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Effects of generalized and specialized adaptive defense by shared prey on intra-guild predation

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HIGHLIGHTS

- We studied effects of adaptive defense by shared prey on an IGP system.
- Prey use generalized and specialized defenses to maximize its fitness.
- Joint use of two types of defenses promotes coexistence of consumers and predators.
- Effective adaptive defense sometimes reduces prey population.
- Joint use of two types of defenses stabilizes oscillations of population densities.

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ABSTRACT

Intra-guild predation (IGP), predation on consumers which share common prey with the predators, is an important community module to understand a mechanism for persistence of complex food webs. However, classical theory suggests that persistence of an IGP system is unlikely particularly at high productivity, while empirical data do not support the prediction. Recently, adaptive defense by shared prey has been recognized to enhance coexistence of species and stability of the system. Some organisms having multiple predators in IGP systems employ two types of defenses; generalized defense that is effective against multiple predators and specialized one that is effective against only a specific predator species. We consider an IGP model including shared prey that can use the two types of defenses in combination against the consumer or omnivore. Assuming that the shared prey can change the allocation of defensive effort to increase its fitness, we show that the joint use of two types of adaptive defenses promotes three species coexistence and enhances stability of the IGP system when the specialized defense is more effective than the generalized one. When the system is unstable, a variety of oscillations appear and both the population densities and defensive efforts or only the population densities oscillate. Joint use of defenses against the consumer tends to increase the equilibrium population density of the shared prey with the defense efficiencies. In contrast, efficient generalized and specialized defenses against the omnivore often decrease the prey population. Consequently, adaptive defense by shared prey may not necessarily heighten the population size of the defender but sometimes increases densities of both the attackers and defender in IGP systems.

1. Introduction

Intra-guild predation (IGP), predation on consumers which share common prey with the predators, is ubiquitous in nature (Polis et al., 1989; Arim and Marquet, 2004). This simple system of three species contains indirect ecological interactions such as exploitative competition for shared prey between consumers and omnivores, apparent competition between shared prey and consumers through predation by omnivores and an indirect positive trophic cascade from omnivores to shared prey through consumers (Polis et al., 1989; Diehl, 1993; Holt and Polis, 1997). Since IGP is one of the important community modules, it is crucial to reveal the nature of IGP to understand complex food webs (Holt and Polis, 1997; Holt, 1997; Kondoh, 2008).

Classical theoretical studies on IGP predicted that coexistence of consumers and omnivores was possible only at intermediate productivity and that omnivores or consumers were excluded at

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low or high productivity, respectively (Holt and Polis, 1997; Borer et al., 2003), while empirical studies showed that consumers could coexist with omnivores at high productivity (Amarasekare, 2008; Abrams and Fung, 2010). Accordingly, theoreticians have modified the classic model to resolve the gap between the empirical observations and theoretical predictions (Heithaus, 2001; Mylius et al., 2001; HilleRisLambers and Dieckmann, 2003; Holt and Huxel, 2007). Some of them have focused on adaptive behavior of organisms, such as diet choice by predators (Křivan, 2000; Křivan and Diehl, 2005) or induced defense by prey (Kimbrell et al., 2007; Nakazawa et al., 2010; Urbani and Ramos-Jiliberto, 2010).

Induced defense is morphological or behavioral shifts of prey to avoid predation, which is widely observed in nature (Lima and Dill, 1990). If there are multiple predators, prey may develop a single defensive trait effective against many predators (generalized defense) or different traits against different predators (specialized defense) (Sih et al., 1998; Relyea, 2003). Examples of the former are reducing activity for mating or foraging to avoid encounters with predators (Huang and Sih, 1991; Krupa and Sih, 1998; Relyea and Werner, 1999; Van Buskirk, 2001), or changing morphology to prevent predation (Van Buskirk and McCollum, 2000; Relyea, 2001; Van Buskirk, 2001). Examples of the latter are taking different behavior or morphology at different locations or against different modes of predation (Rahel and Stein, 1988; Soluk and Collins, 1988; Gonzalez and Tessier, 1997; Krupa and Sih, 1998; Hoverman and Relyea, 2007).

Theoretical studies focused on generalized defense showed that predators less competitive in exploitative competition for the common prey were often excluded by generalized defense (Lima, 1992; Matsuda et al., 1993, 1996; Kimbrell et al., 2007). Kimbrell et al. (2007) studied an IGP system and suggested that coexistence of consumers and omnivores by virtue of adaptive generalized defense was realized only when the predation rate on the consumers by the omnivores was intermediate. In contrast, theoretical studies focused on specialized defense suggested that, since prey tended to allocate more effort toward more consumptive predators, competitive exclusion could be prevented (Lima, 1992; Matsuda et al., 1996; Kondoh, 2007; Nakazawa et al., 2010). Nakazawa et al. (2010) studied an IGP system with two kinds of specialized defenses by shared prey effective against each of consumers and omnivores and suggested that coexistence of consumers and omnivores was realized by adaptive specialized defense when the predation rate on consumers was low as well as intermediate. Consequently, joint use of the specialized defenses against consumers and omnivores may enhance the three species coexistence more than the generalized one does. However, specialized defense often makes the IGP system unstable, especially in highly productive environments (Nakazawa et al., 2010).

Some organisms use these two types of defenses in combination. For example, anuran tadpoles (*Rana pirica*) become a bloated bulgy morph to avoid predation by swallowing type predators, salamander larvae (*Hynobius retardatus*), or increase tail fin depth and become a high-tail morph to avoid predation from biting type predators, dragonfly larvae (*Aeshna nigroflava*) by improving their swimming performance (Kishida and Nishimura, 2005; Kishida et al., 2009). The former defense is effective only against salamander larvae, while the latter is effective against both predators, and thus functions as a generalized defense (Kishida and Nishimura, 2005). Although such joint use of two types of defenses is observed in nature, most of previous theoretical works have focused on either one of the specialized or generalized defense, and rarely studied both of them.

In this study, we extend the model of Nakazawa et al. (2010), considering both generalized and specialized adaptive defenses by shared prey in an IGP system. We describe population dynamics by using a Lotka–Volterra model with dynamics of defense efforts of the shared prey. We assume that shared prey allocate defensive efforts toward specialized and generalized defenses so as to increase its fitness. Questions to answer in this article are (1) whether joint use of two types of adaptive defenses promotes three species coexistence at high environmental productivity, (2) how the joint use affects stability and dynamics of the system, and (3) how the two types of defenses shape the abundance of each species.

2. Model

In this article, we extend the model of Nakazawa et al. (2010) which considers predator-specific adaptive defenses by shared prey in an IGP system. We assume that shared prey can employ both generalized defense against consumers and omnivores and either one of two kinds of specialized defenses effective against consumers or omnivores. Population dynamics are described by a Lotka–Volterra model as follows:

$$\frac{dR}{dt} = \left(rC - \frac{R}{k} - D_N a_{NR} N - D_P a_{PR} P\right) R \quad (1-\mathrm{A})$$

$$\frac{dN}{dt} = (b_{NR} D_N a_{NR} R - a_{PN} P - m_N) N \quad (1-\mathrm{B})$$

$$\frac{dP}{dt} = (b_{PR} D_P a_{PR} R + b_{PN} a_{PN} N - m_P) P \quad (1-\mathrm{C})$$

where R, N and P represent the population densities of shared prey, consumers and omnivores, respectively. The parameter k is the inverse of density dependence of the shared prey and closely related to the carrying capacity (we consider this as a measure of productivity). r is the intrinsic growth rate of shared prey. a_{ij} is the attack rate of species i on species j ($i \in \{N, P\}$, $j \in \{R, N\}$). b_{ij} is the conversion efficiency of species i consuming species j ($i \in \{N, P\}$, $j \in \{R, N\}$). m_i is the density-independent mortality of species i ($i \in \{N, P\}$). D_i represents effects of defense by shared prey against predator species i, or fractional decrements in the attack rate. We assume that the reduction in attack rates of predators due to each defense is described as follows:

$$D_i = 1 - f_{gi} e_g - f_{si} e_{si} \ (i \in \{N, P\}) \quad (2)$$

where e_g and e_{si} represent the efforts toward the generalized defense and the specialized one against species i, respectively ($i \in \{N, P\}$) and f_{gi} and f_{si} represent the efficiencies of the generalized defense and the specialized one against species i, respectively ($0 \le f_{si}, f_{gi} \le 1$, $i \in \{N, P\}$). We assume that shared prey can invest effort to each of the defenses within a limit, $0 \le e_{si} + e_g \le 1$ ($i \in \{N, P\}$). Although attack rates from predators decrease with increasing effort to defense, shared prey incurs costs in the intrinsic growth rate. We assume that the cost of defense is described as follows:

$$C = 1 - c_g e_g - c_{si} e_{si} \quad (3)$$

where c_g and c_{si} represent the coefficients of costs of the generalized defense and the specialized one against species i ($0 \le c_g, c_{si} \le 1$, $i \in \{N, P\}$).

Here, we assume that shared prey can adaptively change the effort toward each defense to increase its own fitness described by W. We define the fitness as the per-capita growth rate of the shared prey ($W = (dR/dt)/R$). The dynamics of each effort to reduce the attack rates is expressed by the replicator equation, which is used in