

REPORT

The population consequences of natural enemy enhancement, and implications for conservation biological control

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Abstract

We explore models for the management of invertebrate pests by enhancing the efficacy or local abundance of existing natural enemies. Different aspects of natural enemy biology had different effects on prey density. Enhancement of enemy search rate or prey conversion efficiency showed the greatest potential for reducing prey density, while maximum consumption rate by predators, and parasitoid fecundity, had less effect. The effect on prey density of increased natural enemy longevity depended on its interaction with other parameters. The degree of manipulation needed to achieve a given reduction in prey populations was largely determined by the enemy's potential reproductive rate. Spatial "attraction" of enemies to a target site had an almost linear effect on local prey density. We conclude that successful conservation biological control benefits from a directed approach, targeting the most important aspects of natural enemy ecology, and that there is considerable potential for further research in this area.

Keywords

Metapopulation, modelling, parasitism, predation.

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INTRODUCTION

Many pest populations may be managed by enhancing the performance and local abundance of the existing community of natural enemies, a practice which has been termed "conservation biological control" (Barbosa 1998; Pickett & Bugg 1998; Letourneau & Altieri 1999; Landis *et al.* 2000). As practised, it is perhaps the oldest and most widespread form of biological pest control, with roots in the many traditional cultural practices which influence the distribution and abundance of natural enemies in crops. However, there is still relatively little theory underlying the practice.

Conservation biological control is an application of food web dynamics (Polis & Winemiller 1996), but it also represents a gap in the theory. Many insect predators and parasitoids exhibit life history omnivory, so that provision of supplementary plant foods may enhance the local abundance or performance of natural enemies and improve top-down control of pests (Polis & Strong 1996). While population models have been used to examine the effects of allochthonous (externally-derived) subsidies on communities (Huxel & McCann 1998; Callaway & Hastings 2002), in these systems it is typically the lower trophic levels (plants or

herbivores) which receive subsidies. Conservation biological control, on the other hand, is concerned with the effects of subsidies for predators and parasitoids. In addition, food web studies are primarily motivated by broad-scale ecological issues such as the relationships between complexity, stability, and resilience of communities. Similarly, work on intraguild predation has focussed on stability and coexistence of predators (Polis *et al.* 1989; Holt & Polis 1997), with very few empirical and theoretical studies addressing the effects on prey (Rosenheim *et al.* 1995). While this and other work supports the general basis for conservation biological control (Gurr *et al.* 2003), it is of limited use in its tactical application, and there has been little work to date using quantitative population dynamics to optimise practice.

We address this lack of quantitative guidance by analysing simple enemy-prey population models in the context of conservation biological control, and in particular the role of resource subsidies. Such subsidies, in the form of pollen or nectar, can enhance components of natural enemy performance in a range of laboratory and field situations. Predators and parasitoids subsidized in this way may show increased longevity (e.g. Dyer & Landis 1996; Heimpel *et al.* 1997; Jacob & Evans 2000; Johanowicz & Mitchell 2000;

Sagarra *et al.* 2001) and higher fecundity (e.g. Jervis *et al.* 1993; Wheeler 1996), while the female-biased sex ratio of parasitoid offspring may be increased (e.g. Berndt *et al.* 2002). In addition, resource subsidies can affect the spatial distribution of natural enemies in and around crops (e.g. Thomas *et al.* 1992; Liang & Huang 1994).

The demonstrated potential of conservation biological control has often resulted in the adoption of a “shotgun” approach characterized by mass planting of a wide range of flowering species in the expectation that there will be some net benefit to pest management (Gurr *et al.* 2003). More directed strategies that incorporate morphological/physiological compatibility of flower and natural enemy species are likely to increase the chances of success, and also minimize the risk of adverse effects. For example, provision of inappropriate resource subsidies may actually increase pest damage by diverting natural enemies from carnivory (e.g. Cottrell & Yeargan 1998), by enhancing higher-order predators or hyper-parasitoids (e.g. Stephens *et al.* 1998), or by benefiting the pest itself (e.g. Baggen & Gurr 1998). Such risks highlight the need for a solid underpinning of ecological theory to guide conservation biological control practice.

In this paper, our aim, therefore, is to uncover some general principles as a starting point for further theory development, and to form a basis for targeted experiments in the field and laboratory. We focus on insect pests of productive sectors, since these systems are perhaps the best studied and most amenable to management. First, we examine the degree to which natural enemy performance must be enhanced, and what aspects of enemy biology should be targeted to increase the likelihood of successfully managing invertebrate pests. Second, we explore the effects of spatial attraction of natural enemies to target areas for pest control. Ultimately, we hope that such analyses will lead to more directed management and greater success of conservation biological control in the field.

MODELS

Natural enemy enhancement: basic population model

We begin with a simple model for the change in a prey population, N , and its dominant natural enemy, P , through time, t . Although a suite of natural enemies is typically present, for ease of interpretation we model only the dominant one; the milder prey regulation resulting from secondary enemies might be considered as helping to determine K , the prey carrying capacity. Note that the quantity P refers to the population of natural enemies that actually attacks the prey, so for parasitoids this will be only the females. We assume that prey and enemy populations have overlapping generations, which is appropriate for a range of pests such as aphids and mites. As conservation

biological control is practised on systems where pests may be abundant, we include the potential for prey self-limitation governed by the logistic equation. Additionally, we assume that enemy attack follows a saturating functional response, in this case using Holling’s Type 2 function (Holling 1959). Although generalist predators are typically modelled using a Type 3 functional response, they tend to show a Type 2 response with their preferred prey (Hassell 1978).

Given these assumptions, the model is

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \frac{afPN}{f + aN}, \quad (1a)$$

$$\frac{dP}{dt} = \frac{cafPN}{f + aN} - \frac{P}{g}, \quad (1b)$$

where r is the prey intrinsic rate of increase, K is the prey equilibrium in the absence of predation (the prey “carrying capacity”), a is the search rate of natural enemies, f is the maximum consumption rate, c determines the number of enemies recruited per prey attack, and g is mean duration of the attacking enemy life stage. It is useful to define two further parameters: the maximum number of attacks possible in an enemy’s lifetime, F , given by fg , and the total area searched by an average enemy over its lifetime, \mathcal{A} , given by ag (Table 1).

The Type 2 functional response captures the effect of prey abundance on enemy attack rate. When prey are rare ($N \rightarrow 0$) then the attack rate of natural enemies is limited by a , their searching efficiency. When prey are abundant ($N \rightarrow \infty$), however, the attack rate is constrained by f , the maximum rate at which attacks may be processed. The maximum number of attacks possible in an enemy’s lifetime, $F = fg$, will be determined in part by the effect of any handling time associated with attacks (Holling 1959), but for parasitoids may depend largely on their available egg load (Barlow & Wratten 1996; Getz & Mills 1996).

Natural enemy attraction: metapopulation model

Gurr *et al.* (2003) conducted a simple modelling analysis of conservation biological control, including a parameter for

Table 1 Default model parameter values

Parameter	Unit	Predator	Parasitoid
r , prey rate of increase	day ⁻¹	0.2	0.2
K , prey carrying capacity	m ⁻²	5000	5000
g , enemy longevity	days	50	5
c , conversion efficiency		0.01	0.1
f , maximum attack rate	day ⁻¹	10	10
F , maximum total attacks		500	50
a , search rate	m ² day ⁻¹	0.001	0.001
\mathcal{A} , lifetime search area	m ²	0.05	0.005

net immigration of enemies. Here we adopt a more robust approach by actually simulating pest and enemy populations across a spatial arrangement of crop sites. A square coupled map lattice of seven by seven local populations was used, with local dynamics governed by the basic model (eqns 1a and 1b). Hosts and enemies were assumed to emigrate to the surrounding eight locations at rates μ_N and μ_P respectively, and lattice boundaries were assumed to be “reflecting”, so that dispersers bounce back from the lattice edges (Comins *et al.* 1992). Conservation biological control was simulated in the central lattice square by reducing the rate of enemy emigration from that site by a multiplying factor $1 - \varepsilon$, where $0 \leq \varepsilon \leq 1$. Normal emigration is simulated by $\varepsilon = 0$, while $\varepsilon = 1$ means that enemies do not emigrate at all from the conservation biological control area. Thus, ε is a measure of natural enemy “attraction” to an area in which conservation biological control is practised, where the attraction arises from reduced emigration rather than increased immigration.

Special care was taken when formulating the metapopulation model, as realistic simulation of dispersal in continuous time is problematic. Heedless mathematical treatment of unrealistically small dispersal densities may lead to conclusions, which are biologically unreasonable (Mollison 1991). Several alternatives are available for avoiding such mathematical artefacts (Kean 1999), and we resolved this potential problem in the following way. First, dispersal was implemented daily, a coarser time scale than for the local population dynamics which were integrated numerically using the fourth-order Runge-Kutta technique (a particularly accurate method for simulating continuous processes, see Kreyszig 1988) on a 15-min time step. Second, local populations of host and enemy were initialized at the equilibrium densities suggested by the basic non-spatial model, thereby avoiding unrealistically small local population sizes during transient dynamics. Third, any quantities $<10^{-3}$ were rounded down to zero, including local populations and cohorts of dispersers. In practice, such rounding was seldom required since the former precautions ensured that unrealistically small quantities arose only very rarely in the simulations conducted.

Default parameter values

Default model parameter values (Table 1) were chosen to be representative of the types of field populations to which conservation biological control is usefully applied. The host parameters were modelled on a typical pest aphid (Dixon 1998), with an intrinsic rate of increase $r = 0.2 \text{ day}^{-1}$ and carrying capacity $K = 5000 \text{ m}^{-2}$ leaf area. Different parameter sets are appropriate for predators and parasitoids. Predators such as coccinellids (ladybirds/ladybugs) and syrphids (hoverflies) are typically longer-lived than parasitoids (g greater), and may attack more prey (F greater), but generally

have greater consumption requirements (c lower). Hypothetical but realistic parameter values, based on a range of studies in the literature, are $g = 50$ days, $F = 500$, and $c = 0.01$ for predators, and $g = 5$ days, $F = 50$, and $c = 0.1$ for parasitoids. The default search rate, $a = 0.001 \text{ day}^{-1}$, is assumed to be the same for predators and parasitoids; this value is lower than those typically measured in simplified laboratory systems (Hassell 1981) which tend to overestimate field values (Weidenmann & O’Neil 1991).

RESULTS

Equilibrium solutions

The model results are presented only in terms of the equilibrium solutions, since these give the long-term average outcomes that might be expected, i.e. the densities towards which prey and enemy populations will tend. In practice, simulation of realistic scenarios suggested relatively brief (<1 year) transient dynamics, even from extreme initial densities. By dealing with the equilibrium outcomes we also minimize the effects of any temporal assumptions implicit in the models, such as the effectively instantaneous conversion of attacked prey into searching enemies.

The equilibrium prey and enemy populations, N_{eq} and P_{eq} were obtained by solving the model equations when $dN/dt = dP/dt = 0$, yielding

$$N_{\text{eq}} = \frac{f}{a(\mathcal{R}_g - 1)}, \quad (2a)$$

$$P_{\text{eq}} = r \left(\frac{1}{a} + \frac{N_{\text{eq}}}{f} \right) \left(1 - \frac{N_{\text{eq}}}{K} \right). \quad (2b)$$

The parameter combination \mathcal{R}_g represents the enemy’s net reproductive rate in the presence of unlimited prey, and we denote this quantity R_p . Similarly, the combination f/a gives the “half-saturation density” for the enemy, i.e. the host density at which enemy attacks occur at half their maximum rate. The host equilibrium, therefore, is determined by the enemy’s half-saturation density, f/a , divided by the amount that its potential reproductive rate exceeds unity, $R_p - 1$. From eqn 2b, coexistence of prey and enemy requires $P_{\text{eq}} > 0$ and therefore $N_{\text{eq}} < K$.

Using the methods of Rosenzweig & MacArthur (1963), the stability of the model equilibrium can be shown to depend on two conditions. First, persistence of the natural enemy population requires $R_p > 1$; in other words, the enemy population must be able to increase when prey are abundant. Second, stability requires that $N_{\text{eq}}/K > 1/(R_p + 1)$, implying that intraspecific competition between prey (determined by the proximity of their populations to the carrying capacity) is sufficient to prevent their escaping control by the natural enemy population.

The default parameter values suggest a stable equilibrium with $N_{eq} = 2500 \text{ m}^{-2}$ for prey and $P_{eq} = 125 \text{ m}^{-2}$ for either predator or parasitoid. This equilibrium prey density is equivalent to half the prey carrying capacity; such suppression is unlikely to be economically adequate for many pests, suggesting our default systems may be good candidates for conservation biological control.

The model can help guide conservation biological control practice by suggesting the effort required to achieve a particular target reduction in pest density. Using a prime (') to indicate a new value, we define q as the required proportional reduction in prey density, $q = 1 - N'_{eq}/N_{eq}$, which is analogous to the host suppression measure used by classical biological control theorists (e.g. Beddington *et al.* 1978). This expression, together with eqn 2a, can then be used to calculate the proportional change in a particular natural enemy parameter that would be required to reduce the prey equilibrium to N'_{eq} . Similarly, the maximum host suppression possible by enhancing one aspect of natural enemy biology is found by making the appropriate parameter value very large in eqn 2a. These results are shown in Table 2. For example, the formulae in Table 2 suggest that to achieve a 20% reduction in equilibrium prey density ($q = 0.2$) using a natural enemy for which the default predator parameters apply ($R_p = 5.0$) would require a 20% increase in recruitment efficiency ϵ , or a 25% increase in search rate a . This target cannot be achieved by manipulating enemy attack rate f or fecundity F alone.

Effects of enemy longevity

The effects of enemy longevity, g , on the equilibrium prey population are complicated by the fact that it may also affect search and attack rates. For example, if a parasitoid is egg-limited in the field (e.g. Heimpel *et al.* 1998) then increasing its longevity would have little effect on how many prey are attacked. Similarly, the provision of floral resources may increase enemy longevity, but the effect might actually be less prey suppression if enemy search rate declines as it spends time exploiting the floral resources. If F is defined as $f\bar{g}$, the maximum number of attacks possible by an enemy,

and A is defined as ag , the area searched by an enemy in its lifetime, then the effect of enemy longevity on the equilibrium prey population now depends on which aspect of the enemy's biology is independent of longevity: f or F , and a or A .

For example, if search rate, a , and maximum attack rate, f , are independent of longevity (case 1; Table 2, Fig. 1), then increased longevity leads to a greater lifetime search area and more attacks. This results in the equilibrium prey abundance, given by eqn 2a, decreasing towards zero with increasing enemy longevity (Fig. 1). A second case arises if a and F are constant, so that increased enemy longevity leads to greater lifetime search area but decreased potential attack rate (case 2; Table 2, Fig. 1), giving $N_{eq} = F/(ag(cF - 1))$. For the default parameter values, this result is very similar to

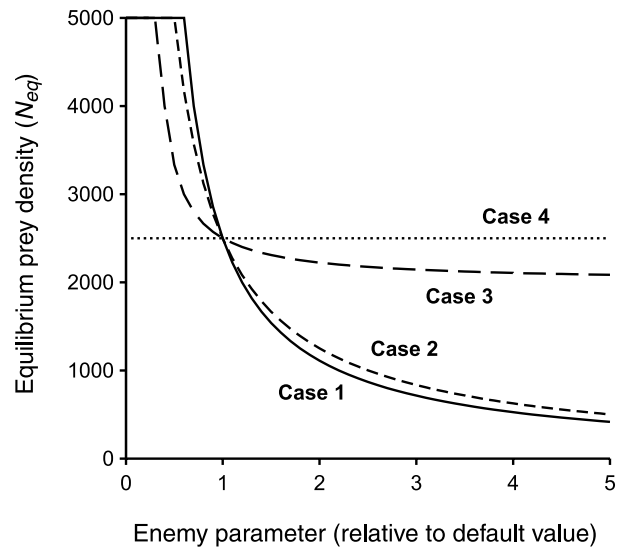


Figure 1 Effects of natural enemy parameters on equilibrium host density, given default predator or parasitoid parameter values. The different lines refer to the parameter which is adjusted: case 1 shows the results for ϵ , or g if a and f are constant; case 2 applies to a or A , or g if a and F are constant; case 3 applies to f or F , or g if A and f are constant; case 4 applies for g if A and F are constant (see text and Table 2).

Table 2 Model solutions for the proportional increase in natural enemy parameter values required to achieve a q proportional reduction in equilibrium prey population, N_{eq} , and the minimum prey density, which may be achieved. Note that natural enemy persistence requires that $R_p > 1$, and stability requires that $RP > K/N_{eq} - 1$

Case	Natural enemy parameter	Prop. increase required for q prop. reduction in N_{eq}	Minimum N_{eq} possible
1	ϵ , or g if a and f unaffected	$\frac{q(R_p-1)}{(1-q)R_p}$	$\rightarrow 0$
2	a or A , or g if a and F unaffected	$\frac{q}{1-q}$	$\rightarrow 0$
3	f or F , or g if A and f unaffected	$\frac{q(R_p-1)}{1-qR_p}, q \leq \frac{1}{R_p}$	$\rightarrow \frac{1}{F\bar{g}}$
4	g if A and F unaffected	∞ (no reduction possible)	$\frac{F\bar{g}}{A(R_p-1)}$

the previous case, suggesting that the main benefit in terms of reduced prey density arises through longevity's affect on search area rather than potential attacks. This conclusion is supported by the third case, when enemy longevity allows more attacks, but in the same total area, so that A and f are constant (case 3; Table 2, Fig. 1) and $N_{\text{eq}} = fg/(A(cf - 1))$. Here, prey abundance approaches $1/Ac$ as enemy longevity increases, which is a smaller suppression than that possible if lifetime search area increases with longevity (cases 1 and 2), although the difference may be negligible if either A or c are very large. Finally, equilibrium host abundance, $N_{\text{eq}} = F/(A(cF - 1))$, is unaffected by enemy longevity if neither lifetime search area, A , nor maximum total attacks, F , are affected (case 4; Table 2, Fig. 1).

To manage prey abundance by manipulating natural enemy longevity, therefore, it is important to know how enemy searching and attack potentials vary over the lifespan of the enemy. For example, if a parasitoid tends to search and deposit its eggs all within the early stages of adulthood, then neither total search area nor the maximum potential number of attacks are likely to be affected by increasing enemy longevity (case 4; Table 2, Fig. 1) and there will be little affect on prey abundance. On the other hand, if increasing enemy longevity increases the potential number of attacks but not the total search area covered (case 3; Table 2, Fig. 1), then enabling enemies to live longer will have some, but limited, potential to reduce prey density. Greater prey reduction is possible by enhancing enemy longevity when this allows them to search further in their lifetime (cases 1 and 2; Table 2, Fig. 1). The model quantifies the effects, and suggests that increasing enemy longevity via resource subsidies is most successful at reducing prey density when it increases lifetime search area rather than total potential attacks.

Effects of enemy recruitment efficiency and search rate

The recruitment efficiency parameter, ϵ , represents the mean number of enemies recruited from each prey attacked, or the inverse of the number of prey needed to mature and sustain an adult natural enemy. Therefore, the value for ϵ will be closely related to the relative body sizes of prey and enemy (Yodzis & Innes 1992). For parasitoids, only female adults attack the prey, so ϵ must take into account the sex ratio of parasitoid offspring. Nevertheless, ϵ will typically be greater for parasitoids than for predators since the former generally require only a single host for development, and for gregarious parasitoids ϵ might conceivably be greater than 1. The effect of recruitment efficiency on prey equilibrium is the same as for longevity under case 1 (Table 2; Fig. 1). Prey equilibrium is relatively sensitive to ϵ (Fig. 1), and enhancing ϵ has the potential to substantially reduce prey populations.

Similarly, changes in search rate or total search area (case 2) has substantial effects on equilibrium prey density.

Effects of enemy fecundity

The basic model suggests that prey population size is relatively less sensitive to the maximum attack rate of enemies (Fig. 1). Even as the attack rate, or parasitoid fecundity, becomes very large, equilibrium prey density cannot be suppressed to a value $< 1/Ac$ (Table 2), although this may be close to zero if Ac is large. We investigated the effects of enemy fecundity in more detail, using a parasitism model featuring explicit egg loads of

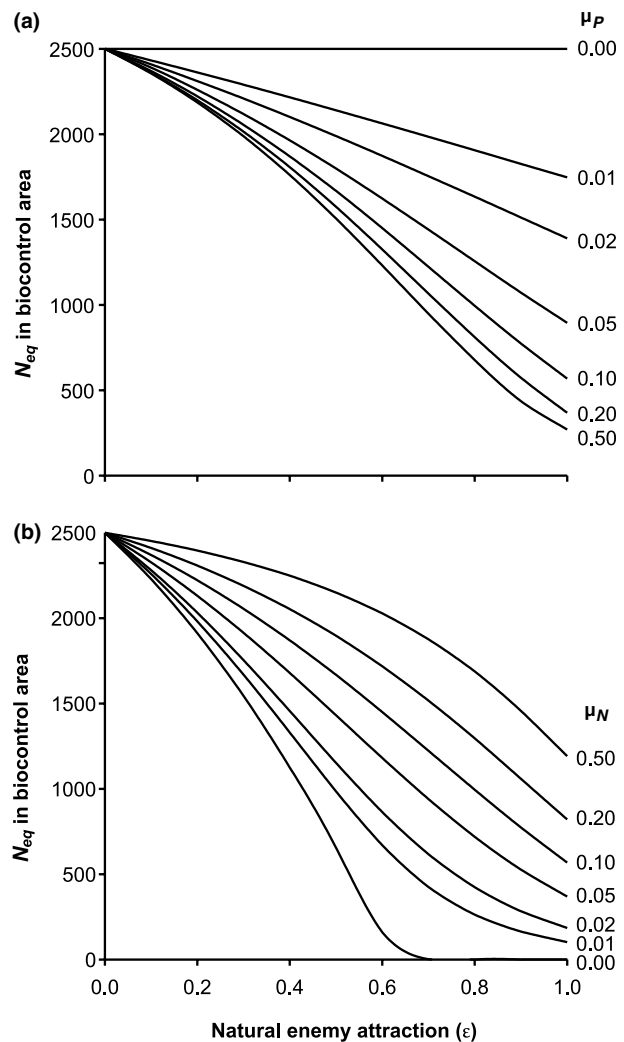


Figure 2 Effects of reduced natural enemy emigration (i.e. increased attraction to a managed site) on local pest equilibrium density in the metapopulation model. (a) Prey dispersal rate $\mu_N = 0.1 \text{ day}^{-1}$ and contours for different values of the natural enemy dispersal rate, μ_P (b) $\mu_P = 0.1 \text{ day}^{-1}$ and contours shown for μ_N .

female parasitoids (Shea *et al.* 1996, model 2). Here, the egg load of maturing parasitoids was assigned according to contrasting scenarios: (1) all parasitoid recruits being endowed with exactly F eggs (i.e. zero variance in egg load), or (2) egg loads uniformly distributed from 0 to $2F$ across parasitoid recruits (i.e. high variance). In the former case, the model suggested that egg load affects equilibrium prey density only if the egg load was relatively close to that required for parasitoids to persist in the system. Hence, increasing parasitoid fecundity had little effect on prey density except when egg load was close to that required for parasitoid persistence. For the second, high variance scenario, however, equilibrium host density was more sensitive to increases in parasitoid fecundity, although the same maximum potential suppression of prey was possible.

Effects of natural enemy attraction

The metapopulation model suggested how equilibrium prey density is affected by natural enemy ‘‘attraction’’ (arising through reduced emigration) to a local site. Enemy attraction reduced prey densities to the greatest extent when enemy dispersal rate was high (Fig. 2a) or prey dispersal rate was low (Fig. 2b). Interestingly, the effects on prey density of a range of natural enemy attraction levels was fairly linear, suggesting that a particular management strategy which attracts enemies twice as much as another should result in approximately twice as much reduction in prey density. Importantly, any prey reduction resulting from natural enemy attraction was largely restricted to the attractive site. The net drain of enemies into the biological control area resulted in slightly elevated prey densities in immediately surrounding areas, although this effect was very small compared to the prey reduction achieved in the attractive area.

DISCUSSION

Natural enemies may be used as tools to manage pest populations in two ways: by attracting natural enemies to a site, thereby boosting their local populations and the impact that they have on pests; and by enhancing the performance of existing natural enemies in terms of their fecundity, longevity, search ability, and conversion efficiency. One management technique which is receiving increased research attention (Landis *et al.* 2000) is the provision of floral foods (nectar and pollen) for use by predators and parasitoids. The modelling analysis suggests that such practices can have different effects on pest density depending on how the particular subsidy affects the dominant natural enemy. Perhaps the most fundamental and immediate effect of resource subsidies is to attract natural enemies from surrounding areas, resulting in increased local enemy abundance through increased tenure time and reduced

emigration (Harmon *et al.* 2000). The metapopulation model suggests that this might cause a substantial reduction in local prey density, especially if the natural enemy has high mobility relative to that of its prey, as is often the case. Although the results suggest an approximately linear relationship between natural enemy attraction and the resulting prey equilibrium, the model assumed that attraction results solely from suppressing emigration, and any increase in immigration due to attractive sensory cues was ignored. Therefore, the results are likely to be conservative. Natural enemy attraction is likely to be the most useful mechanism for conservation biological control in ephemeral crops such as wheat and rice, since the effects arising from enhanced enemy performance may take longer to be fully realized. In such situations, a complementary modelling approach may be more appropriate, focusing on the effects of conservation biological control on the rate of increase of pests (e.g. Wilby & Thomas 2002).

In terms of natural enemy performance, perhaps the most useful conclusion from the modelling presented here is that the success of a conservation biological control program may depend largely on the potential reproductive rate, R_p , of the target natural enemy. This quantity measures how many adult female offspring may be produced by each female natural enemy in the presence of unlimited prey, and is very closely related to the ‘‘maximum growth rate’’ which Hochberg (2000) showed is a useful parameter for managing parasitoid populations for conservation purposes. As a composite parameter, R_p may be relatively easily estimated from appropriate laboratory or field studies, without the need to estimate longevity, fecundity, and conversion efficiency explicitly. In the simple systems captured by the modelling, R_p may then be used to set management goals using the formulae of Table 2. For example, for a natural enemy with $R_p = 4$ and a constant search rate and total fecundity, Table 2 suggests that a 20% reduction in prey density will require a 19% increase in conversion rate (which includes sex ratio for parasitoids), a 25% increase in enemy longevity, or a 300% increase in enemy fecundity (i.e. maximum potential attacks). On the other hand, a slower-growing natural enemy with $R_p = 2$ would require a 12.5% increase in conversion rate, a 25% increase in enemy longevity, or a 33% increase in fecundity to achieve the same 20% reduction in prey. Such results could be used as benchmarks to guide conservation biological control practice, perhaps by helping to determine the composition, total area, and spatial arrangement of floral resources planted around or within a target crop. A particular question for further research to address is whether the formulae for success listed in Table 2 differ significantly for models which incorporate more realistic biological details such as stage structure (e.g. Wilby & Thomas 2002),

and therefore whether our conclusions stand up as “rules of thumb” for guiding conservation biological control practices.

The model suggests that the greatest proportional prey reduction arises from enhancing the conversion efficiency of enemies, which may be possible if resource subsidies affect the female-biased sex ratio of parasitoid offspring (e.g. Berndt *et al.* 2002). The second most influential enemy parameter is its searching ability, which might be manipulated if resource subsidies allowed enemies to spend a greater proportion of their available time actively searching. Natural enemy fecundity, or attack potential, appears to be readily manipulated by resource subsidies (e.g. Jervis *et al.* 1993; Wheeler 1996; Berndt *et al.* 2002), but the model suggests that this has relatively less potential to reduce prey density except when conversion efficiency and search ability are non-limiting. This might help to explain why Lane *et al.* (1999) found no significant correlation between parasitoid fecundity and the success of classical biological control programmes. The modelling highlights that the natural enemy parameters that are the easiest to manipulate in the laboratory or field may not necessarily be those that have the greatest effect on pest density, although it should also be noted that these effects may be of secondary importance if the main effect of management is on spatial attraction of natural enemies. In practice, the most useful management options will depend on the specific characteristics of the targeted natural enemy, together with the degree to which each of its attributes may be affected by management. For example, although the fecundity of a parasitoid may have less influence on prey density than its searching ability, its egg load may be far more amenable to enhancement by conservation biological control practices. Such detailed information, especially on searching ability, might be most readily obtained using video technology (Wratten 1994), although the more general principles based on R_p may be sufficient for effectively managing many systems.

In order to derive simple, general conclusions about the population dynamics of natural enemy enhancement we have used a simple, general approach to the modelling. Further work should explore some of the complexities inherent in real systems. For example, we have assumed a tight coupling between a single prey species and its dominant natural enemy, while field systems may contain several important enemies attacking a range of prey species. Likewise, we assume that the effects of seasonality, stochasticity, and age structure are negligible, and that model equilibrium solutions provide a reasonable indication of the prey population densities to be expected. In the field, the situation may be more complicated. For example, equilibrium solutions may suggest that conservation biological control is ineffective under normal field conditions, yet it might prove invaluable during exceptional seasons or

during occasional prey outbreaks. We have explored the effects of direct manipulation of specific natural enemy characteristics, but in reality the mechanisms for such changes are likely to affect more than one aspect of enemy or prey ecology. Further modelling and field experiments are needed to address these issues, and the simplified and relatively well-studied communities typical of classical or inundative biological control systems may be particularly well suited for experiments in conservation biological control.

It is becoming clear that successful conservation biological control will require a more directed approach than is typically practised (Gurr *et al.* 2003). Conservation biological control should be conducted in such a way as to target those aspects of the dominant enemy's biology, which are likely to have the greatest effect on prey density. Where greater knowledge of pest life history is available it may also be possible to target specific phenological stages. For example, Phillips *et al.* (1998) suggested that a specialist parasitoid might cause greater suppression of its host, a pest weevil, if parasitoid longevity could be increased in early summer when a critical cohort of weevils encloses. This is a case where classical biological control might benefit from targeted conservation biological control (i.e. “integrated biological control”, Gurr & Wratten 1999). Similarly, a better understanding of how predator and parasitoid characteristics affect prey populations may help us to choose more effective agents for classical or inundative biological control, and to better understand the ways in which natural food webs operate.

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