Decision theory and biodiversity management: How to manage a metapopulation

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ABSTRACT

An objective of nature conservation is to manage threatened species so that their chance of extinction is minimised. This paper explores the application of Markov decision theory as a tool to choosing between management options for a threatened species. Specifically, the problem of minimising the extinction probability of a metapopulation is considered. A presence–absence stochastic metapopulation model is used to model the dynamics of the population. The two management options considered are to make a new patch of habitat, or to reintroduce the species to a suitable but empty patch. The best strategy employed will depend on the current state of the metapopulation. This management problem is an illustration of the application of decision theory to making optimal state-dependent decisions for conservation in an uncertain environment. If applied conservation biology is to be successful it is essential that more conservation theory within an explicit decision-making framework is developed.

Key words: Markov decision theory, metapopulation dynamics, conservation biology, biodiversity management

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Introduction

Many ecological theories and concepts, e.g. island biogeography theory, metapopulation theory, theories of coexistence, and the notion of a minimum viable population size, have been developed to help us make decisions in applied nature conservation. Generally these theories are not particularly useful because they are not enclosed within a management framework. Most existing theories only indicate which management strategies are useful, without enabling those strategies to be ranked. For example island biogeography tells us that big patches of suitable habitat are better than small patches, and corridors linking habitat patches are useful. However, island biogeography theory does not indicate how to trade off reserve size with connectedness, that is, should a revegetation program concentrate on making corridors between patches or on increasing the size of existing patches.

Where time and money are limited, it is vital to choose the best management options within the constraints of those resources. To help managers achieve the best result with the resources available, existing theories of population ecology need to be merged with decision theory tools. This union of decision theory and ecological theory can lead to a theory of applied conservation management. This paper gives one example of how that union can occur.

Over the past decade there has been increasing interest in modelling the dynamics of spatially structured populations. One class of ideas and models used to understand the dynamics of populations that are not spatially homogeneous is metapopulation theory (Hanski 1991; Verboom *et al.* 1991; Mangel and Tier 1993; Adler and Nuernberger 1994; Hanski 1994). Metapopulations are made up of a number of local populations. The simplest kind of metapopulation model follows the dynamics of the number of patches that are occupied, ignoring local population dynamics (Levins 1969). In this case the two processes of local extinction and colonisation drive the dynamics of the metapopulation (Fig. 1). This is often referred to as a presence–absence metapopulation model and is the kind of metapopulation model used in this paper (Richter-Dyn and Goel 1972).

This paper explores the application of Markov decision theory to decision making in applied nature conservation (Intriligator 1971), in particular the optimal management of a metapopulation. Using decision theory tools in nature conservation is not new, but it is rare (Maguire 1986; Ralls and

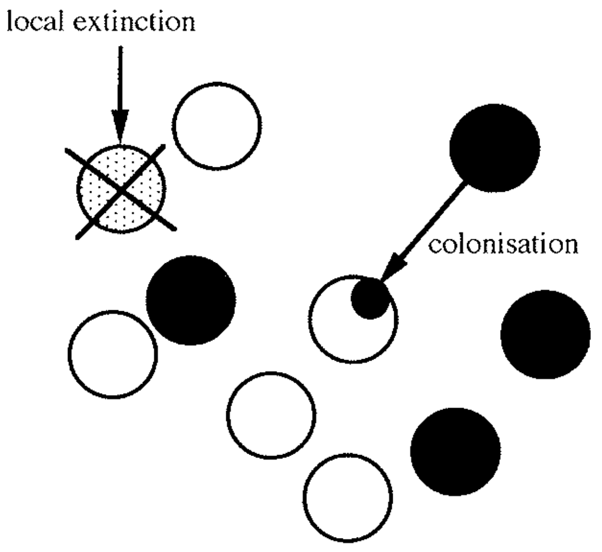

Fig. 1. A schematic diagram of a metapopulation in which the species is either present in (●), or absent from (O), a patch. The dynamics of the metapopulation is driven by the extinction and colonisation processes.

Starfield 1995). Moore (1990) outlined a process where Markov decision theory could be used to manage vegetation succession, representing the only application of this tool to nature conservation.

In this example the objective is to minimise the likelihood of extinction of the metapopulation, the standard objective in applied threatened-species management (Burgman *et al.* 1993). Two real management options for minimising the likelihood of metapopulation extinction are to make more patches of suitable habitat or reintroduce the species to suitable empty patches. I show how Markov decision theory can be used to choose between these two management options and enable optimal management decisions to be made in an uncertain environment. Hopefully, this paper will be a step towards accepting the utility of these methods.

Model

Solving a management problem using Markov decision theory (Intriligator 1971) has two parts. First the stochastic dynamics of the system are modelled, in this case the dynamics of a metapopulation. This is the simplest stochastic metapopulation model possible – a presence-absence model that is not spatially explicit. Second is the decision theory, where the stochastic dynamic programming equations need to be formulated and rewards defined for the outcome of the management.

The metapopulation model

It will be assumed that the interest is in a metapopulation where all the patches are identical and it is equally likely that colonisation of a patch occurs from any occupied patch. This type of non-spatial model has been used widely to explore aspects of metapopulation dynamics (Levins 1969; Richter-Dyn and Goel 1972) and although it is somewhat unrealistic the lack of a formal spatial structure may be relatively unimportant. It will also be assumed that patches are either occupied or unoccupied. A presence–absence model like this ignores the possibility that different patches may contain different numbers of individuals – however where local population dynamics operate rapidly on the time scale of the extinction/colonisation processes that determine the dynamics of metapopulations this is a reasonable simplification (Hanski and Thomas 1994).

A discrete time and discrete state space stochastic model is used for this sort of metapopulation. In any time step (henceforth referred to as years) our state variables will be the number of occupied patches, i, and the number of suitable patches, m, which may be occupied or unoccupied. The total number of patches that could be occupied is not constant, because we allow for the possibility of creating suitable new habitat. This variation in the number of suitable patches is not normally incorporated into metapopulation models. Each year any patch that is unoccupied may be colonised, and any patch that is occupied may experience a local extinction and become unoccupied. Without loss of generality, it is also assumed that the annual sequence of events is colonisation followed by extinction. The following equations describe the dynamics of this metapopulation in the absence of management.

Let β be the per patch colonisation rate – namely the probability that an empty patch is colonised by one of the occupied patches. The probability that an empty patch is colonised in one year is then

$$c = 1 - (1 - \beta)^i \, . \tag{1}$$

Let e be the probability that an occupied patch becomes unoccupied in one year, that is the local population extinction rate. It is also assumed that the probability of local extinction is independent of the state of the other patches, such that there is no rescue effect (Hanski and Gyllenberg 1993).

For a system with a constant number of patches, m, the state of the system at a particular time is simply the probability there are i full patches at time t, denoted as $p_i(t)$. To determine the probability of moving from one state to another, let A be the transition matrix that defines the probability of going from one state to another in each year so that

$$p(t+1)=p(t)A \ , \tag{2}$$

where $\mathbf{p}(t)$ is the vector describing the probability of being in any state, with components $p_i(t)$ as defined above. The elements of A; $a_{ij}(m)$ are the probabilities of moving from i occupied patches to j occupied patches in one year, assuming there are m suitable patches in the system. The equation for the transition probabilities in terms of the colonisation and extinction parameters is

$$a_{ij}(m)=\sum_{k=0}^{m-i}\binom{m-i}{k}c^{k}(1-c)^{m-i-k}\binom{i+k}{i+k-j}e^{i+k-j}(1-e)^{j}$$
$$\mathit{for} \quad i+k-j\geq 0 \, . \tag{3}$$

The stochastic metapopulation dynamics are fully described by Eqns 2 and 3. The probability of being in any state at some future time, given an initial state, can be calculated by iterating Eqn 2.

Dynamic programming equations

The objective of Markov decision theory is to determine the state-dependent optimal decision for controlling a stochastic process. To use this method the 'pay-off' values for achieving a certain state of the system need to be defined. Also, the management options need to be described mathematically, and the dynamic programming equation needs to be defined. In this example the pay-off will be 1 if the population persists (is not extinct) and 0 otherwise. The optimal management strategy is found by back-stepping through time, choosing the optimal decision for each year assuming that subsequent decisions are made optimally.

At any year a value is assigned to being in a particular state. Let $J_t(i,m)$ be the value of being in state (i,m) at time t (i of the m patches occupied). To find the value of being in that state, values first need to be given to the state of the system at some terminal time T at which success is measured. If the metapopulation survives to year T the value is 1, and 0 otherwise, so

$$J_T(0,m)=0$$
$$J_T(i,m)=1 \quad \mathit{for} \ 0<i\leq m \, . \tag{4}$$

To calculate the optimal strategy for the penultimate time, T–1, the value of being in state (i,m) is expressed in terms of the value of being in state (i,m) at the terminal time T, weighted by the chance of moving to each of those future states. This enables the best strategy for the penultimate time to be chosen and hence the value of each state at the penultimate time. The process is iterated backwards through time using the general equation relating present value to future value

$$J_T(i,m)=r\sum_{j=0}^{m}a_{i+1j}(m)J_{t+1}(j,m)+(1-r)\sum_{j=0}^{m+1}a_{ij}(m+1)J_{t+1}(j,m) \ , \tag{5}$$

where r = 1 if a reintroduction is done and r = 0 if a new patch is made instead. It is assumed that reintroductions and patch construction are always successful and they have equal cost because only one or the other can be done in a single year. The first summation term in Eqn 5 is the expected value of being in state (i,m) in year t if we chose to reintroduce the species to an empty patch, while the second summation term is the expected value of being in state (i,m) in year t if we chose to make a new patch. Equation 5 requires two logical restrictions. The number of patches occupied after a colonisation cannot be more than the number of suitable patches m, and the total number of suitable patches after a patch is created, m + 1, cannot be more than n, a ceiling set on the number of suitable patches that can exist.

From Eqn 5 the value of r that maximises $J_t(i,m)$ for every year and state (i,m) can be found. Because we are interested in a long-term optimal strategy, that is a strategy that minimises the long-term extinction probability, the process was backstepped to a terminal time $T = 100$. All the results presented here are 'equilibrium' optimal strategies, that is they are the strategies that maximise long-term persistence of the metapopulation. The results are found numerically because the Monte Carlo simulation is not required.

Results

First a particular example is examined in detail, before considering the consequences of worse environmental conditions on the optimal decision. Unless otherwise stated there is a maximum of 12 patches ($n = 12$), the final time step being $T = 100$, the per patch extinction probability is $e = 0.2$, and the patch colonisation rate parameter is $\beta = 0.05$.

Figure 2 displays the optimal strategy choice for the baseline parameter choice. All the possible combinations of total patch number, and number of patches occupied, are shown with an r indicating that the optimal strategy is to do a reintroduction, otherwise the optimal strategy is to make a new patch. By thinking about the problem some of the results can be quickly explained. When $m = 12$ no more patches can be made so the optimal strategy will always be to reintroduce the species. When $i = m$ (the leading diagonal of the results diagram), all the patches are occupied, reintroduction is not possible, and the optimal strategy is to make a new patch. When $i = m = 12$ neither strategy is possible. In between these extremes either strategy is possible. In general the reintroduction strategy is optimal when the number of occupied patches is small or the fraction of occupied patches is low.

Besides considering the optimal strategy at a particular time it is useful to follow a likely trajectory of strategies. Consider a specific circumstance, say with $m = 5$ and $i = 4$. Then the optimal strategy is to begin by making a new patch, forcing $m = 6$. The number of patches can only increase so, in the absence of extinction the state of the system will inevitably move to the right (more patches). Whether the number of occupied patches increases or decreases depends on chance. Consequently a management scenario for a particular population will generally involve both strategies in the short

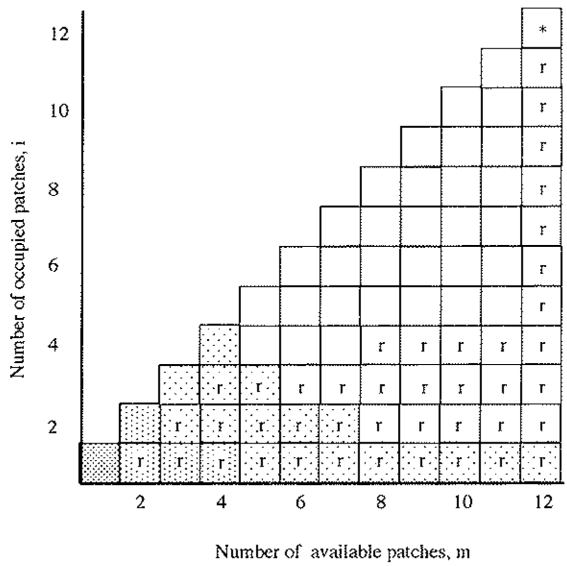

Fig. 2 The optimal strategy for the baseline example: $n = 12$, $e = 0.2$, $\beta = 0.05$ and $T = 100$. States in which the optimal strategy is to reintroduce the species to an empty patch are indicated with an r, otherwise the best strategy is to make a new patch (except for the state (12,12) where neither strategy is possible). The shading indicates the probability of extinction within the next 100 years if the population starts in that state and assuming we continue to make optimal decisions. Darker shading is an indication of a higher likelihood of extinction.

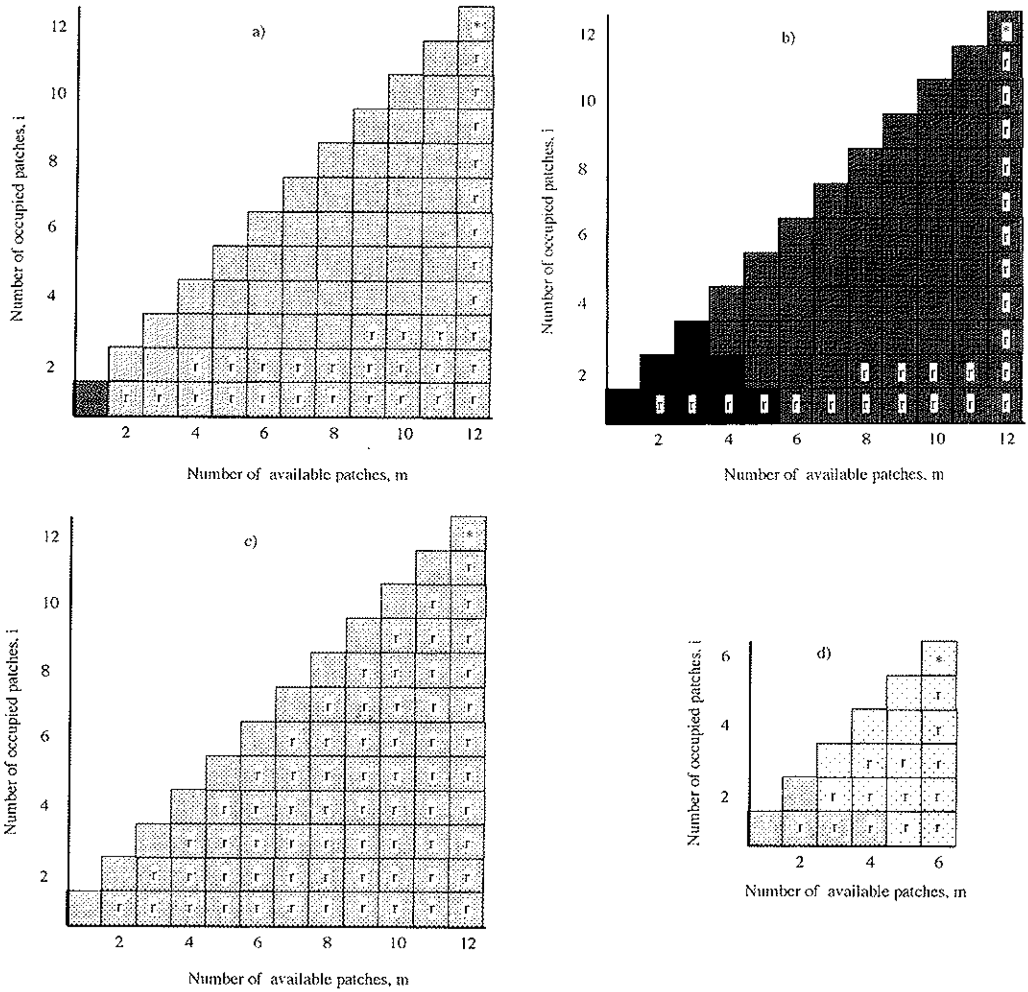

Fig. 3. Optimal strategies for a range of environments that are worse than the baseline case: a) $e = 0.3$, the per patch extinction rate is higher, b) $e = 0.4$, a further increase in extinction rate, c) $\beta = 0$, no natural colonisations and d) $n = 6$, a maximum of only six patches. As with Fig. 2, darker shading is an indication of a higher likelihood of extinction.

term, with the patch construction option becoming less frequent as time passes until the only available strategy is to do repeated reintroductions.

The long-term extinction probability increases as we move down (fewer occupied patches) and to the left (fewer suitable patches). This is indicated by the darker shading in the lower left corner of Fig. 2.

Figure 3 shows the response of the optimal strategy to worse environmental conditions. If the extinction rate increases, reintroductions become a less favoured option. At the highest extinction rate (Fig. 3b), it is only profitable to do a reintroduction when one or two of the patches are occupied, otherwise it is best to make a new patch if possible. Under these circumstances the extinction rate is high and the best chance for the population to persist for a substantial period is if there are many patches. Note that making more patches is a long-term strategy.

Another way of making the environment worse for the metapopulation is to allow no natural colonisations by setting $\beta = 0$. In the absence of management this would mean that the metapopulation is doomed. However, because we can artificially colonise patches, the metapopulation has a reasonable chance of persisting over 100 years. In this case a worse environment means reintroduction is generally the best option, the reverse effect to increasing the extinction rate. Finally the environment can be made worse in the model by halving the maximum number of patches that can be made (reducing n, see Fig. 3d). Although extinction rates increase slightly, the optimal strategy remains virtually unchanged. When the maximum number of patches is doubled to $n = 24$ the optimal strategy also remains unchanged.

Discussion

These brief examples show that it is difficult to make generalisations about what is the best management strategy. No simple rules were derived by exploring numerous examples. Every situation needs to be modelled to find the best management policy.

The example presented here can be extended in several ways. Reintroductions are rarely assured, and it is possible to associate a risk of failure with either the reintroduction or patch construction strategy. It is also possible to relax the assumption that only one action can be done in a single year. We could allow for several reintroductions and/or patch constructions. This example explored the trade-off between only two management options. There are other options that can be modelled, for example, a temporary reduction in the extinction rate (reflecting say predator control) or an increase in the colonisation rate by corridor construction. We can even include an explicit monetary budget, where the project receives income and that money can be used for different strategies including saving.

There are many possible extensions to the existing model. Day and Possingham (1996) explore a metapopulation model with explicit spatial structure. Optimal strategies for this sort of model could be determined for specific cases using their model coupled to the Markov decision theory process outlined here. Greater realism could be added to our example in many ways. For example, it is possible to make the reintroduction process uncertain, allow more than one reintroduction, put a time delay on our ability to create a new patch, and allow suitable patches to become unsuitable with a certain probability.

Markov decision theory enables explicit decisions to be made about management of a metapopulation that depend on the current state of the metapopulation. An enormous number of different problems can be explored in the Markov decision theory framework. The most profitable paths for future research will involve specific examples (e.g. Morton this volume pp. xx) and searches for generalisations and rules of thumb that provide robust solutions in most situations.

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