POPULATION RESPONSE TO RESOURCE SEPARATION IN
CONSERVATION BIOLOGICAL CONTROL

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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.

Keywords: Insect parasitoid, hyperparasitism, matrix model, Diaeretiella rapae, floral
resources
I. 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 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.,
However, flight is energetically expensive (Casas et al., 2003) and insects may experience a trade-off 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 multi-trophic 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 20-30% (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 \( \lambda \), 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

\[
\lambda X = AX, \quad \text{(Eqn. 1)}
\]

where \( X \) is the population vector with a stable age distribution, \( A \) is the transition matrix, and \( \lambda \) 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, young adult, and mature adult). Both young and mature adults could oviposit in host larvae. Many parasitoid species oviposit in host insects in one habitat ("host patch") and then forage for nectar and pollen in nearby patches of plants. In our model, we explored the effects of these two processes on parasitoid populations separately and in combination. In particular, we modelled (i) a decline in adult survival with increasing distance of floral resources from the host patch, (ii) a decline in adult reproductive rates, and (iii) the combination of both. We parameterized the
model survival and fecundity rates from life table data we generated for an earlier project in which *Diaeretiella rapae* parasitism of the cabbage aphid *Brevicoryne brassicae* was recorded for 25 days (see Stark et al., 2004 for details). Declines in rates associated with spatial dissociation of floral resources were calibrated using a negative exponential function in accordance with the observations of Tylianakis et al. (2004) (Table 1).

We also considered the effects of patch separation on hyperparasitism pressure on the primary parasitoid larvae/pupae. For this, we posited that increasing distance from the host patch would correlate with either (iv) increased survival or (v) decreased survival for larval stages. The former scenario (iv) corresponds to hyperparasitoid foraging behavior that becomes less effective when adults have to expend more energy to use far-flung floral resources. The latter scenario (v) corresponds to hyperparasitoids that forage for hosts in a more focused, non-systematic way, and increased spatial dissociation of floral resources facilitates their easily finding concentrated areas of primary parasitoid host patches. Both hyperparasitoid scenarios (vi and v) encompassed the combined effects on adult survival and reproductive rates from scenario (iii) above. In our model, then, we incorporated increasing or decreasing larval survival gradients due to hyperparasitism with increasing separation of floral resources and the host patch to implicitly model the two different hyperparasitoid scenarios. Similar to the decline in rates in scenarios (i)-(iii), increasing survival probabilities were calibrated using a positive exponential function, and decreasing survival probabilities were generated using a negative exponential (Table 1). For all model runs, as stipulated by classic host-parasitoid models (e.g. Nicholson and Bailey 1935), we assumed that parasitoids are not egg-limited.

### 2.3. Simulations

For each scenario listed above, we conducted matrix multiplications until the population vector reached a stable age distribution, at which time we solved for $\lambda$, the population growth rate. We then compared growth rates among the different scenarios (i – v) as a means of determining the relative importance of direct and indirect effects of spatial dissociation of floral resources from hosts on primary parasitoids. We also calculated elasticity values for survival and reproductive rates for our projection matrix (Morris and Doak 2002). Calculating elasticities for a matrix model allows us to determine the relative influence of each life history parameter value (survival and fecundity) input into the model on population growth outcomes.

In the current application of our model, this provides a means of assessing the importance of the different influences (e.g. changes in survival and reproduction of adults due to spatial dissociation of floral resources, changes in larval survival due to hyperparasitism) on *D. rapae* growth and survival. To determine elasticities, we measured the proportional change in population growth ($\lambda$) corresponding to a very small (1%) change in each in each vital rate $r_i$ (reproduction and survival rates) while all other parameter values were held constant at their initial (control, or no resource separation) values. We then calculated elasticities by dividing the proportional change in the population growth rate by the corresponding proportional change in the vital rate, for each vital rate respectively. This is equivalent to estimating the slope of the curve generated by plotting each vital rate against its corresponding change in population growth, i.e.
\[ E_i = \frac{\partial \lambda / \lambda}{\partial r_i / r_i} \]  
(Eqn. 2)

where \( E_i \) is the elasticity for a given vital rate \( r_i \) (Morris and Doak 2002).

3. Results

Positive population growth for all distances simulated was shown when adult primary parasitoid survival alone declined (scenario i) with increasing spatial dissociation of floral resources (Figure 1). Declines in adult reproductive output alone (scenario ii) resulted in \( \lambda > 1 \) for all distances except the farthest, whereas the combination of decreasing both adult survival and reproductive (scenario iii) resulted in negative population growth (\( \lambda < 1 \)) for \( d > 1 \) (Figure 1). The elasticity values for adult (young and mature combined) survival (\( E = 0.129 \)) and reproductive output (\( E = 0.29 \)) indicate the relative importance of each of these vital rates for \( D. \) rapae populations (Table 2) and reflect the greater population decline seen for reduced adult reproductive output with increasing spatial dissociation of nectar resources (Figure 1). The elasticity value for larval survival (corresponding to the effects of hyperparasitism) was somewhat smaller than the elasticity value of the combination of adult survival and reproductive output (\( E=0.29 \) vs. \( E=0.418 \), respectively). Overall, the effect of adding hyperparasitism into the mix on the primary parasitoid population differed depending on how resource dissociation altered hyperparasitism behavior. When hyperparasitism pressure increased with increasing dissociation of floral resources (scenario v), it rendered the primary parasitoid population growth negative (\( \lambda < 1 \)) for \( d > 1 \) (Figure 1, “hyperparasitism pressure increases with distance”). However, when hyperparasitism pressure decreased with increasing dissociation of floral resources (scenario iv), \( \lambda \) dropped below one for all distances (Figure 1, “hyperparasitism pressure declines with distance”). Overall then, our model results illustrate the strong but variable effects that hyperparasitism may have on the primary parasitoid population growth rate, either driving the parasitoids to extinction or allowing for some positive population growth, depending on the details of how hyperparasitoids aggregate to primary parasitoid patches.

4. Discussion

The results of our simulation model illustrate the complex relationship that the spatial dissociation of floral resources may have on primary parasitoids, either directly via foraging and reproductive tradeoffs, or indirectly via hyperparasitism – with the outcome depending on the foraging behavior of hyperparasitoids. The results presented here were based on parameter values taken from life tables developed for \( D. \) rapae, but the patterns are likely to hold for other parasitoid species. Field tests explicitly incorporating spatial dissociation distances into experimental designs are critically needed to better understand these multi-trophic interactions.

In our simulations, adding hyperparasitism to reductions in adult survival and reproduction due to spatial dissociation was enough to drive the primary parasitoid population growth below one, even though it had a lower elasticity value than that of the adult survival and reproduction rates combined (Table 2). Furthermore, the addition of hyperparasitism drove the primary parasitoid population growth rate negative (corresponding to \( \lambda < 1 \)) either with very little spatial dissociation of floral resources or only for larger values of spatial dissociation (Figure
1), depending on whether or not the effect on larval survival increased or decreased with increasing spatial separation of resources.

The details of how hyperparasitoids respond to the spatial distribution of floral resources may be critical in determining the overall effects of within-field biological control. Field studies such as one conducted by Holler et al. (1993) have demonstrated that hyperparasitoids can substantially undermine biological control in cereal fields. Other studies have indicated that the influence of hyperparasitoids on primary parasitoids may be quite substantial, depending on their foraging behavior. Hyperparasitoids foraging in a density-dependent fashion may serve as an evolutionary driver for increased patchiness of primary parasitoid distributions across host insect populations as a means of “spreading the risk” (Mackauer and Volkl, 1993). Our simulations suggest that more experiments in which the details of both primary and secondary parasitoid responses to spatial deployment of supplemental resources are needed. Laboratory/field estimates of hyperparasitism rates as a function of spatial dissociation of supplemental resources could give us a better idea of how hyperparasitism interacts with the tradeoffs in primary parasitoid flight energy expenditure and adult survival and fecundity.

Beyond this, lab/field experiments could also generate parameter estimates of survival and fecundity for primary parasitoids facing such tradeoffs.

Landscape structure is recognized as an important determinant for species diversity and population persistence; habitat loss and fragmentation are often implicated in declines in species richness (Fahrig, 2003). The underlying assumption in the majority of these studies is that all resources required for reproduction and population persistence are found within a focal patch, recognizable as a unique landscape element, surrounded by a matrix of no particular value to the species (Haila, 2002). In the case of biological control, spatially separated resources such as those considered in our model could generate a gradient of effects on parasitoid survival and reproduction within one area with differences in vital rates (and ensuing population growth) between the edge and the interior of a crop plot. Recent field studies have highlighted the importance of the landscape matrix and location (edge vs. interior) of host populations on parasitism rates (Cronin 2003); spatial dissociation of essential floral resources could be easily included in future experiments and models of these scenarios.

The interface of foraging behavior and habitat spatial scale may be especially important for hyperparasitoids aggregating to patches of hosts (Chow 2000); Schooler et al. (1996) demonstrated that hymenopteran hyperparasitism on *Aphidius ervi* could be either density-dependent or independent, depending on the size of alfalfa field plots. Hyperparasitoids may accrue greater benefits than their primary parasitoid hosts from extra floral resources, further complicating their influence on population regulation (Araj et al. 2006). Finally, hyperparasitism may affect primary parasitoid population dynamics sufficiently to disrupt biological control of the host (Holler et al. 1993). Details of both hyperparasitoid aggregation behavior and physiology, then, should be included in further models of tri-trophic interactions incorporating dissociation of floral resources and primary parasitoid distributions. Parameter estimation of the effects of primary and secondary parasitoids based on field studies should be a priority; models couched in terms of mathematical inverse problems parameterized with population dynamics stemming from simple census data can provide good estimates of the different effects of landscape treatments on arthropod populations (Adams et al. 2005, Banks et al. 2008).
In conservation biological control, it is imperative that we bring to bear lessons from this larger ecological context. Field studies aimed at linking parasitoid dispersal ability, spatial deployment of floral resources, and parasitism rates are making great progress towards more precise protocols for enhancing CBC (Lavandero et al. 2005). Additionally, more models such as Bianchi and van der Werf’s recent (2004) exploration of the role of non-crop habitats as sources of alternative prey can help guide the design and execution of field experiments aimed at better understanding the mechanisms driving CBC in a landscape context. Because both temporal and spatial separation of resources are important, phenological as well as positional effects need to be considered (Bowie et al. 1995). Several theoretical frameworks, including patch and metapopulation models, can be applied to the issue of how biological control agents use multiple resources distributed temporally and spatially. Work exploring the optimal allocation of time spent foraging for host vs. non-host resources could be expanded to incorporate higher trophic levels (Sirot and Bernstein, 1996; Křivan and Sirot, 1997). Certainly issues such as prey density, predator-predator interactions, natural enemy functional response, and the strength of attractiveness as well as accessibility and nutritional value of floral resources are important to consider in determining parasitoid densities and distributions (Chang and Snyder, 2004; Kean et al., 2003; Rebek et al. 2006; Snyder et al., 2006; Straub and Snyder, 2006). Furthermore, secondary parasitoid host-specificity and the presence of higher-order levels of parasitism may also alter interactions among lower trophic levels (Sullivan 1987). These and other factors should be incorporated into models and experiments in order to further explore the nuances of CBC in a landscape context.

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Table 1. Primary parasitoid parameter values used for matrix model. In each case, the first number is the baseline value (no resource separation effects); values in parentheses correspond to exponential decline in value as a function of increasing distance (d) of floral resource from host patch. Survival probabilities and fecundity rates were based on D. rapae life history data developed in an earlier study (Stark et al. 2004), the second row of values for larva/pupa corresponds to a hypothesized increase in survival with increasing resource spatial dissociation, as a function of hyperparasitoid oviposition behavior. Declines or increases were generated using $y = ke^{-d}$ for $d = \{0, 1, 2, 3\}$ (for declines) or $d = \{0, -1, -2, -3\}$ (for increases) for where $k$ is the baseline value.

<table>
<thead>
<tr>
<th>Life Stage</th>
<th>Fecundity Rates</th>
<th>Survival Probabilities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>N/A</td>
<td>0.9</td>
</tr>
<tr>
<td>Larva/Pupa</td>
<td>N/A</td>
<td>0.9 (0.9, 0.33, 0.12, 0.04)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.9 (0.04, 0.12, 0.33, 0.9)</td>
</tr>
<tr>
<td>Young Adult</td>
<td>7 (7, 2.6, 0.9, 0.3)</td>
<td>0.9 (0.9, 0.33, 0.12, 0.04)</td>
</tr>
<tr>
<td>Mature Adult</td>
<td>6 (6, 2.2, 0.8, 0.3)</td>
<td>0.5 (0.5, 0.18, 0.07, 0.02)</td>
</tr>
</tbody>
</table>

Table 2. Elasticities for primary parasitoid vital rates used in matrix model simulations.

<table>
<thead>
<tr>
<th>Life stage parameter</th>
<th>Elasticity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg survival</td>
<td>0.29</td>
</tr>
<tr>
<td>Larva/Pupa survival</td>
<td>0.29</td>
</tr>
<tr>
<td>Young Adult survival</td>
<td>0.097</td>
</tr>
<tr>
<td>Mature Adult survival</td>
<td>0.032</td>
</tr>
<tr>
<td>Young Adult fecundity</td>
<td>0.193</td>
</tr>
<tr>
<td>Mature Adult fecundity</td>
<td>0.097</td>
</tr>
</tbody>
</table>

Figure 1. Population growth outcomes of separation of floral resources from parasitoid host patch for five different scenarios: (i) adult survival only is affected, (ii) adult fecundity only is affected, (iii) both adult survival and fecundity are affected, (iv) adult survival and reproduction are affected and hyperparasitism exerts an increasingly negative effect on larval survival with increasing resource dissociation, and (v) same scenario as (iv) except hyperparasitoids exert an increasingly positive effect.
effect on larval survival with increasing resource dissociation. Distance “0” represents no spatial separation of resources; distance “3” represents the maximum separation.
Figure

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