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Adaptive evolution of attack ability promotes the evolutionary branching of predator species

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ABSTRACT

In this paper, with the methods of adaptive dynamics and critical function analysis, we investigate the evolutionary branching phenomenon of predator species. We assume that both the prey and predators are density-dependent and the predator's attack ability can adaptively evolve, but this has a cost in terms of its death rate. First, we identify the general properties of trade-off relationships that allow for a continuously stable strategy and evolutionary branching in the predator strategy. It is found that if the trade-off curve is weakly concave near the singular strategy, then the singular strategy may be an evolutionary branching point. Second, we find that after the branching has occurred in the predator strategy, if the trade-off curve is convex–concave–convex, the predator species will eventually evolve into two different types, which can stably coexist on the much longer evolutionary timescale and no further branching is possible.

1. Introduction

Understanding the mechanism of species diversification remains a core problem in evolutionary ecology (Abrams, 1991; Brown and Vincent, 1992; Matsuda and Abrams, 1994; Boudjellaba and Sari, 1998; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000; Grant and Grant, 2002; Bowers et al., 2003; Ackermann and Doebeli, 2004; Ma and Levin, 2006; Tobler and Hastings, 2011). Particularly, it is not well understood which demographic or environmental factors may promote the diversity of predator species. Yet it is well known that two types of predator species with linear functional response can coexist on a single prey species when the two predators engage in direct conflicts and interfere with each other (i.e., interference competition, Abrams and Ginzburg, 2000; Amarasekare, 2002). However, there has been little discussion about whether such a coexistence is also evolutionarily stable, and whether the two predator species may evolve from a single ancestor via evolutionary branching in a simple one-predator–one-prey system. The classical ecological models that demonstrate equilibrium coexistence do not address evolutionary stability, whereas the evolutionary models that show the evolutionarily stable coexistence usually fix the environmental conditions (Geritz et al., 2007). When an eco-evolutionary feedback loop is taken into account, the environmental conditions necessarily coevolve and accordingly the spectrum of possible population dynamical behavior becomes a lot richer (Diekmann et al., 2005). This viewpoint affects not only the intuition of evolutionary biologists, but also their theoretical tools.

When ecological and evolutionary dynamics occur on a similar timescale, we should couple the evolutionary and population dynamics. However, if mutations occur infrequently such that a mutant strategy either has spread or has been excluded, and the populations have reached their ecological equilibriums by the time the next mutants come along, then the two dynamics can be decoupled (Geritz et al., 1998). In fact, in the latter case, the evolutionary processes can be described by an adaptive dynamical system (Metz et al., 1992; Dieckmann and Law, 1996; Geritz et al., 1998; Dieckmann and Doebeli, 1999; Geritz et al., 2007; Kisdi, 2006). Adaptive dynamics is a mathematical theory that explicitly links population dynamics to a long-term evolution driven by mutation and natural selection. A particularly intriguing phenomenon revealed by the theory of adaptive dynamics is the evolutionary branching, that is, a change from a monomorphic to a dimorphic population (Geritz et al., 1998).

Based on the framework of adaptive dynamics, many different models and approximation schemes have been developed in order to understand the actual mechanisms of the evolutionary diversification of predator species. Doebeli and Dieckmann (2000) investigated the coevolutionary dynamics of predator–prey interactions and found that the evolutionary branching in the prey species can sometimes induce the secondary branching in the predator species. They argued that whether this can happen depends on the distance of the two prey branches. When only the attack ability of

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predator species evolves, Hoyle et al. (2008) found that the evolutionary branching requires that the evolving predator species exhibits an intra-specific competition (see also Bowers et al., 2005). Recently, with the method of critical function analysis, we investigated the adaptive evolution of foraging-related traits when a predator species feeds on two alternative prey species and found that the 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; Rueffler et al., 2006). However, in the previous study, the interference competition among the predator individuals is not considered and there has been little discussion about whether the adaptive evolution of attack ability can promote the diversity of predator species in a simple one-predator–one-prey system. In addition, after the branching has occurred in the predator strategy, it is still unknown whether the coexistence of the two resultant predators can be maintained over evolutionary time and how this evolution depends on the trade-off relationship between the capture rate and the death rate of predator species.

In this paper, we aim to address two questions. One is under what ecological and evolutionary conditions a predator species will change from monomorphism to dimorphism in a simple one-predator–one-prey system. The other is whether the two predator species evolving from a single ancestor can continue to coexist on the much longer evolutionary timescale. We assume that both the prey and predators are density-dependent and an improved attack ability of predator species results in an increased natural death rate of them (e.g., the Lions; with a larger body size and tooth size the Lions can catch more food, but at the same time it is difficult for them to adapt to the climate and surrounding environment, hence their death rate is also increased). Focusing at first on a monomorphic predator species, we use the new method of critical function analysis (Geritz et al., 2007) to identify the general properties of trade-off functions that can induce the evolutionary branching in the predator strategy and show how the shape of trade-off relationships affects the evolutionary outcomes. After the branching has occurred in the predator strategy, we proceed to investigate the final evolutionary equilibrium of such a dimorphic predator species and identify the trade-off characteristics that support an evolutionarily stable dimorphism. 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; Geritz et al., 2007; Kisdi, 2006; Hoyle et al., 2008; Zu and Takeuchi, 2012). In this approach, the evolutionary dynamics is studied using the concept of invasion fitness (Metz et al., 1992). Additional quantitative information about the speed of adaptive movement is embodied in the canonical equation which describes how the expected trait values will change on a very long timescale when the mutations are very small and rare (Dieckmann and Marrow, 1995; Dieckmann and Law, 1996; Diekmann et al., 2005).

The organization of this paper is as follows. In the next section, we present the formulations of mathematical model and derive the invasion fitness for mutant predators. In Section 3, by using the method of critical function analysis (Geritz et al., 2007), we investigate the monomorphic evolutionary dynamics. In Section 4, we study the dimorphic evolution and give an example of evolutionarily stable coexistence. Numerical simulations are also presented respectively in Sections 3 and 4 to illustrate the feasibility of our main results. A brief discussion is given in Section 5.

2. Model description

In this section, we first develop a population dynamical model for an evolving predator species. From this demographic model, we will derive the invasion fitness that we use to investigate the evolutionary dynamics of predator species.

2.1. Population dynamics

The population model we consider is a Lotka–Volterra predator–prey model. In particular, the crowding effect of predator species is considered, i.e., the predator individuals may interact directly through interference competition (Abrams and Ginzburg, 2000). In other words, we assume that the predators are aggressive and engage in direct conflicts, they may kill one another in competitive fights, which leads to an increased death rate when their density is higher. The rate at which such aggressive predator–predator encounters occur is assumed to be proportional to the predator density. Moreover, we assume that the 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 capture rate of predator species is proportional to its phenotypic trait. Without loss of generality, we assume that the capture rate of predator species equals to x, predators with different capture rates represent different types. In order to maximize the individual fitness, the predator species will improve its trait to adapt to the prey species, so the predator's attack ability can adaptively evolve, but this has a cost in terms of its death rate d. In other words, if the predator species improves its attack ability, then its death rate will also be increased, d and x are trade-off related such that $d(x)$ is a monotonically increasing function of x. To give a concrete mechanism, let x denote the body size of the predator, with a larger body size the predator species can catch more prey, but with a larger body size it is difficult for them to adapt to the climate and surrounding environment, hence their death rate will be increased. In other words, an intrinsic cost to large body size is to be expected. Therefore, the population model is given by

$$\begin{cases} \dfrac{dN}{dt} = N\,(r - k_1 N) - xNP, \\ \dfrac{dP}{dt} = axNP - (d(x) + k_2 P)\,P, \end{cases} \tag{1}$$

where

$$d'(x) > 0, \quad x \in [0, 1],$$

N and P denote respectively the population densities of the prey and predator species at time t, r is the per capita intrinsic growth rate of the prey species, k_1 measures how sensitive the prey species is to crowding and k_2 measures the per capita effect of direct predator density dependence, the predator species transforms the consumed prey into predator offspring with efficiency a, $d(x)$ is the per capita natural death rate of the predator species, which is such that $d(x)$ is a twice continuously differentiable and increasing function with respect to x, but the exact nature of this relationship is unknown. Without loss of generality, we scale the capture rate x such that x varies continuously between 0 and 1. The other parameters are positive. Moreover, we think of the attack ability as a phenotypic trait of the predator species. A trait can change if it gives a higher fitness to its bearer. The predator species with different attack abilities represent different types.

When

$$arx > k_1 d(x), \tag{2}$$

setting the right-hand sides of (1) to 0, we obtain a globally asymptotically stable ecological equilibrium $(N^*(x), P^*(x))$, where

$$\begin{cases} N^*(x) = (rk_2 + xd(x))/(k_1k_2 + ax^2), \\ P^*(x) = (arx - k_1 d(x))/(k_1k_2 + ax^2). \end{cases} \tag{3}$$

Notice that the stable ecological equilibrium $(N^*(x), P^*(x))$ is determined by the trait value x and the trade-off function $d(x)$. It is important to appreciate that, on the timescale of ecological dynamics, the species may not coexist for some trait values and trade-off