Population response to resource separation in conservation biological control

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ARTICLE INFO

ABSTRACT

Enhancement of resources to improve the impact of natural enemies in agroecosystems is an important component of conservation biological control. As many organisms depend on more than one resource throughout their life cycle it is necessary to take into account the distance separating vital resources and how it may affect natural enemy population development. It is also important to examine possible interactions with the fourth trophic level. In this study life history values for the parasitoid *Diaeretiella rapae* are incorporated into a mathematical model to explore these issues. In particular, a matrix model is employed to explore the impact of distance of separation between food (nectar in flowering plants) and reproductive (hosts found in the crop field) resources on the primary parasitoid population growth rate. Furthermore, the effects of spatial dissociation of resources on hyperparasitoids are considered. The results suggest that primary parasitoid population dynamics are influenced mainly by limitations in reproduction and by the response of parasitoids to separation of floral resources and host patches. Furthermore, hyperparasitism may cause primary parasitoid populations to decline and undermine biological control, depending on the extent to which hyperparasitoids systematically search for patches of primary parasitoids. The approach provides an initial theoretical framework to natural enemy use of multiple resources.

1. Introduction

Despite its status as one of the oldest means of controlling insect pests, conservation biological control (CBC), which focuses on modifying the environment in order to facilitate biological control of pests, has only recently received substantial consideration in academic circles as a viable alternative or supplement to other forms of biological control (Barbosa, 1998). In the past decade, there has been an increase in the number of studies exploring management schemes for enhancing native predators and parasitoids for efficient biological control (Landis et al., 2000; Marino et al., 2006). A reoccurring theme has been the diversification of agroecosystems, an idea stemming from the ecological debate over whether or not diversity enhances stability (May, 1973; Tilman et al., 2001) and prey suppression in predator–prey interactions (Marino and Landis, 1996; Menalled et al., 1999 Tscharntke et al., 2007). Diversification in agroecosystems for CBC may aim to add supplementary resources for natural enemies for increased survival, fecundity, and longevity so as to maximize biological control efficacy (Landis et al., 2000, 2005; Sunderland and Samu, 2000; Wratten and van Emden, 1995).

In spite of increased interest and numerous field studies, CBC has played only a minor role in biological control programs and research (Hopper, 2003). One possible reason for this is that CBC lacks a basic framework on which to build research protocols and predictive models. Although the importance of resource spatial structure has been explored for host–parasitoid interactions (Hassell, 2000; Hassell and May, 1973), little theory has been developed to describe the dynamics of biological control agents relying on more than one resource. Many arthropods important in biological control rely on spatially distributed resources, such as primary and secondary prey, or host and nectar resources. These resources are often spatially and/or temporally separated and may be found in widely different landscape elements. A few recent field studies have explored the influence that separation of floral resources from host patches may have on parasitism rates (e.g., Lavendero et al., 2005). But few studies have directly addressed quantitatively how the distance separating resources necessary for survival and reproduction may affect population growth and persistence. There is a need to develop more basic ecological theory to support situations in which predators or parasitoids rely on both hosts and other supplemental resources for survival.

In this paper, we explore the link between the use of resource patches and population outcomes when a species resides in one patch but relies on a second patch for foraging. One example that is readily amenable to this sort of analysis is that of insect

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parasitoids, which depend upon external resources (e.g., nearby floral resources) to garner energy for reproduction and extend their longevity. The spatial separation (distance) of such resources from patches where parasitoids oviposit warrants consideration in order to determine how it might be manipulated to bolster parasitoid populations and consequently biocontrol success. We explore these phenomena by incorporating life history parameter values for a parasitoid of economically important agricultural pests into a Leslie matrix model. Our goal is not to provide a detailed model of parasitoid population dynamics, but rather to illustrate some simple patterns that we hope will inspire further modelling and field work.

Recent field studies have provided evidence that increased floral subsidies may confer increased longevity and fecundity on parasitoids (Ellis et al., 2005; Lavendero et al., 2006; Rahat et al., 2005; Rebek et al., 2005; Winkler et al., 2006). However, flight is energetically expensive (Casas et al., 2003) and insects may experience a tradeoff in their lifetime fecundity and their ability to forage for far-flung resources. Recent work indicates that parasitoids that do not feed on supplemental nectar will not survive more than two days in the field, and exhibit dramatically reduced oviposition rates (Winkler et al., 2006). Thus the proximity of floral resources can directly affect both survival and fecundity of adult parasitoids. We would expect a decrease in adult parasitoid survival and fecundity as the spatial separation between resources increases. A recent field study on aphid-parasitoid dynamics demonstrated that parasitism rates declined exponentially with increased distance between host patches and floral resources (Tylianakis et al., 2004).

Another important consideration in biological control is multitrophic interactions. Although classic studies indicate that providing additional plant resources in and around crop fields may attract and positively affect host populations (e.g., aphids on mustard, see van Emden, 1965), more attention is generally paid to the positive effects of nectar and other floral resources on primary and secondary parasitoids. Field studies indicate that higher-order interactions typical of hyperparasitism may be important as regulating factors on parasitoid population dynamics (Lee and Heimpel, 2005; Montoya et al., 2003; van Veen et al., 2002). Hyperparasitism rates of primary parasitoids important for biological control can commonly range from 20% to 30% (Wraight et al., 1993; Mohamed et al., 2000). Although few studies have been designed to explicitly address how hyperparasitoids use floral resources, there is field evidence that hyperparasitoids, like primary parasitoids, depend heavily upon supplemental resources for survival and reproduction (Phillips, 1993). Furthermore, field studies indicate that parasitoids spend more time in high host-density areas than in low-host density areas (Casas, 1989). Thus hyperparasitoids may also aggregate in or near host patches, in which case separating floral resources from high-density host patches may render it more difficult for hyperparasitoids to find hosts. That is, the farther supplemental floral resources are separated from host patches, the lower the hyperparasitism pressure exerted on the primary parasitoid.

A contrasting view is that an increase in separation of floral resources from hosts of the primary parasitoid may make it easier for hyperparasitoids to locate the concentrated patches of primary parasitoids and their hosts. The mechanism driving this scenario would be similar to Root's (1973) resource concentration hypothesis, in which herbivores (hyperparasitoids in this setting) are more easily able to find high-density "monocultures" or patches of host plants (primary parasitoids in this setting). The degree to which hyperparasitoid oviposition is concentrated around parasitoid patches may vary with hyperparasitoid behavior; some hyperparasitoids are more systematic in their foraging (Chow, 2000) whereas others are more focused on patches of primary parasitoids (density-dependent) (Baur et al., 1996; Rosenheim, 1998). In the latter case, we would expect that increased separation of floral resources from primary parasitoid patches would yield more concentrated hyperparasitoid oviposition in primary parasitoid patches, and thereby *increase* mortality in the primary parasitoid with increasing resource spatial dissociation. Thus for the purposes of our modelling exercise here, we also consider the possibility that increasing spatial dissociation of floral resources may result in an increasingly negatively impact on primary parasitoid populations from hyperparasitoids.

In either of these two hyperparasitoid scenarios, separation of floral and host patches may influence adult survival and fecundity as well as larval survival in the primary parasitoid. We hypothesize that increasing spatial separation of resources may decrease vital rates of adult parasitoids, and also affect hyperparasitism rates, with ensuing effects on primary parasitoid population dynamics. To illustrate this, we use a simple model that explores tradeoffs between flight energy expenditures and parasitoid survival and fecundity in order to explore how vital rates interact with the spatial deployment of floral resources in the field.

2. Methods

2.1. General matrix model

We used a Leslie matrix model to determine how spatial separation among host and floral resource patches might affect population outcomes. This may be done by organizing survival and reproduction probabilities into a transition matrix, and then multiplying it by a vector containing the number of individuals in each age class. Repeated multiplication of the population vector by the transition matrix results in a stable population vector, which enables one to solve for λ, a scalar describing population growth. This model, commonly used to compare population growth rates among different species or management scenarios, including biological control (Bommarco, 2001; Caswell, 2001; Kean et al., 2003; Shea and Kelly, 1998), does not consider density dependence, carrying capacity, immigration or emigration. For the current scenario, we assume that densities are low enough that we may ignore density-dependence. Likewise, we assume that within-field dispersal is more important than immigration/emigration in driving population dynamics. Mathematically, the model may be written as

$$\lambda X = AX, \tag{1}$$

where X is the population vector with a stable age distribution, A is the transition matrix, and λ is the population growth rate. Solutions of this equation for which $\lambda > 1$ describe a growing population; those for which $\lambda < 1$ describe a declining population, and those for which $\lambda = 1$ describe a population with zero growth or decline.

For the model, we simulated population outcomes for four different values of spatial separation of host and floral resource patches, ranging from nearest (no spatial separation) to farthest (maximum spatial separation). The zero spatial separation scenario corresponds to situations in which crop plants may produce their own nectar, or growers are using artificial nectar sprays. For each of these distances, different effects of the spatial separation of the floral resource patch from the host patch (d) were implicitly included in reproduction and survival parameters in the transition matrix (A).

2.2. Parameters

We modelled the persistence of a single primary parasitoid species that relies on two different resource patches, one with food, and one with hosts. We assume overlapping generations, with the population broken down into four life stages (egg, larva/pupa,