



How optimally foraging predators promote prey coexistence in a variable environment



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ABSTRACT

Optimal foraging is one of the major predictive theories of predator foraging behavior. However, how an optimally foraging predator affects the coexistence of competing prey is not well understood either in a constant or variable environment, especially for multiple prey species. We study the impact of optimal foraging on prey coexistence using an annual plant model, with and without annual variation in seed germination. Seed predators are modeled using Charnov's model of adaptive diet choice. Our results reveal that multiple prey species can coexist because of this type of predator, and that their effect is not greatly modified by environmental variation. However, in diverse communities, the requirements for coexistence by optimal foraging alone are very restrictive. Optimally foraging predators can have a strong equalizing effect on their prey by creating a competition–predation trade-off. Thus, their main role in promoting diversity may be to reduce species-average fitness differences, making it easier for other mechanisms, such as the storage effect, to allow multiple species to coexist. Like previous models, our model showed that when germination rates vary, the storage effect from competition promotes coexistence. Our results also show that optimally foraging predators can generate a negative storage effect from predation, undermining coexistence, but that this effect will be minor whenever predators commonly differentiate their prey.

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1. Introduction

Optimal foraging theory is one of the major predictive theories of animal foraging behavior (Perry and Pianka, 1997). Optimal foraging theory encompasses a variety of different models, but all are united by the assumption that a forager will maximize some fitness proxy under some constraint (Pyke et al., 1977). For example, the Charnov model of adaptive diet choice (Charnov, 1976) – the focus of this paper – shows how predators would alter their diet breadth to maximize their calorie intake per unit time. The model assumes that predators are constrained because they must spend time handling their prey; therefore, a predator that consumes low-calorie prey has less time to search for high-calorie prey (Charnov, 1976). The model predicts that predators should always consume high-calorie prey, but should only consume low-calorie prey when high-calorie prey are scarce (Charnov, 1976). Like many optimal foraging models, the Charnov model includes unrealistic assumptions, such as perfect information and perfectly rational behavior (Pierce

and Ollason, 1987). However, like many optimal foraging models, it provides an adequate approximation for foraging behavior in many systems (reviewed in Jaenike, 1990; Krebs and McCleery, 1984), such as insectivorous birds (Krebs et al., 1977), crabs (Elnor and Hughes, 1978), and coyotes (Hernández et al., 2002). In particular, it incorporates several well-documented behaviors: preference hierarchies (Inouye et al., 1980), predator satiation (Kelly and Sork, 2002), and malleable diet choice (Hernández et al., 2002). Such behaviors can cause a predator to affect its prey differentially, and differential effects are a basic requirement for any mechanism that promotes coexistence (Chesson, 2000). Beyond these differential effects, much is unknown about how an optimally foraging predator will affect its prey's ability to coexist in a complex community. In this paper, we analyze how an optimally foraging granivore can affect prey coexistence in a diverse community of annual plants.

Many previous studies have shown that an optimally foraging predator can allow two prey species to coexist if there is a competition–predation trade-off (Abrams and Matsuda, 1996; Genkai-Kato and Yamamura, 1999; Gleeson and Wilson, 1986; Krivan, 2003); however, this result is not unique to optimal foraging. Rather, a competition–predation trade-off can allow two species to coexist, even if the predators consume prey at constant per capita rates, i.e. have a linear or Type I functional response

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(Armstrong, 1979; Holt et al., 1994; Levin, 1970). However, if every species has a linear functional response, then two species is an upper limit to the number of prey that can coexist (Levin, 1970). But, if any species have nonlinear functional responses or malleable behavior, additional prey species may be able to coexist (Levin, 1970). Hambäck (1998) considered a community of three prey species, but did not find three-species coexistence without invoking an additional mechanism. As far as we are aware, no study has examined if optimal foraging can allow more than two species to coexist.

Optimal foraging leads to a form of frequency-dependent predation, which has been shown in other circumstances to be a strong promoter of species coexistence (Chesson and Kuang, 2010). For example, when frequency-dependent predation arises due to a learning constraint, predators will attack abundant prey species disproportionately more (McNair, 1980; Murdoch, 1969). This generates a low-density advantage for prey species, potentially allowing them to recover if they fall to low densities (Chesson and Kuang, 2010; Kuang and Chesson, 2010). Such behavior can allow a potentially unlimited number of prey species to coexist (Chesson and Kuang, 2010). However, there is an important distinction between frequency-dependence arising from learning constraints and frequency-dependence arising from optimal foraging. An optimally foraging predator does not reduce its attack rate on a prey species because that species is rare. Instead, it excludes a prey-species from its diet based on the abundance of higher-calorie prey (Charnov, 1976). Such behavior creates important asymmetries, as high-calorie prey are never ignored.

A deeper understanding of optimal foraging will be particularly important for understanding communities of desert annual plants. Seed predation is thought to play a major role in allowing desert annuals to coexist (Brown and Heske, 1990; Davidson et al., 1984). For example, long-term experiments near Portal, AZ, have shown that when rodents are excluded, the annual community becomes dominated by plants with large seeds (Allington et al., 2013; Brown and Heske, 1990). Granivorous rodents show strong preference hierarchies based on seed size (Brown and Heske, 1990; Inouye et al., 1980), and thus models of optimal foraging, or adaptive diet choice more generally, are likely applicable. Environmental variation is also thought to drive coexistence in these systems (Angert et al., 2009; Chesson et al., 2013; Pake and Venable, 1996). Thus, a model for annual plants provides an opportunity to study how predators interact with yearly variation in the environment. Annual plant models have previously been used to study a diverse set of interactions between consumers and the environment (e.g., Chesson and Kuang, 2010; Kuang and Chesson, 2008; Kuang and Chesson, 2009; Mordecai, 2014).

In previous models of desert annual communities, environmental variation promotes coexistence through the storage effect (Chesson, 1994; Chesson et al., 2013). Seeds of different species have different germination rates each year due to variation in the weather (Adonakis and Venable, 2004; Facelli et al., 2005). Only individuals who germinate can reproduce. However, when an abundant species has a high germination rate, competition will be high; thus, very abundant species are unable to take advantage of favorable years for germination (Chesson, 1994). Species can gain a low-density advantage by germinating under different conditions, because they are more likely to germinate in years when competition is low, and remain dormant in the seed bank when competition is high (Chesson, 1994).

In a variable environment, natural enemies can generate a storage effect that is analogous to the storage effect from competition (Chesson and Kuang, 2010). Generalist pathogens and predators with a Type III functional response will become more active when prey are abundant (Chesson and Kuang, 2010; Mordecai, 2014). Thus, abundant species will face high consumption rates in years

where they have a high germination rate. In this case, species at low-density gain an advantage because they are likely to germinate when consumption rates are low, and are likely to remain dormant when consumption rates are high (Chesson and Kuang, 2010). Thus, the storage effect from consumers is similar to the storage effect from competition, but it is generated by apparent competition instead of resource competition.

In this paper, we study how seed predators that behave according to the Charnov model of adaptive diet choice affect the coexistence of annual plants (Charnov, 1976). We examine the effect of predators both when germination rates are constant, and when they vary. This model allows us to analyze how a major form of predator behavior interacts with environmental variation, and how it affects prey coexistence in a diverse community. Our work suggests that unlike frequency dependent predation due to a learning constraint (Chesson and Kuang, 2010; Kuang and Chesson, 2010), optimal foraging promotes coexistence mainly by making species competitively similar, rather than by generating a low-density advantage. Our model also suggests a new mechanism through which predators can undermine coexistence: a negative storage effect caused by predator satiation.

2. Model and analysis

Our model is based upon the life history of desert annual plants, which are competing in the presence of seed predators (Kuang and Chesson, 2008). All variables are listed in Table 1. Our population variable, $N_j(t)$, is the number of seeds of species j at the start of year t , before germination. At the beginning of each year, some fraction of the seeds from each species germinate, $G_j(t)$. A fraction s of the ungerminated seeds will survive and be present in the seed bank the following year. Seeds that germinate compete for resources and grow into adult plants that produce new seeds. Adults of species j produce $Y_j e^{-C(t)}$ seeds on average, where Y_j is proportional to seed yield in the absence of competition, and $C(t)$ is the effect of resource competition defined as the reduction in \ln seed yield due to competition. After seeds are produced, the new seeds are exposed to predators, and have the chance $\exp\{-A_j(t)\}$ of surviving predation. Surviving seeds enter the seed bank, where they are protected from predators and competition, and can germinate in future years. Taken together, the yearly finite rate of increase of species j , $\lambda_j(t)$, is

$$\lambda_j(t) = (1 - G_j(t))s + Y_j G_j(t) e^{-C(t) - A_j(t)}, \quad (1)$$

and the population growth rate is $r_j(t) = \ln \lambda_j(t) = \ln N_j(t+1) - \ln N_j(t)$.

Resource competition is modeled as

$$C(t) = \ln \left\{ \alpha_1 + \alpha_2 \sum_{j=1}^n G_j(t) N_j(t) \right\}, \quad (2)$$

where α_1 and α_2 are competition parameters, and n is the number of competing species. For small population densities, each germinating seed produces approximately Y_j/α_1 seeds; for high population densities, seed production is inversely proportional to the number of plants. Modeling competition with two competition parameters allows us to consider both lottery competition (i.e., when $\alpha_1 = 0$, which assumes no maximum reproductive output and complete resource use), and forms of competition where species have a maximum reproductive output (i.e., when $\alpha_1 > 0$). However, this parameter flexibility leads to slight awkwardness in the defining of Y_j , as it is not exactly seed yield, but merely proportional to it, and zero competition is not $C(t) = 0$, but

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