Adaptive evolution of foraging-related trait in intraguild predation system☆

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ABSTRACT

This paper considers a tri-trophic food chain in which the top predator (intraguild predator) also feeds on the basal resource. We refer to the model as intraguild predation. We analyze its dynamics from an evolutionary perspective. The attack rate or foraging effort of the middle species (intraguild prey) for the basal resources is assumed to be evolvable and is also assumed to be traded off with the vulnerability to being attacked by the top predator. We focus on the analysis of the evolutionary dynamics of the attack rate using the adaptive dynamics approximation of mutation limited evolution. In particular, the critical function analysis is applied. This study reveals that the evolutionary dynamics of the intraguild predation system is completely characterized by the concavity of the trade-off function and admits trichotomous dynamic scenarios: (1) when the trade-off function is more concave than the critical function, an evolutionary singular strategy exists and is a repeller; (2) when the trade-off function is less concave than the critical function, the evolutionary singular strategy is convergence stable and turns into an evolutionary branching point, in which case the monomorphic intraguild prey will split into two different types; (3) when the trade-off function is convex, the evolutionary singular strategy turns into a continuous stable strategy and is uninvadable. Our theoretical analysis suggests that the adaptive foraging behavior may strongly influence the community stability. Consequently, it may promote the diversity of intraguild prey and the persistence of the system on the evolutionary timescale, which highlight a more comprehensive mechanistic understanding of the intricate interplay between ecological and evolutionary force. This modeling approach provides a venue for research on indirect effects from an evolutionary perspective.

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1. Introduction

Intraguild predation (IGP), being known as a mixture of competition and predation, refers to a three-species module in which the top predator feeds from two trophic levels (i.e., it is an omnivore) by consuming the intermediate predator and the shared resource. It has been suggested in theory that the communities with IGP are not persistent on the ecological time scale [1]. However, in reality, the IGP system is ubiquitous in ecosystems [1–3]. From the perspective of ecology, various theoretical hypotheses and experimental researches have contributed to explaining this discrepancy [4–8]. Although the prevailing ecological models using emergent properties of some observed food webs are able to depict food-web interactions satisfactorily, they fail to provide clear mechanisms explaining the evolution of dynamic properties of food webs [9].

A key problem in community ecology is to understand how individual-level traits give rise to population-level trophic interactions. Recent experimental studies on IGP suggest that, the intermediate predator has evolutionary consequence by evolving traits that increase its ability to consume the shared resource, and complex food webs may emerge from evolutionary assembly processes [5,10,11]. Consideration of adaptive processes may provide approaches to understanding the structure and functioning of ecosystems. Many characteristics are likely to play roles in ecosystems and a large set of traits determine the strength of trophic interactions. The traits are numerous and usually are not explicitly identified. It is almost impossible to understand the evolutionary dynamics by considering a large number of traits, either theoretically or experimentally. Foraging behavior may be an important trait that allows many complex ecological systems to exist [12] and has been extensively studied [13–15]. It affects an animal's fitness, and plays an important role in an animal's ability to survive and reproduce [16]. The evolution of foraging behavior has potentially
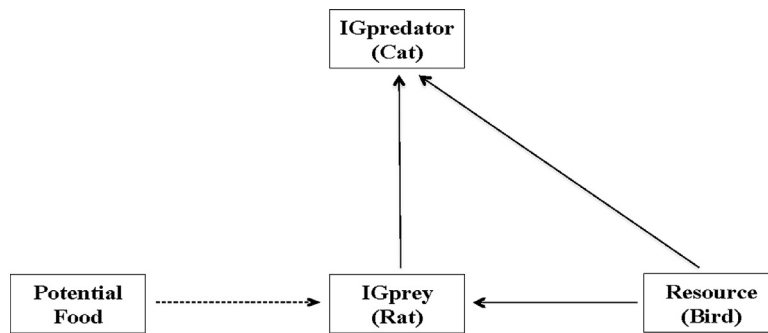
Fig. 1. Schematic diagram of the intraguild predation (IGP) system with a typical example (bird-rat-cat) explored in Fan et al. [23]. The direction of the arrows indicates the energy flow.

profound effects across multiple scales of biological organization from individuals to ecosystem and has important implications for interaction strengths, population dynamics, and eventually the structure and functioning of food-webs and other ecological networks [12]. There has been a growing body of research focusing on the evolution of foraging behavior [7,13,15].

In IGP, the intermediate predator evolves antipredator behavior while balancing costs (perceived predation risk) and benefits (resource intake), any of which may alter the structure of the food web, to determine its foraging effort [5,17]. However, the evolutionary consequences of IGP systems have not received much attention. It will be interesting but challenging to study the evolutionary response of IGP systems. Okuyama and Ruyle [7] construct a simple mathematical model and show that both IGP and adaptive foraging behaviors may strongly influence community dynamics, and the adaptive foraging may facilitate the persistence of the IGP system. But they fail to characterize the dynamical aspects of trait evolution and to expound the rich evolutionary dynamics of the IGP system.

This study is interested in the interplay of ecological and evolutionary processes in IGP system: how will ecological interactions shape selective pressures acting on individual adaptive traits? How will in return the adaptive trait evolution influences population dynamics and community structure? In particular, we focus on the trait evolution of IGprey in IGP system. An adaptive dynamics model with foraging effort being the single biological trait subject to evolution is formulated to expound the ecological consequences of the trade-off between resource acquisition and risk of predation mortality mediated by foraging activity. The principal aim of this paper is fourfold. First, we formulate and explore an ecological model for intraguild predation system consisting of IGpredator, IGprey, and basal resource, and then formulate an evolutionary model of IGprey's trait (i.e., foraging behavior). Second, we investigate under what conditions the adaptive evolution of foraging ability promotes the IGprey to evolutionary stability and diversity. Third, we analyze how the key parameters influence the evolutionary dynamics of the IGprey. Fourth, we investigate the question under what condition, the two sub-populations can coexist on much longer evolutionary time scale when the IGprey species undergoes evolutionary branching. The ecological model is constructed with the help of Lotka–Volterra theory. Our main approach is based on the theory of adaptive dynamics [18–20].

2. Formulation of ecological model

Consider a simple unidirectional IGP community consisted of an intraguild predator (IGpredator, i.e., the top predator), an intraguild prey (IGprey, i.e., the intermediate predator), and a basal resource. The IGpredator being an oligophage both feeds on IGprey and competes with it for the shared basal resource. This double threat of competition and predation can produce substantial negative effects on IGprey. The IGprey depends not only on the basal resource but also on some other complementary potential food. IGprey plays the role of both predator and prey, and exhibits both foraging activity and anti-predator behavior. A simple IGP system can be found widely in the natural aphid communities [21] and in lake food webs [22]. A typical example of such an IGP module is the bird-rat-cat system well explored in Fan et al. [23], where the IGpredator, IGprey, and basal resources are named as superpredator, mesopredator, and prey in the field of biological invasion (see Fig. 1 for a schematic diagram of IGP system).

To develop a mathematical framework that can incorporate the biological details in IGP system, denote by $x \in [0, 1]$ the foraging effort of IGprey, which is considered as the consumption or attack rate of IGprey on basal resource and is assumed to be proportional to the foraging time of IGprey. The vulnerability function of IGprey is represented by $c(x)$. When IGprey spends more time or put more efforts on preying the basal resource (higher x), the probability of encountering with IGpredator increases and IGprey admits higher risk of being preyed by IGpredator (larger $c(x)$). Hence, the foraging effort x and the vulnerability function $c(x)$ are linked via a trade-off relation. This kind of trade-off has been discussed in other studies [17,24]. Based on the above-mentioned discussion, it is assumed that $c(x)$ is an increasing function of foraging effort x, that is $c'(x) > 0$ for $x \in [0, 1]$.

The dynamics of the three species IGP community are given by the following mathematical model modified from the basic IGP model of Holt and Polis [1]

$$\begin{cases} \dfrac{dR}{dt} = rR\left(1 - \dfrac{R}{k}\right) - aRP - xNR, \\ \dfrac{dN}{dt} = sN + e_1 xNR - c(x)NP - d_1 N, \\ \dfrac{dP}{dt} = e_2 aPR + e_3 c(x)NP - d_2 P, \end{cases} \quad (1)$$

where P, N and R denote the densities of IGpredator, IGprey, and basal resource, respectively. The basal resource is assumed to grow in a logistic manner, r is the intrinsic growth rate of resource reproduction and k is the carrying capacity of basal resource. The parameter s is the supplement rate of potential food for IGprey. The parameters d_1 and d_2 are the background mortality rates of IGprey and IGpredator, respectively. The parameter a is the per capita consumption or attack rate of IGpredator on basal resource. The parameter e_i ($i = 1, 2$) is the number of IGprey or IGpredator offspring resulting from basal resource consumption. The parameter e_3 is the number of IGpredator offspring resulting from IGprey. Model (1) is a special case of the BRC model explored in Fan et al. [23].

The focal system (1) admits five possible equilibria and the stability can be achieved by standard qualitative analysis as those in