Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management

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Summary

1. Establishing biological control agents in the field is a major step in any classical biocontrol programme, yet there are few general guidelines to help the practitioner decide what factors might enhance the establishment of such agents.

2. A stochastic dynamic programming (SDP) approach, linked to a metapopulation model, was used to find optimal release strategies (number and size of releases), given constraints on time and the number of biocontrol agents available. By modelling within a decision-making framework we derived rules of thumb that will enable biocontrol workers to choose between management options, depending on the current state of the system.

3. When there are few well-established sites, making a few large releases is the optimal strategy. For other states of the system, the optimal strategy ranges from a few large releases, through a mixed strategy (a variety of release sizes), to many small releases, as the probability of establishment of smaller inocula increases.

4. Given that the probability of establishment is rarely a known entity, we also strongly recommend a mixed strategy in the early stages of a release programme, to accelerate learning and improve the chances of finding the optimal approach.

Key-words: biological control agent establishment, decision theory, metapopulation model, optimization, population invasion.

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Introduction

Biological control is one of a number of approaches that have been used to mitigate or control the negative impacts of pests and weeds. Biological control involves introducing natural enemies, biocontrol agents, to help reduce the harmful impact of a pest. It is a relatively benign method of pest control (Waage & Mills 1992), although there are concerns about non-target effects (Simberloff & Stiling 1996; Louda *et al.* 1997).

Unfortunately, as is frequently acknowledged, we are far from being able to predict whether introductions of a species will succeed (Elton 1958; Crawley 1986; Drake *et al.* 1989; Kareiva 1996; Rejmánek &

Richardson 1996; Williamson 1996). Certainly there seems to be little general theory to help the practitioner decide what factors might assist the establishment of biocontrol agents, although some guidelines do exist (Memmott *et al.* 1996). The establishment failure rates for planned introductions are high. For example, Hall & Ehler (1979) and Stiling (1990) estimated success rates of approximately 35% for biocontrol agents released to control insect pests, and Julien, Kerr & Chan (1984) estimated that approximately 59% of exotic agent introductions for weeds established successfully. It would be extremely useful to have robust rules of thumb for those who need to make decisions in the face of this uncertainty.

Biological control practitioners typically have a limited number of individual agents with which they hope to found populations in as many places as possible as quickly as possible (Memmott *et al.* 1996). The central question we ask here is: What size and

number of populations should be released to maximize the overall chance of success? For example, if there are 1000 insects available for release, and some number of populations need to be established in the next few years, should 100 be released at each of 10 sites, or 10 at each of 100 sites? Or should some other strategy be used? There is evidence that larger releases establish more successfully (Hopper & Roush 1993; Memmott, Fowler & Hill 1998), but releasing all available agents at only one site runs the risk of complete failure as a result of one catastrophic event (Memmott *et al.* 1996). This important dilemma has rarely been addressed in the literature (but see Grevstad 1996; Memmott *et al.* 1996; Memmott, Fowler & Hill 1998). In this paper we bring decision theory to bear upon the problem.

Ecological theory provides a foundation for applied population biologists, but it is not couched within a decision-making framework. Decision theory allows managers to attempt to maximize the benefits of their actions. By working within such a framework we can develop a theory of applied population biology that enables us to choose between options. The process involves a number of stages. First, there must be a clear statement of the objective. Next, the management options must be listed. The system and its dynamics, including any constraints, are then described. Even as a verbal exercise this approach is immensely useful. When couched in the precise language of mathematics, and coupled with numerical decision-making tools, it becomes an even more powerful tool.

Stochastic dynamic programming (SDP) is a formal mathematical approach to decision theory. It is a mathematical programming algorithm for solving complex, stochastic, state-dependent optimization problems, that are, in general, impossible to analyse and understand within a purely analytic framework. It has a long history of use in economics and engineering (Bellman 1957; Intriligator 1971) and, with advances in computing technology, is being used more and more in the study of population level problems (Clark 1990; Possingham 1996). SDP is invaluable in comparing alternative management plans, based on both environmental and economic costs and benefits (Watt 1968; Walters & Hilborn 1978; Kennedy 1981, 1986). It is becoming more common in the field of conservation (Maguire 1986; Ralls & Starfield 1995; Possingham 1997) and has been used in pest and weed control (Watt 1963; Shoemaker 1982; Plant & Mangel 1987; Pandey & Medd 1991; J. Moore & H. P. Possingham, unpublished data), fisheries (Walters 1978, 1986; Hilborn & Walters 1992) and wildlife management (Reed 1974; Anderson 1975; Milner-Gulland 1997; Possingham & Tuck 1998).

The work we present here uses a rigorous SDP approach to calculate the optimal strategy set, and hence to generate rules of thumb for the practitioner trying to establish a biological control agent in the field. In addition it indicates which aspects of the biology of the agent it is most important to understand well, in order to enhance the chance of successful establishment.

Methods

The full model involves applying SDP to a stochastic metapopulation model. The model was developed to help choose the release strategy (how many insects released at how many sites) that will maximize the establishment of as many populations of the agent as possible in up to P sites, by some terminal time T, with only N insects available for release each year. The measure of success we use is the number of established sites at the terminal time.

The terminal time, T, reflects time constraints imposed by funding bodies. P reflects limited availability of suitable sites for agent release; such land must be set aside and protected from other forms of control for the duration of the programme. We assume that the practitioner has N insects that have been cultured for release. These insects can be released at empty sites, i.e. sites at which no biocontrol agents are present. We assume that the releases are independent (sites are far enough apart that the populations do not interact) and that all sites are of equal quality from the point of view of the agent (e.g. the pest or weed density is the same at each). We initially allow two types of release, either of small or of large inocula of the agent. For example, $N/10$ insects could be released at 10 sites (all small) or $N/2$ at 2 sites (both large). Alternatively, a mixed strategy could be adopted, where $N/10$ are released at each of 2 sites and $4N/10$ at each of another 2 sites. We discuss the potential benefits of the latter strategy below.

To predict the success of a release, we need a simple model of the dynamics of the population at a site. Assume that a site can be described as being in one of three possible states: an empty site, an insecure site or an established site (Fig. 1). A site is described as empty if the agent is absent. At an insecure site, the agent is present, but the population is small and has a relatively high probability of extinction. At an established site, the agent is well established and is relatively unlikely to go extinct. Furthermore, the population at an established site can be used as a source of other individuals to augment those from the main breeding population in future releases.

STATE TRANSITIONS

Three separate processes are involved in the transitions between these three states. First, there is the
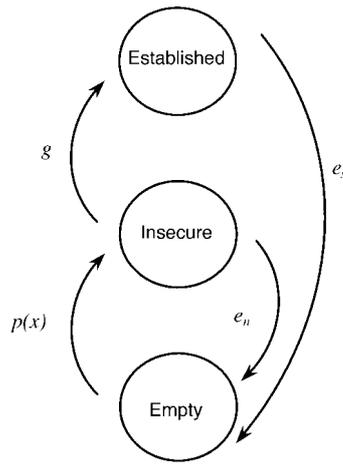
Fig. 1. State transitions in the metapopulation model for an individual site. The system can be in one of three possible states: empty, insecure or established. Transitions between these states can occur due to the processes of colonization ($p(x)$), extinction (e_s and e_n) and growth (g).

process of colonization, in which groups of individual agents released at a site may establish. Given the size of an inoculum (i.e. the number of agents released), x, we assume there is an associated probability of establishment, $p(x)$. If the population does persist, it becomes an insecure site. Secondly, all the populations in the system have some probability of going extinct. Established populations have a lower probability of local extinction, e_s, than insecure populations, e_n. Thirdly, all insecure populations have some probability, g, of growing to become established populations during the course of the next time interval ($g + e_n \leq 1$). The states and transitions between them are described in Fig. 1.

To define the system dynamics we need to define the transition probabilities associated with the three processes of population growth, extinction and colonization. These transition probabilities are then combined to give the overall probability of moving from any state to any other state in one time interval.

TRANSITIONS FROM INSECURE TO ESTABLISHED SITES DUE TO POPULATION GROWTH

The number of established sites can increase as a result of the successful growth of insecure sites. Let $P_g(i,n)$ be the probability that i insecure sites become established sites, given that there were n insecure sites to begin with. Using the definition that g is the probability that each insecure site grows to become an established site, and assuming independence of sites:

$$P_g(i, n) = \binom{n}{i} g^i (1 - g)^{n-i} \qquad \text{eqn 1}$$

where $\binom{x}{y}$ is the binomial coefficient, i.e.

$$\binom{x}{y} = \frac{x!}{y!(x - y)!},$$

which is the number of ways of choosing y successes in x attempts in any order. Note that $i \geq 0$.

LOCAL EXTINCTION

Local extinction reduces the number of established and insecure sites. Let $P_e((i,j),(s,n))$ be the probability that i of s established sites, and j of n insecure sites, go extinct in one time step. Assuming that the extinction events are independent we can calculate that:

$$P_e((i, j), (s, n)) = \binom{s}{i} e_s^i (1 - e_s)^{s-i} \binom{n}{j} e_n^j (1 - e_n)^{n-j}.$$

$$\text{eqn 2}$$

Note that $s \geq i \geq 0$ and $n \geq j \geq 0$.

COLONIZATION

Finally, we need to estimate the state transition probabilities associated with the colonization process, which is the part over which the manager has some control. We define the probability of establishment $p(x)$ of an inoculum of size x by the function:

$$p(x) = p_m (1 - e^{-ax^2})^2 \qquad \text{eqn 3}$$

where p_m is the maximum probability of establishment and a is a constant. This functional form generates a sigmoidal curve (Fig. 2) and represents an increasing probability of establishment with increasing numbers of insects released. It incorporates an upper limit to the probability of establishment (p_m) as well as the possibility of depensation (an Allee effect; Lewis & Kareiva 1993). Depensation arises if there is a greatly reduced probability of establishment at low densities. Biologically, this may arise because mates are hard to find when there are few individuals at the site. The constant a determines the shape of the establishment curve (Fig. 2), with larger values of a shifting the curve to the left and making it steeper.

Assume that we make z_s small releases and z_l large releases, where x_s and x_l are the sizes of the small and large releases, respectively. Let $P_c(i,(s,n))$ be the probability of i successful colonizations given the initial state of the system (s,n). Let j of the new colonizations be due to the z_s small releases, each of which establish with probability $p(x_s)$. Then $(i - j)$ new colonizations are due to the z_l large releases, each of which establishes with probability $p(x_l)$. Assuming that these colonization events are inde-
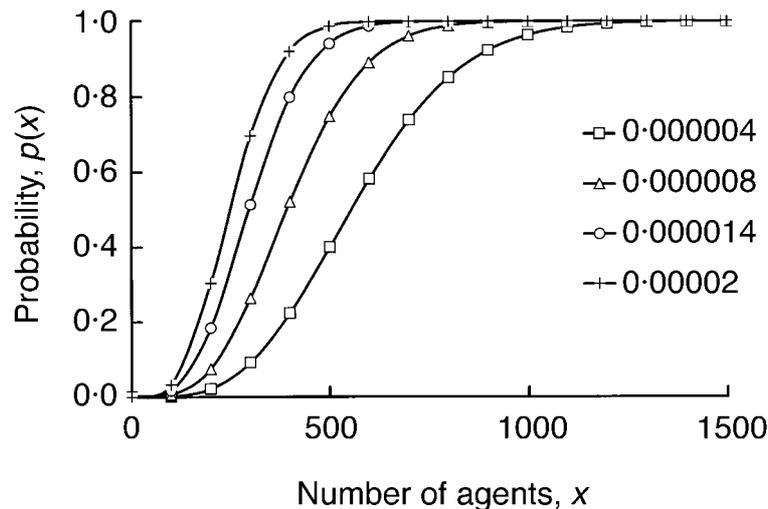
Fig. 2. Probability of establishment curves $p(x)$ for inocula of different sizes, x. The curves are defined by $p(x) = p_m(1 - e^{-ax^2})^2$, and the value of a alters the steepness of the curve.

pendent, and summing over all possible values of j for each i:

$$P_c(i, (s, n)) = \sum_{j=0}^{i} \binom{z_s}{j} p(x_s)^j (1 - p(x_s))^{z_s - j}$$

$$\times \binom{z_l}{i-j} p(x_l)^{(i-j)} (1 - p(x_l))^{z_l - (i-j)}. \qquad \text{eqn 4}$$

Again, $z_s \geq j \geq 0$ and $z_l \geq (i - j) \geq 0$. Note that the total number of releases made is constrained by the number of empty sites available (no releases are made onto sites that are already occupied).

Equations 1, 2 and 4 were used to construct three transition matrices for all transitions between all possible states of the system: a colonization matrix, **C**, an extinction matrix, **E**, and a growth matrix, **G**. All three matrices are square matrices of size $(P + 1) \times (P + 1)$ (as there are P patches, there are $P + 1$ possible occupied states: 0, 1, 2, 3, ... P). We assume that the sequence of events in a year is ordered colonization, extinction and growth, i.e. releases are made, any extinctions that are going to happen do so, and then any extant insecure sites can grow. Thus the overall transition matrix, **T**, for the transition from one year to the next is the product of these three matrices. The time interval is chosen to be 1 year, as this is the usual length of time between sets of releases (for a univoltine insect).

MANAGEMENT STRATEGIES

We now define the possible management strategies more explicitly. Strategy 1 (S1: many small releases) involves releasing $x_s = X/s_s$ insects at $s_s = \min(s_d,$ empty) sites (i.e. s_d sites, or fewer if there are less than s_d empty sites remaining). Strategy 2 is a mixed strategy, incorporating aspects of both strategies 1 and 3, and we return to it in a moment. Strategy 3 (S3: few large releases) involves releasing $x_l = X/l_l$ insects at $l_l = \min(l_d,$ empty) sites (again, with the same caveat if fewer empty sites remain). The parameters s_d and l_d are the default numbers of small and large releases for the strategies, and X is the total number of insects available.

The mixed strategy 2 (S2: mixed) is slightly more complicated. In this case, there will be z_l sites with 'large' inocula and z_s sites with 'small' inocula where:

$$l_m = \min(l_d, \text{empty}) \qquad \text{eqn 5}$$

$$s_m = \min(l_d, \text{empty} - z_l)$$

i.e. the number of 'large' sites is chosen first. Here the strategy is to release 4/10 of the insects available at each of 2 sites, and 1/10 of those available at each of 2 other sites. In other words, the number of insects at small sites is $X/(5 s_m)$, while at large sites $4X/(5 l_m)$ are released.

The number of empty sites is a constraint on the number of releases that can be made. For example, if the small release tactic is 'release $N/5$ insects at each of 5 sites' and there are only four sites empty, then we have a problem. In this work we have defined the number of small sites as the minimum of the default value or the number of empty sites (in this example $s_s = \min(5,4) = 4$ and $X/4$ insects would be released at each site). When there are very few empty sites, s_s and l_l are equal and strategies 1 and 3 are identical. In this case the model has been

defined so that if there are l_d sites or less, the strategy is S3.

PARAMETERS AND ADDITIONAL FUNCTIONS

The parameters used in the baseline scenario are presented in Table 1. The values in this scenario were chosen to provide a reference point representative of a general weed or insect pest control problem. However, all parameters were varied systematically across plausible ranges. This approach covers the realistically possible state space, and ensures the general applicability of our results to a wide range of situations.

In a real system, there is a pay-off to early and successful establishment of well-established sites. This comes as an augmentation of the number of agents available for release, as extra insects can be collected from a well-established site. These extra insects are added to the N available from rearing to increase the total number, X, released. In this study we have used a step function. As soon as we have one established population we have $f(s)$ extra insects available to add to the N we have reared from cultures, i.e.:

$$X = N \text{ if } s = 0 \qquad \text{eqn 6}$$

$$X = N + f(s) \text{ if } s > 0.$$

In the baseline scenario we have set $f(s)$ equal to a constant, reflecting the situation when the cost of visiting extra sites to collect more insects restricts the number of sites visited to 1 (but see later for a relaxation of this assumption).

Now it is necessary to determine the value function, $J_T(s,n)$, after T years, i.e. the value attributed to being in any of the possible states at the end of the release programme. Thus $J_T(s,n)$ is an end condition. Let the value, V, of having s established and n insecure sites (i.e. of being in any state (s,n) of the

system) be:

$$v = \frac{s + \dfrac{n}{4}}{P}, \qquad \text{eqn 7}$$

where P is the number of sites. In this formulation we have attributed a value of $1/P$ to each established site, and each insecure site is worth 25% of that value. We also investigated other possible forms, including step functions and monotonically increasing linear and curvilinear (s-shaped) functions.

MODEL SOLUTION

Finding the optimal solution involves backwards iteration in time (Mangel & Clark 1988). If we know the value of any of our final system states at the end time T, we can calculate the values associated with any state at the previous time interval (the product of the transition probability from that state to a final end state, multiplied by the value of that final state and then summed over all possible final states). This process can then be iterated back from T, through $T - 1$, $T - 2$, to find the optimal strategy set at $t = 0$. Thus for each backward transition, the value function, $J_{t-1}(s,n)$, at time $t-1$ is determined by that at time t by:

$$J_{t-1}(s, n) = \max_{K=1,2,3} \sum_{i=0}^{P} \sum_{j=0}^{P-i} \mathbf{T}_K((s, n)(i, j)) J_t(i, j),$$

$$\text{eqn 8}$$

where $\mathbf{T}_K$ is the transition matrix when you use strategy K ($K = 1,2,3$) (Mangel & Clark 1988).

Results

We used the model to calculate the long-term, steady-state optimal strategy set for the system. The optimal decision set settles down very rapidly, and seems to be largely independent of the time frame, T, over which we wish to establish the agent.

Table 1. Baseline parameters used in the model. In order to generate the results, we varied these parameters systematically across plausible ranges

Parameter	Definition	Baseline value
P	Number of sites under consideration	10
T	Time horizon	5 or 10
N	Total number of insects available from quarantine	1000
e_s	Extinction probability of established sites	0·0
e_n	Extinction probability of insecure sites	0·6
g	Growth probability of insecure sites	0·2
a	Shape parameter in probability of establishment curve, $p(x)$	0·000014
s_d	The default number of small releases	6
l_d	The default number of large releases	2
$f(s)$	Extra insects available for release if at least one established site is established	400
p_m	Maximum probability of establishment of any released inoculum	1·0

However, the best decision clearly depends on the state of the system (i.e. it depends on the number of established and insecure sites; Fig. 3).

We now describe our results, using Fig. 3 to illustrate the important points. Each part of the figure (a, b, c) depicts the optimal strategy set for a parti-
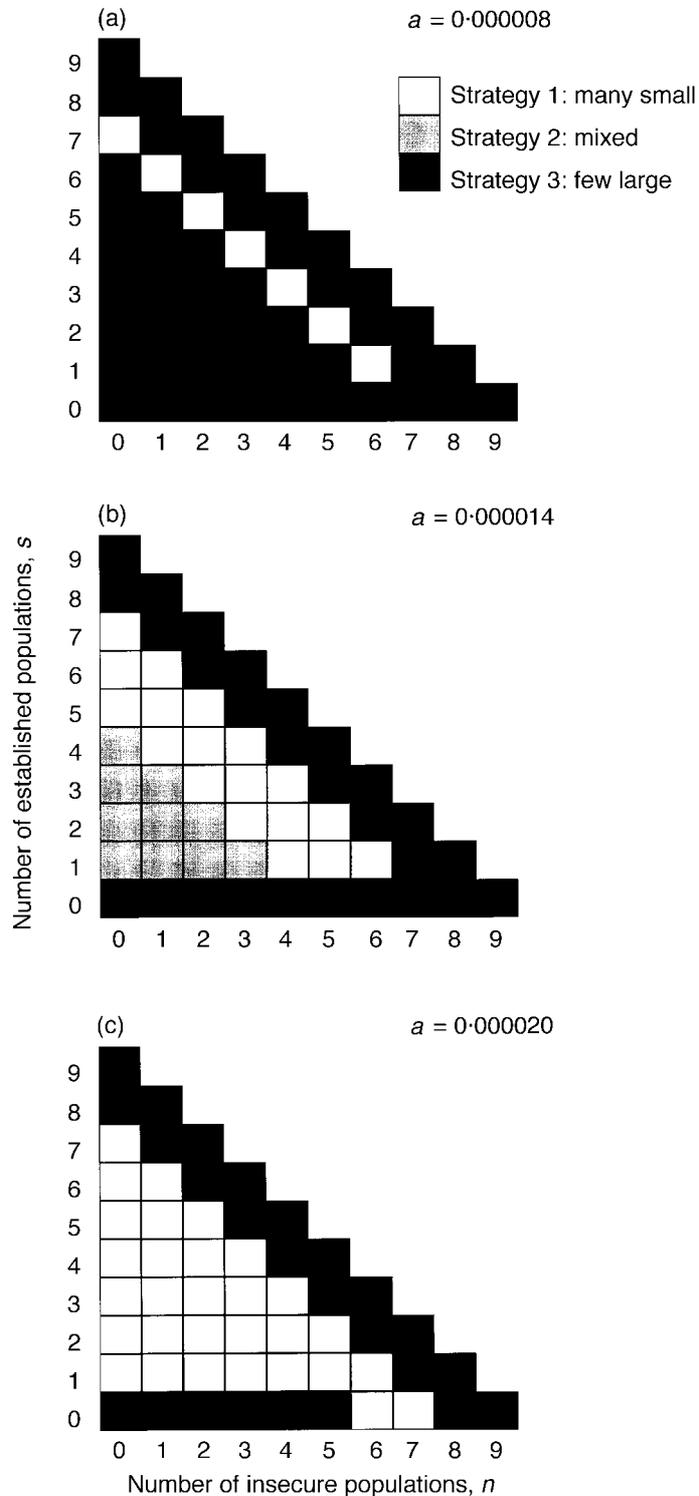

Fig. 3. Optimal strategy sets for a increasing from (a) $a = 0.000008$ to (b) $a = 0.000014$ to (c) $a = 0.000020$. All other parameters are as defined for the baseline scenario (Table 1). Each box represents a possible state of the system, and the key indicates the optimal decision to make for that particular state. Note that when there are no empty sites available, no releases can be made.

cular combination of parameters. Each box represents a possible state of the system, and the key indicates the optimal decision to make for that particular state. For example, in the case when $a = 8 \times 10^{-6}$ (Fig. 3a) the optimal decision for a system in which there are 2 insecure populations and 5 established populations is S1 (many small).

BASELINE SCENARIO

Consider first the baseline scenario (Table 1 and Fig. 3b), which uses parameter values that lie in the middle of the ranges considered. In this case, the optimal strategy is to make a few large releases when the number of established populations is zero, regardless of the number of insecure populations, n. This reflects the benefit to be obtained from having one established population. When the total number of populations (established or insecure) is four or less, then a mixed strategy is optimal. At higher numbers (up to seven) of populated sites, then S1 (many small releases) is best. The fact that S3 (few large) is again optimal when the total number of established and insecure sites is close to P (in this case $P = 10$) reflects the constraint on the system that there are few empty sites available at all. If P is increased, say to $P = 20$, it can be seen that this result is an artefact of the limit on the number of sites available, and would be less likely to arise in a real field situation.

PARAMETERS OF IMPORTANCE IN THE MODEL

As the value of the parameter, a, is changed from its baseline value, the optimal strategy set changes. If a is reduced to 8×10^{-6} (Fig. 3a), then we see that the optimal strategy set for nearly every combination of established and insecure sites is S3; a few large releases. This is because at this value of a, the probability of establishment of small inocula is so small that only larger releases have any chance of establishment. At higher values of a ($a = 2 \times 10^{-5}$; Fig. 3c), however, the probability of establishment of smaller inocula increases sufficiently to make the optimal strategy, in most cases, to release many small inocula. Note, however, that it is still optimal to make fewer, larger releases when there are no well-established sites.

The model indicates that one of the most important considerations for the practitioner is the relationship between inoculum size and probability of establishment. As the parameter a increases, we see a marked shift in the optimal strategy set (Fig. 3a,b,c). It is vital to know the probability of establishment of inocula of different sizes in order to choose the best release strategy for the agents. Clearly, in the initial stages of a release programme

this is not going to be well-defined, and we will return to this point later.

The number of insects available also has a big effect on the optimal strategy choice. This is a related point, as release sizes 'small' and 'large' are relative. For a fixed probability of establishment curve, the number of insects in a release dictates the establishment probability just as much as changing the probability curve does. However, larger releases usually have a higher establishment probability (Memmott *et al.* 1996). The number of extra insects available from established sites also contributes to determining the optimal strategy; if there is a large benefit to having an established site, then there is a greater value to establishing at least one large population early on in the release programme. Thus when there are few or no established sites, the optimal strategy is S3 (Fig. 3a,b,c), but once sites are established, S1 is often better (Fig. 3c). The mixed strategy, which serves as a bet-hedging mechanism (including some of the benefits of having a larger number of releases, with the benefit of having some larger inocula in case of adversity), appears to be a relatively poor choice, appearing only at intermediate values of a (Fig. 3b).

PARAMETERS OF LITTLE OR NO EFFECT

In decision-based modelling, it is also vital to know what is unimportant with respect to the best decision. In this case, other parameters and variables have little or no effect on the optimal strategy. The optimal strategy is a stationary one (using $T = 5$, 10 or 20 generates the same optimal strategy set). Extinction and growth probabilities for established and insecure sites make little difference (the exception being that the mixed strategy is less common at high e_n). We investigated a number of different forms for the value function, V, including step functions and monotonically increasing linear and curvilinear (s-shaped) functions, and none of these made a significant difference to the qualitative trends. In addition, the maximum probability of establishment, p_m (the asymptote in Fig. 2) does not affect the optimal strategy set because this is a linear equation.

The release strategies were defined to be flexible with respect to the number of empty sites available. Thus the number of potential sites for establishment, P, only affects the optimal strategy for certain states near the boundary where very few sites are empty (Fig. 3a; S1 is the optimal strategy). If the number of sites overall is increased, the line of S1s moves out towards that boundary. In a programme with a great many (or infinite) possible release sites, it seems clear that the optimal strategy for all these scenarios would be S3.

How much better is it to use the optimal strategy instead of a fixed one? Comparison of the values of

different terminal states indicates that the optimal strategy can be twice as good as the worst strategy for some states over 5 years. However, the relative benefit does depend on the state of the system, and simulations comparing fixed with variable strategies show that S3 (a few large releases) can often be nearly as good as the optimal strategy.

Discussion

For established populations, there has been some very sophisticated theoretical work addressing the spread of invaders (Okubo 1980; Lewis & Kareiva 1993; Kot, Lewis & van den Driessche 1996), in particular the different modes of spread as embodied in stratified diffusion (Shigesada, Kawasaki & Takeda 1995). There are also a number of theoretical and comparative studies that address the factors affecting small population establishment (Richter-Dyn & Goel 1972; Lande 1988; Pimm, Jones & Diamond 1988; Hopper & Roush 1993; Haccou & Iwasa 1996; Veltman, Nee & Crawley 1996). However, while they provide general insight, none of these directly addresses the management decisions that face biocontrol practitioners. Some recent experimental work has begun to examine and make predictions about optimal establishment for particular species introductions (Grevstad 1996; Memmott *et al.* 1996; Memmott, Fowler & Hill 1998), although there are insufficient studies to be able to draw generalizations. The work we present here complements this experimental approach with an applied theory framework.

The optimal strategy set is most sensitive to the relationship between the probability of establishment and the release sizes (Fig. 3), which indicates that it is very important to have a clear idea about this process (e.g. is there depensation?). Often, such information is not available, although we can see that there are some emergent rules of thumb. For example, it is clear that if there are no well-established sites in the field, the pay-back in extra insects for future releases that is gained from establishing such a site means that a few larger releases should be recommended, rather than many small ones (see the bottom row in Fig. 3a,b,c). However, the importance of knowing the functional form of the establishment probability curve for an agent is paramount for most other states of the system (compare Fig. 3a,b,c). If the shape of this curve is known, then an optimal strategy can be used, but if not, what is a manager to do?

Unfortunately, many practitioners release the same number of agents at all sites, even when they have little or no idea of the likelihood of establishment. If no sites establish, then failure is complete. Not only do no agents establish, but no real information (other than that too few were released!) is

gained. Furthermore, even successful establishment may not be optimal. If there is establishment, who is to say that fewer agents might not have fared just as well? In practice, often if one release size works, the same number of insects is used at every subsequent release with no certainty that opportunities are not being wasted. Given the cost of rearing agents, this can be a waste of resources. Making smaller releases would increase the number of successful releases, and hence the efficiency with which the landscape is provided with control agents.

This observation brings us to an additional motivation for using a mixed rather than a single strategy approach in the initial stages of a release programme. As a bet-hedging tool, the mixed strategy performs relatively poorly for a particular probability of establishment curve; S2 is optimal only over a very narrow range of values of *a* (Fig. 3b). However, the mixed strategy (generating two data points) will allow an unknown curve for $p(x)$ to be defined much more precisely than a single strategy (generating only one data point) will. It is always possible to get single strategies that are better than mixed strategies but, at least initially, these will be unknown. There is tremendous scope for learning about the system by having a spread of initial release sizes. Once the establishment curve has been defined, then future releases can converge on the optimal size.

Such an approach is an example of using active adaptive management; management with a plan for learning about the managed system (Walters 1986; Parma *et al.* 1998). Clearly, there will be a trade-off between learning and achieving the desired result (Mangel & Clark 1988). However, in situations where management actions are to be repeated many times, either in space or in time (e.g. in biocontrol redistribution programmes) then such an approach can be extremely profitable.

Unfortunately, explicitly modelling the learning process is relatively complicated, and has not been included in the model presented here. Modelling learning often involves a Bayesian approach, with each time step allowing the update of prior probabilities by the individual that is making decisions (Stephens & Krebs 1986; Hilborn & Mangel 1997). There are some SDP models that incorporate learning (Walters 1986; Mangel & Clark 1988) but it quickly becomes computationally costly to include (Kennedy 1981; Mangel & Clark 1988). Note that learning requires monitoring, so that if there is a cost associated with monitoring, there may be a downside to many 'small' releases.

There are a number of caveats pertaining to our work. For example, we have assumed that all sites are equally hospitable, but spatial variation in the quality of sites might incline us more to a risk-reducing strategy (more small introductions). The model

is pseudospatial and hence we do not explicitly address the question of how far apart releases should be. Nevertheless, an underlying assumption is that these inocula are released far enough apart that they do not interact with each other. This will obviously depend on the biology of the agent concerned, but it seems likely that the assumption that they do not interact is conservative from the point of view of understanding establishment. In addition, we have not addressed issues of population genetics and the risks of inbreeding in small isolated populations (Lande 1988). Finally, there will always be considerations that are particular to the species in question. These may include choice of safe sites with suitable soil type and climate where the pest is healthy and where there is easy access for redistribution and monitoring. It is also important that the site has low priority for other types of control (a common problem is farmers mowing or spraying weeds where releases have been made).

Finally, we make a plea for more cross-disciplinary interactions between conservationists and pest control workers (Shea *et al.* 1998). The process of biocontrol agent release is analogous to reintroducing a threatened species. If experiments are constrained by the number of available individuals for release in biological control, how much more restricted are conservation efforts? Insights from biocontrol release, and studies of invasive species, can provide guidance to conservationists dealing with rare and endangered species.

MANAGEMENT IMPLICATIONS

We present guidelines that can improve the design and efficiency of biocontrol release programmes. The optimal strategy depends on the success of previous releases and the relationship between inoculum size and probability of establishment. Given the importance of knowing the probability of establishment of inocula of different sizes, we advocate using mixed strategies in the initial stages, in order to facilitate learning. Once this information has been gained, the practitioner can move towards making optimal decisions based on the current state of the system: larger releases when there are few established sites (in order to augment the numbers available for release in future years) or when the probability of establishment of small releases is low; and more, smaller releases at other times.

Acknowledgements

References

Anderson, D.R. (1975) Optimal exploitation strategies for an animal population in a Markovian environment: a theory and an example. *Ecology*, **56**, 1281–1297.

Bellman, R.E. (1957) *Dynamic Programming*. Princeton University Press, Princeton, NJ.

Clark, C.W. (1990) *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*, 2nd edn. Wiley-Interscience, New York, NY.

Crawley, M.J. (1986) The population biology of invaders. *Philosophical Transactions of the Royal Society of London, B*, **314**, 711–731.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. & Williamson, M. (1989) *Biological Invasions: A Global Perspective*. Scientific Committee on Problems of the Environment (SCOPE). Wiley, New York, NY.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.

Grevstad, F. (1996) Establishment of weed control agents under the influences of demographic stochasticity, environmental variability and Allee effects. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds V.C. Moran & J.H. Hoffmann), pp. 261–267. University of Cape Town, Cape Town, South Africa.

Haccou, P. & Iwasa, Y. (1996) Establishment probability in fluctuating environments: a branching process model. *Theoretical Population Biology*, **50**, 254–280.

Hall, R.W. & Ehler, L.E. (1979) Rate of establishment of natural enemies in classical biological control. *Bulletin of the Entomological Society of America*, **25**, 280–282.

Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.

Hilborn, R. & Walters, C.J. (1992) *Quantitative Fisheries Stochastic Assessment: Choice, Dynamics and Uncertainty*. Chapman & Hall, New York, NY.

Hopper, K.R. & Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology*, **18**, 321–331.

Intriligator, M.D. (1971) *Mathematical Optimisation and Economic Theory*. Prentice Hall, Englewood Cliffs, NJ.

Julien, M.H., Kerr, J.D. & Chan, R.R. (1984) Biological control of weeds: an evaluation. *Protection Ecology*, **7**, 3–25.

Kareiva, P. (1996) Developing a predictive ecology for non-indigenous species and ecological invasions. *Ecology*, **77**, 1651–1652.

Kennedy, J.O.S. (1981) Applications of dynamic programming to agriculture, forestry and fisheries: review and prognosis. *Review of Marketing and Agricultural Economics*, **49**, 141–173.

Kennedy, J.O.S. (1986) *Dynamic Programming: Applications to Agriculture and Natural Resources*. Elsevier, London, UK.

Kot, M., Lewis, M.A. & van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.

Lande, R. (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.

Lewis, M.A. & Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, **43**, 141–158.

Louda, S.M., Kendall, D., Connor, J. & Simberloff, D. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science*, **277**, 1088–1090.

Maguire, L.A. (1986) Using decision analysis to manage endangered species populations. *Journal of Environmental Management*, **22**, 345–360.

Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ.

Memmott, J., Fowler, S.V., Harman, H.M. & Hayes, L.M. (1996) How best to release a biological control agent. *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds V.C. Moran & J.H. Hoffmann), pp. 291–296. University of Cape Town, Cape Town, South Africa.

Memmott, J., Fowler, S.V. & Hill, R.L. (1998) The effect of release size on the probability of establishment of biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. *Biocontrol Science and Technology*, **8**, 103–115.

Milner-Gulland, E.J. (1997) A stochastic dynamic programming model for the management of the saiga antelope. *Ecological Applications*, **7**, 130–142.

Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York, NY.

Pandey, S. & Medd, R.W. (1991) A stochastic dynamic programming framework for weed control decision making: an application to *Avena fatua* L. *Agricultural Economics*, **6**, 115–128.

Parma, A.M., Amarasekare, P., Mangel, M., Moore, J., Murdoch, W.W., Noonburg, E., Pascual, M.A., Possingham, H.P., Shea, K., Wilcox, C. & Yu, D. (1998) What can adaptive management do for our fish, forests, food and biodiversity? *Integrative Biology, Issues, News and Reviews*, **1**, 16–26.

Pimm, S.L., Jones, H.L. & Diamond, J. (1988) On the risk of extinction. *American Naturalist*, **132**, 757–785.

Plant, R.E. & Mangel, M. (1987) Modeling and simulation in agricultural pest management. *SIAM Review*, **29**, 235–262.

Possingham, H.P. (1996) Decision theory and biodiversity management: how to manage a metapopulation. *Frontiers of Population Ecology* (eds R.B. Floyd, A.W. Sheppard & P.J. De Barro), pp. 391–398. CSIRO Publishing, Melbourne, Australia.

Possingham, H.P. (1997) State-dependent decision analysis for conservation biology. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems and Biodiversity* (eds S.T.A. Pickett, R.S. Ostfeld, M.S. Shachak & G.E. Likens), pp. 289–304. Chapman & Hall, New York, NY.

Possingham, H.P. & Tuck, G. (1998) Fire management strategies that minimise the probability of population extinction for early and mid-successional species. *Statistics in Ecology and Environmental Monitoring* (eds D. Fletcher, L. Kavaliers & B.J.F. Manly), pp. 157–167. University of Otago Press, Dunedin, New Zealand.

Ralls, K. & Starfield, A.M. (1995) Choosing a management strategy: two structural decision-making methods for evaluating the predictions of stochastic simulation models. *Conservation Biology*, **9**, 175–181.

Reed, W.J. (1974) A stochastic model for the economic management of a renewable animal resource. *Mathematical Biosciences*, **22**, 313–337.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Richter-Dyn, N. & Goel, N.S. (1972) On the extinction of a colonizing species. *Theoretical Population Biology*, **3**, 406–433.

Shea, K., Amarasekare, P., Kareiva, P., Mangel, M., Moore, J., Murdoch, W.W., Noonburg, E., Parma, A.M., Pascual, M.A., Possingham, H.P., Wilcox, C. & Yu, D. (1998) Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution*, **13**, 371–375.

Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modeling stratified diffusion in biological invasions. *American Naturalist*, **146**, 229–251.

Shoemaker, C.A. (1982) Optimal integrated control of univoltine pest populations with age structure. *Operations Research*, **30**, 40–61.

Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology*, **77**, 1965–1974.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, NJ.

Stiling, P. (1990) Calculating the establishment rates of parasitoids in classical biological control. *American Entomologist*, **36**, 225–282.

Veltman, C.J., Nee, S. & Crawley, M.J. (1996) Correlates of introduction success in exotic New Zealand birds. *American Naturalist*, **147**, 542–557.

Waage, J.K. & Mills, N.J. (1992) Biological control. *Natural Enemies: The Population Biology of Predators, Parasites and Diseases* (ed. M.J. Crawley), pp. 412–430. Blackwell Scientific Publications, Oxford, UK.

Walters, C.J. (1978) Some dynamic applications in fisheries management. *Dynamic Programming and its Applications* (ed. M.L. Puterman), pp. 233–246. Academic Press, New York, NY.

Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Macmillan, New York, NY.

Walters, C.J. & Hilborn, R. (1978) Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics*, **9**, 157–188.

Watt, K.E.F. (1963) Dynamic programming, 'look ahead programming', and the strategy of insect pest control. *Canadian Entomologist*, **95**, 525–536.

Watt, K.E.F. (1968) *Ecology and Resource Management*. McGraw-Hill, New York, NY.

Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London, UK.