



Top predators induce the evolutionary diversification of intermediate predator species



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HIGHLIGHTS

- Top predators promote the diversity of intermediate predators.
- The shape and strength of trade-offs determine evolutionary branching.
- The dimorphic intermediate predators can be evolutionarily stable.
- After branching, one of the two branches may go extinct.

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ABSTRACT

We analyze the evolutionary branching phenomenon of intermediate predator species in a tritrophic food chain model by using adaptive dynamics theory. Specifically, we consider the adaptive diversification of an intermediate predator species that feeds on a prey species and is fed upon by a top predator species. We assume that the intermediate predator's ability to forage on the prey can adaptively improve, but this comes at the cost of decreased defense ability against the top predator. First, we identify the general properties of trade-off relationships that lead to a continuously stable strategy or to evolutionary branching in the intermediate predator species. We find that if there is an accelerating cost near the singular strategy, then that strategy is continuously stable. In contrast, if there is a mildly decelerating cost near the singular strategy, then that strategy may be an evolutionary branching point. Second, we find that after branching has occurred, depending on the specific shape and strength of the trade-off relationship, the intermediate predator species may reach an evolutionarily stable dimorphism or one of the two resultant predator lineages goes extinct.

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1. Introduction

Understanding why and how evolutionary branching of intermediate predator species comes into being remains an important question in evolutionary ecology (Brown and Vincent, 1992; Abrams and Matsuda, 1993; Matsuda and Abrams, 1994; Boudjellaba and Sari, 1998; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000; Abrams and Chen, 2002; Nowak and Sigmund, 2004; Diekmann et al., 2005; Ma and Levin, 2006). Although predator–prey interactions are ubiquitous in nature and intermediate predator species show tremendous diversity, the

underlying demographic and environmental factors are not well understood.

Based on the framework of adaptive dynamics (Geritz et al., 1998; Dieckmann and Doebeli, 1999), many different models have been developed in order to understand predator diversification. Doebeli and Dieckmann (2000) investigated the coevolutionary dynamics of predator–prey interactions and found that branching in the prey can induce secondary branching in the predator. Based on the standard predator–prey model, Landi et al. (2013) found that prey branching is induced by the predation pressure, and is favored when prey intraspecific competition is highly sensitive to the resident–mutant phenotypic mismatch, while predator branching is not possible when prey and predators are present in an equal number of morphs. When only the attack ability of predator species evolves, Hoyle et al. (2008) found that evolutionary branching requires that the evolving predator species exhibits

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intra-specific competition and a trade-off with a weakly decelerating cost (see also Bowers et al., 2005; Zu and Wang, 2013). Besides, Geritz et al. (2007) investigated the evolution of handling time in a nonequilibrium predator–prey system and found that evolutionary branching and long-term coexistence of cycling predators is possible. Recently, Zu et al. (2011) investigated the adaptive evolution of foraging-related traits when a predator species feeds on two alternative prey species and found that evolutionary branching of predator species is possible if there is a small switching cost between the two capture rates (see also Ma and Levin, 2006). Kooi (2015) studied the dynamics of a predator–prey system where predators fight for captured prey besides searching for and handling of the prey. He found that for low costs the predator population is monomorphic (only hawks) while for high costs the predator population is dimorphic (hawks and doves). In these studies, the predators underwent branching, but it was not assumed to be itself exposed to a top predator.

However, in reality, the population community structures are much more complicated, and predators may often themselves exposed to top predators (Abrams and Ginzburg, 2000). Many examples can be found in Freedman and Waltman (1977); Hastings and Powell (1991) and Sun and Loreau (2009). Yet, there has been little discussion about how the presence of a top predator will affect the evolution of an intermediate predator species. For the tritrophic food chain model, without considering evolutionary stability, Kirlinger (1988) found that two types of intermediate predators with linear functional responses can coexist with a single prey species when there exists a top predator species (i.e., the top predator species mediates coexistence). It is, however, not well understood whether such a coexistence is also evolutionarily stable, and whether the two intermediate predator species may evolve from a single ancestor via evolutionary branching.

In this paper, we aim to examine two questions. First, under what ecological and evolutionary conditions an intermediate predator species will change from monomorphism to dimorphism. Second, whether the dimorphic intermediate predators can evolutionarily stably coexist, or whether adaptive evolution of a foraging-related trait can lead to the extinction of one of the two resultant predator lineages. Our main approach is based on the theory of adaptive dynamics and critical function analysis (Metz et al., 1992; Dieckmann and Law, 1996; Geritz et al., 1998; Dieckmann and Doebeli, 1999; de Mazancourt and Dieckmann, 2004; Dieckmann et al., 2005; Kisdi, 2006; Geritz et al., 2007; Hoyle et al., 2008; Zu et al., 2011).

2. Materials and methods

2.1. Population dynamics

We assume that the intermediate predator species is caught by a top predator species (Kirlinger, 1988; Abrams and Ginzburg, 2000). Therefore, the population model is given by

$$\begin{cases} \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - c_p NP, \\ \frac{dP}{dt} = a_p c_p NP - d_p P - c_T PT, \\ \frac{dT}{dt} = a_T c_T PT - d_T T, \end{cases} \quad (1)$$

where N , P and T denote respectively the population densities of the prey, intermediate predator and top predator species at time t , r is the per capita intrinsic growth rate of the prey species, K is the environmental carrying capacity of the prey species, c_p and c_T are respectively the capture rates of the intermediate predator and top predator species, a_p and a_T are respectively the conversion

efficiencies of the intermediate predator and top predator species, d_p and d_T are respectively the per capita natural death rates of the intermediate predator and top predator species (Gurney and Nisbet, 1998). All the parameters are positive. We next incorporate the trade-off structure into model (1).

2.2. Trade-off structure

We assume that the intermediate predator species is characterized by a single phenotypic trait x of interest, such as horn size or body size, that determines its attack ability and the attack ability of intermediate predator species is proportional to its phenotypic trait. Without loss of generality, we assume that the capture rate c_p of the intermediate predator is equal to x . The phenotypic trait x scales between zero and one. This scaling is achieved by means of the transformation $\log(l/l_{\min})/\log(l_{\max}/l_{\min})$, where l is the real trait value and l_{\min} and l_{\max} are minimum and maximum trait values, respectively (Schwinning and Fox, 1995). Moreover, we assume that only the intermediate predator species can adaptively evolve, but the evolution of the intermediate predator will almost inevitably be subject to a trade-off, that is, increasing x has a cost in terms of a reduced defense ability on the top predator. Thus the capture rate c_T of the top predator species and x are related by a trade-off, such that $c_T(x)$ is a monotonically increasing function of x . For the simplicity of notation, we use $c(x)$ instead of $c_T(x)$. To give a concrete mechanism, let x denote the body size of intermediate predator species, with a larger body size the intermediate predator species can catch more prey, but with a larger body size it is much easier for them to be detected and caught by a top predator, hence the capture rate of the top predator will increase. Therefore, in case of a monomorphic intermediate predator species, the population model (1) is changed to

$$\begin{cases} \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - xNP, \\ \frac{dP}{dt} = a_p x NP - d_p P - c(x)PT, \\ \frac{dT}{dt} = a_T c(x)PT - d_T T, \end{cases} \quad (2)$$

where $c(x)$ is a twice continuously differentiable function with respect to x and $x \in [0, 1]$.

Moreover, it should be noted that if the trade-off function $c(x)$ is a linear function with respect to x , then as the benefit through the improvement of foraging ability increases, the cost due to the change in the defensive ability increases at a constant rate, in this case we say there is neither a decelerating cost nor an accelerating cost. However, if a part of the trade-off curve is convex, then in this segment each unit of improvement in the foraging ability comes at an ever increasing cost in the anti-top predator ability, i.e., the cost increases quicker than the benefit. Hence, in this case, we say there is an accelerating cost in the convex part of the trade-off curve. On the contrary, if a part of the trade-off curve is concave, then in this segment each unit of improvement in the foraging ability comes at an ever decreasing cost in the anti-top predator ability. Hence, in this case, we say there is a decelerating cost in the concave part of the trade-off curve (Egas et al., 2004; White and Bowers, 2005; Hoyle et al., 2008).

Setting the right-hand sides of (2) to 0, we obtain a strictly positive ecological equilibrium $(N^*(x), P^*(x), T^*(x))$, where

$$\begin{cases} N^*(x) = \frac{K(ra_T c(x) - xd_T)}{ra_T c(x)}, \\ P^*(x) = \frac{d_T}{a_T c(x)}, \\ T^*(x) = \frac{Ka_p x(ra_T c(x) - xd_T) - d_p ra_T c(x)}{ra_T c^2(x)}. \end{cases} \quad (3)$$

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