous studies (Matsuda *et al*., 1994, 1996).

With respect to suppression of the shared prey, introduction of two predators was less effective than that of either one of two predators in most cases even if the shared prey employed adaptive defense (lower panels of Figs. 1–3). In other words, it seems typical that introduction of two natural enemies disturbs biological control when the pest employs predator–nonspecific defense. Exceptionally, when f_P and a_{NP} were sufficiently low and a_{RP} was intermediate, introduction of two predators was more effective than that of a single one (Fig. 3b). This might happen because the almost non–defended omnivore (low f_P) became much superior to the intermediate predator in suppressing the shared prey, but the intermediate predator still existed and complemented the control by the omnivore. This mechanism seems different from the one in our companion paper in which adaptive defense was effective against both predators (high f_P and f_N) but the low rate of IGP (low a_{NP}) and the constraint on the total defensive effort made it difficult for the shared prey to successfully defend themselves against both predators (Ikegawa *et al*., in review). Although the predator–specificity of the defenses and the trade–off between defensive efforts against two predators are important factors to understand more efficient suppression of the pest by two natural enemies, there may be another mechanism other than weak IGP (Briggs and Borer, 2005) or alternative resources (Daugherty *et al*., 2007) to make introduction of multiple natural enemies successful.

In future, we should collectively consider the predator–specific or nonspecific defense by prey species and various feeding modes of predator species (e.g. switching predation, prey preference etc.), and examine their joint effects on equilibrium states and suppression of the prey species. Behavioral plasticity shown by both pests and natural enemies may lead to qualitative changes in the outcomes of biological control by introduction of multiple natural enemies (Rosenheim, 1998; Stiling and Cornelissen, 2005; Janssen *et al*., 2006). Our results suggest that examining behavioral traits of pests and natural enemies in agricultural systems may be important to determine optimal methods for biological control, and that mathematical analyses are useful for evaluating and predicting the effects of the method on the efficiency of biological control.

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