

## A Stochastic Metapopulation Model with Variability in Patch Size and Position

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### ABSTRACT

Analytically tractable metapopulation models usually assume that every patch is identical, which limits their application to real metapopulations. We describe a new single species model of metapopulation dynamics that allows variation in patch size and position. The state of the metapopulation is defined by the presence or absence of the species in each patch. For a system of  $n$  patches, this gives  $2^n$  possible states. We show how to construct and analyse a matrix describing transitions between all possible states by first constructing separate extinction and colonisation matrices. We illustrate the model's application to metapopulations by considering an example of malleefowl, *Leipoa ocellata*, in southern Australia, and calculate extinction probabilities and quasi-stationary distributions. We investigate the relative importance of modelling the particular arrangement of patches and the variation in patch sizes for this metapopulation and we use the model to examine the effects of further habitat loss on extinction probabilities.

### 1. INTRODUCTION

There has been much recent interest in incorporating spatial structure into models of population dynamics (Pulliam, 1988; Howe *et al.*, 1991; Verboom *et al.*, 1991a; Verboom *et al.*, 1991b; Mangel and Tier, 1993; Adler and Nuernberger, 1994). Traditionally, population models make the restrictive assumption that populations are well mixed and have no spatial structure. These assumptions imply that interaction between any two individuals in the population is equally likely. One method for incorporating spatial structure is to use the concept of a metapopulation (Andrewartha and Birch, 1954; den Boer, 1968), which allows the chance of interaction between individuals to vary according to their relative location.

A metapopulation refers to a population inhabiting a collection of discrete patches (Levins, 1969; Hanski, 1991). Each patch is homogeneous and contains a local population in which individuals mix freely. The extinction of local populations and the recolonisation of empty patches are key features of metapopulation dynamics. Many metapopulation models, including both stochastic and deterministic models, rely on the assumption that the system comprises either an infinite or a very large number of identical patches (MacArthur and Wilson, 1967; Levins, 1969; Richter-Dyn and Goel, 1972; Nisbet and Gurney, 1982; Chesson, 1984; Woolhouse, 1988; Hanski, 1991; Hastings, 1991; Gotelli and Kelley, 1993; Hanski and Gyllenberg, 1993). This assumption simplifies mathematical analyses, but such models may miss properties of species restricted to small numbers of patches.

It is important to be able to explore the effect of the relative size and spatial position of patches. Variation in the size and quality of patches (Pulliam, 1988; Howe *et al.*, 1991) and variation due to different spatial arrangements of patches will have different effects on population dynamics (Doak *et al.*, 1992; Holt, 1992; Adler and Nuernberger, 1994). Previous attempts to model these aspects of metapopulation dynamics have relied largely on Monte Carlo simulations (Boyce, 1992; Burgman *et al.*, 1993; Hanski and Thomas, 1994; Possingham *et al.*, 1994). Other approaches incorporating some form of heterogeneous spatial structure use an array of interlocking cells (Pulliam *et al.*, 1992; Perry and Gonzalez-Andujar, 1993). These detailed models also involve simulation, especially if they include stochastic effects. Hanski (1994a; 1994b) looks at presence-absence data for metapopulations and uses this to estimate probabilities of patch extinction and recolonisation. From these probabilities, he uses simulation to predict the future state of a metapopulation.

Other authors develop and analyse dynamic metapopulation models which incorporate variation in patch sizes without resorting to simulation. Anderson (1991) considers a stochastic continuous time metapopulation model which explicitly models the size of each local population in a collection of variable sized patches. To ensure analytical tractability, Anderson's model does not include density dependence. Hanski and Gyllenberg (1993) allow continuous variation in

patch size using a partial differential equation model. Cantrell and Cosner (1994) look at the effects of patch size and geometry in a biogeographic context.

Akçakaya and Ginzburg (1991) formulate a presence-absence transition matrix metapopulation model with distinct local extinction and recolonisation phases. They give details of this model for a two patch metapopulation and look at the effects of environmental correlation of local extinctions in a three patch metapopulation. Gyllenberg and Silvestrov (1994) also present a stochastic presence-absence model which allows variation in patch size and spatial location of each patch. These models have similarities to the model we present here. However, the model we present has significant differences in presentation and formulation and in the methods of analysis.

The extinction of a species involves elements of chance, so we feel it is important to include stochastic influences when modelling a metapopulation occupying a small number of patches. In a continuous state space model, the decision of whether to round up or down is crucial if a model predicts that 2.5 patches are occupied (Gilpin, 1992). If the number of occupied patches is large, such a decision has little effect on the predictions of the model. Here we use a discrete state space to address metapopulation extinction, thereby avoiding such rounding problems.

In this paper, we describe and analyse a new stochastic presence-absence metapopulation model which allows for differences in size and quality of patches and incorporates the explicit spatial distribution of patches. The principal issues we address are: (i) estimating extinction probabilities and (ii) calculating the probability distribution function of the state of the system, given that the metapopulation is not extinct. We relax the assumption that all patches are identical. We focus our attention on presence-absence models, formulating a model with a discrete, finite state space because this allows us to avoid the mathematical and computational complications (Iwasa and Mochizuki, 1988) which arise from stochastic models which track the number of individuals in each patch.

We apply our model to malleefowl, *Leipoa ocellata*, inhabiting fragments of habitat in the Bakara region, southern Australia. We consider an existing system of eight patches, where the patches range in size from 100 to 2700 hectares. For this metapopulation, we calculate extinction probabilities and the quasi-stationary distribution. We also examine the effect of patch removal on the metapopulation extinction probability.

To illustrate the influence of variation in patch size, we analyse this same system assuming that all patches have the same area, but maintaining the same total area of habitat. We also explore the effect of explicit spatial structure, by analysing both of these systems with the additional assumption that all patches are equally accessible.

## 2. THE MODEL

Consider a population that can inhabit a finite number of patches. Let the state of this metapopulation be described at discrete time points by the presence or absence of the species in each patch of habitat. The discrete time steps will often be annual, but may be chosen to suit the breeding cycle of the particular species being studied. A patch of habitat is considered to be occupied, at time  $t$ , if there are any individuals present in the patch. If there are no individuals present in a patch, it is considered to be empty.

A discrete time frame, also suggested by Gilpin (1992), reflects the fact that for many species, the dispersal of juveniles, and hence the colonisation of empty patches, occurs only during a short time period following the breeding season. Extinction of occupied patches is assumed only to occur in the longer time periods between dispersal. Separation of the local extinction and colonisation phases in time has been suggested by several authors (Akçakaya and Ginzburg, 1991; Hansson, 1991; Sabelis et al., 1991; Burgman et al., 1993).

If the time step is annual, the repeating cycle is census-extinction-colonisation-census- ... The timing of the census, taking place just after the colonisation phase, is arbitrary and could equally well have been taken just before the colonisation phase (Akçakaya and Ginzburg, 1991). This choice of discrete time frame suggests that the number of patches occupied is likely to first decrease and then increase between each time step. Hence the choice of census time determines whether the local peaks or local troughs are sampled, but has no influence on the overall metapopulation dynamics.

Assume that the system under study has  $n$  patches of suitable habitat, numbered from 1 to  $n$ . Let the state of the system at any given time,  $t$ , be the set of patches which are occupied at time  $t$ . We represent this by an  $n$ -dimensional vector  $\mathbf{u}(t) = (u_1(t), u_2(t), \dots, u_n(t))$ , where the components are zero-one variables,  $u_i(t) \in \{0, 1\}$ . If  $u_i(t) = 0$  then patch  $i$  is empty at time  $t$  and if  $u_i(t) = 1$  then patch  $i$  is occupied at time  $t$ . The zero vector,  $\mathbf{0} = (0, 0, \dots, 0)$ , represents extinction of the metapopulation. As each of the  $n$  patches can be in one of 2 different states, the system has  $2^n$

possible states. It may be useful to order these states in some logical fashion and index them by the integers from 1 to  $2^n$ , although the exact details are not important.

For a stochastic model, we need to assign probabilities that the system is in each of the  $2^n$  possible states at any particular time. This requires a  $2^n$ -dimensional state probability vector,  $w(t)$ , where the entry  $w_j(t)$  represents the probability of being in state  $j$  at time  $t$ . As  $w(t)$  is a probability vector, its elements sum to one,  $\sum_{j=1}^{2^n} w_j(t) = 1$ .

For example, a two patch system has four possible states, (0, 0), (1, 0), (0, 1), and (1, 1) with corresponding state indices 1 to 4. The state probability vector (0, 0, 0, 1) represents the system being in state 4, the state with both patches occupied. If the state probability vector is (0.05, 0.25, 0.2, 0.5) then the metapopulation has probabilities 0.05, 0.25, 0.2, and 0.5 of being in states (0, 0), (1, 0), (0, 1), and (1, 1), respectively.

### 2.1. Transition Matrix

To understand the dynamics of the system, we need to construct a matrix,  $T_n$ , which contains the transition probabilities of moving from any state to any other state of the system. This matrix has dimension  $(2^n \times 2^n)$  and is indexed by the states of the system. Hence, if the state probability vector  $w(t)$  represents the probabilities of being in each of the possible states of the metapopulation at time  $t$ , then these same probabilities at the next time step, time  $(t + 1)$ , are given by the entries in  $w(t + 1)$ , where

$$w(t+1) = w(t) T_n.$$

Assuming that the matrix  $T_n$  does not vary with time, the state probability vector of the system at time  $(t + k)$  is

$$w(t + k) = w((t + k - 1) T_n) = (w(t + k - 2) T_n) T_n = \dots = w(t)(T_n)^k.$$

The matrix of one step transition probabilities,  $T_n$ , can be constructed in terms of the individual patch extinction and colonisation probabilities.

We form the matrix  $T_n$  by first constructing two transition matrices, corresponding respectively to the extinction and colonisation processes, and then multiplying these two matrices together. This corresponds to our assumption that extinction and colonisation events occur successively in the annual cycle.

### 2.2. The Extinction Transition Matrix

The extinction transition matrix,  $E_n$ , has dimension  $(2^n \times 2^n)$  and the entries represent the probabilities of transitions from any state in the system to any other state through extinction alone. Single step transition probabilities in the extinction matrix are nonzero only if they represent transitions from state  $\mathbf{u}$  to state  $\mathbf{v}$  where the occupied patches in state  $\mathbf{v}$  are a subset of the occupied patches in state  $\mathbf{u}$ , and hence the set of occupied patches either decreases or remains the same.

To construct the extinction matrix, the annual extinction probabilities,  $a_i$  for each patch,  $i$ , need to be estimated. These extinction probabilities will depend on the species concerned, properties of the patch (e.g., area, habitat quality and boundary length), and stochastic population processes like catastrophes, demography, and environmental variability.

As matrix  $E_n$  contains only extinction probabilities, any entry corresponding to a transition from one state to another which requires colonisation must be zero. If no patch colonisation is required to move from state  $\mathbf{u}$  to  $\mathbf{v}$ , then the entry of matrix  $E_n$  corresponding to this transition is given by the product

$$e_{\mathbf{u}\mathbf{v}} = \prod_{k=1}^n I_1(u_k, v_k),$$

where the function  $I_1(u_k, v_k)$ , the probability that patch  $k$  goes extinct in a transition from state  $\mathbf{u}$  to state  $\mathbf{v}$ , is

$$I_1(u_k, v_k) = \begin{cases} (1 - a_k) & \text{if patch } k \text{ remains occupied} \\ a_k & \text{if patch } k \text{ goes extinct} \\ 1 & \text{if patch } k \text{ remains empty.} \end{cases}$$

These nonzero matrix entries,  $e_{uv}$ , are just products of probabilities that the appropriate occupied patches either remain occupied,  $(1 - a_k)$  terms, or become extinct,  $a_k$  terms, in the next time interval.

For example in a two patch system with state indices 1 to 4 corresponding to states (0, 0), (1, 0), (0, 1), and (1, 1), the extinction matrix is given by

$$E_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ a_1 & (1 - a_1) & 0 & 0 \\ a_2 & 0 & (1 - a_2) & 0 \\ a_1 a_2 & (1 - a_1) a_2 & (1 - a_2) a_1 & (1 - a_1)(1 - a_2) \end{bmatrix}.$$

This formulation assumes that patch extinction is independent of both the state of neighbouring patches and of simultaneous local extinctions of patches. Akçakaya and Ginzburg (1991) formulate a local extinction matrix which allows patch extinctions to be correlated. This feature can be incorporated in this model but this is not done here.

*The rescue effect.* Brown and Kodric-Brown (1977) suggest that migration of individuals into struggling local populations may produce a reduction in the local extinction rate. The magnitude of this reduction, or "rescue effect," will vary with the number of immigrants arriving at a patch. In our model, the number of immigrants depends on the number of occupied patches and their proximity to the patch of interest.

It is possible to incorporate state dependent local extinction probabilities into our model by making the local population extinction probabilities vary with the number of occupied patches. Unless the migration rate is very high, the relative decrease in extinction rate due to the rescue effect will be very small. In this model, the probability of colonisation of an empty patch depends on the number of occupied patches and their proximity to this empty patch. Hence a patch which is likely to be affected by the rescue effect will have a relatively high probability of being recolonised. We choose not to incorporate a rescue effect in the presentation of this model.

### 2.3. The Colonisation Transition Matrix

Next we need to find or estimate annual colonisation probabilities  $b_{ij}$ , the conditional probability that patch  $j$  is colonised from patch  $i$  in one time period, given that initially patch  $i$  is occupied and patch  $j$  is empty. This may be a complicated function incorporating the distance between patches, patch quality, patch size, and asymmetric migration rates. If patch  $j$  is empty, it may be colonised by propagules sent from any of the occupied patches.

To construct the full  $(2^n \times 2^n)$  colonisation matrix,  $C_n$ , we first form an intermediate matrix  $D_n$ , of size  $(2^n \times n)$ . The entries of this matrix,  $d_{uj}$ , represent the probability that patch  $j$  is colonised from at least one of the occupied patches in state  $\mathbf{u}$ . If  $u_j = 1$ , then patch  $j$  is one of the occupied patches in state  $\mathbf{u}$ , and colonisation is not possible, and hence the corresponding matrix entry must be zero. The nonzero entries of matrix,  $D_n$ , are

$$d_{uj} = 1 - \prod_{k=1}^n I_2(u_k, j),$$

where the function  $I_2(u_k, j)$ , the probability that patch  $j$  is not colonised from patch  $k$ , is

$$I_2(u_k, j) = \begin{cases} (1 - b_{kj}) & \text{if patch } k \text{ is occupied in state } \mathbf{u} \\ 1 & \text{if patch } k \text{ is empty in state } \mathbf{u}. \end{cases}$$

These nonzero matrix entries,  $d_{uj}$ , are calculated by finding the probability that patch  $j$  is not colonised by any of the occupied patches in state  $\mathbf{u}$  and subtracting this probability from 1.

The entries of matrix  $D_n$  are used to construct the  $(2^n \times 2^n)$  colonisation matrix,  $C_n$ , which gives the probabilities of transitions from any state in the system to any other state, through colonisation alone. Single step colonisation probabilities are nonzero only if they represent transitions from state  $\mathbf{u}$  to state  $\mathbf{v}$  where the occupied patches in state  $\mathbf{u}$  form a subset of the occupied patches in state  $\mathbf{v}$ , so that the set of occupied patches increases or remains the same. All transitions corresponding to local extinction of patches must be zero.

The nonzero entries of matrix  $C$  are

$$c_{\mathbf{uv}} = \prod_{k=1}^n I_3(u_k, v_k),$$

where the function  $I_3(u_k, v_k)$ , the probability of patch  $k$  being colonised in a transition from state  $\mathbf{u}$  to state  $\mathbf{v}$ , is

$$I_3(u_k, v_k) = \begin{cases} (1 - d_{u_k}) & \text{if patch } k \text{ remains empty} \\ d_{u_k} & \text{if patch } k \text{ is colonised} \\ 1 & \text{if patch } k \text{ remains occupied.} \end{cases}$$

To illustrate these matrices, consider a two patch system again with state indices 1 to 4 corresponding to states (0, 0), (1, 0), (0, 1), and (1, 1). With the same notation as above, the colonisation matrices  $D_2$  and  $C_2$  are

$$D_2 = \begin{bmatrix} 0 & 0 \\ 0 & b_{12} \\ b_{21} & 0 \\ 0 & 0 \end{bmatrix}$$

and

$$C_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & (1 - d_{22}) & 0 & d_{22} \\ 0 & 0 & (1 - d_{31}) & d_{31} \\ 0 & 0 & 0 & 1 \end{bmatrix}.$$

From the entries in matrix  $D_2$ , matrix  $C_2$ , can be written directly in terms of the colonisation probabilities  $b_{ij}$  as

$$C_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & (1 - b_{12}) & 0 & b_{12} \\ 0 & 0 & (1 - b_{21}) & b_{21} \\ 0 & 0 & 0 & 1 \end{bmatrix}.$$

In a three patch system, the matrices  $D_3$  and  $C_3$  are more complicated, with colonisation possible from more than one patch in some cases. For the three patch system, matrix  $D_3$  is

$$D_3 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & b_{12} & b_{13} \\ b_{21} & 0 & b_{23} \\ 0 & 0 & 1 - (1 - b_{13})(1 - b_{23}) \\ b_{31} & b_{32} & 0 \\ 0 & 1 - (1 - b_{12})(1 - b_{32}) & 0 \\ 1 - (1 - b_{21})(1 - b_{31}) & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

where  $b_{ij}$  are the colonisation probabilities. The corresponding  $(8 \times 8)$  matrix,  $C_3$ , can be constructed from  $D_3$  as outlined above and is given in full in the Appendix.

Once the matrices  $E_n$  and  $C_n$  have been constructed, the one step transition matrix,  $T_n$ , is given by the matrix product,  $T_n = E_n C_n$ . For the case with two local populations, the full transition matrix,  $T_2$  is given in terms of the extinction and colonisation probabilities,  $a_i$  and  $b_{ij}$  in the Appendix. Although the matrices  $E_n$  and  $C_n$  are sparse, in general there will be relatively few zeroes in  $T_n$ . Clearly the model allows multiple events to occur in one time period. There is a positive probability that several occupied patches may become extinct and several empty patches may be recolonised in one time step.

### 3. MODEL ANALYSIS

In this section, we discuss methods for exploring metapopulation dynamics, using the transition matrix,  $T_n$ .

The  $m$  step transition matrix can be found by raising the matrix  $T_n$  to the power of  $m, (T_n)^m$ . Hence, for any given number of time steps,  $m$ , and any initial state probability vector,  $w(0)$ , it is possible to find the complete probability distribution,  $w(m)$ . This gives the probability of being in each of the  $2^n$  states, which may be difficult to analyse directly for a system with more than two or three patches.

It is possible to extract more manageable information from this probability distribution. After  $m$  time steps the probability that the metapopulation is extinct is simply the probability of being in the zero state,  $\mathbf{0} = (0, 0, \dots, 0)$ , which is given by the first component of  $w(m)$ .

The probability that patch  $r$  is occupied at time  $m$  can be obtained by summing the components of the state probability vector corresponding to the appropriate states. If the set  $S_1$  is the set of all states with patch  $r$  occupied, then this sum can be written as

$$\sum_{\mathbf{u} \in S_1} w_{\mathbf{u}}(m), \quad \text{where } S_1 = \{\mathbf{u}: u_r = 1\}.$$

Similarly, if  $S_2$  is the set of all states with exactly  $s$  patches occupied, then the probability that exactly  $s$  patches are occupied is

$$\sum_{\mathbf{v} \in S_2} w_{\mathbf{v}}(m), \quad \text{where } S_2 = \left\{ \mathbf{v}: \sum_{i=1}^n v_i = s \right\}.$$

The mean number of patches occupied at time  $m$  can be calculated from these probabilities.

#### 3.1. Quasi-Stationary Distributions

Many models predict only the mean time to extinction of a population (MacArthur and Wilson, 1967; Richter-Dyn and Goel, 1972; Ludwig, 1976; Leigh, 1981; Wright and Hubbel, 1983; Brockwell, 1985; Goodman, 1987; Lande, 1993; Mangel and Tier, 1993; Foley, 1994) and do not make predictions about the system before it reaches extinction. Further, the time to extinction may not have a known distribution, so describing the system by the mean time to extinction can be misleading. For any Markov chain with a single absorption state, extinction in this case, it is possible to calculate the probability of being in any particular state conditioned on nonabsorption. The long-term limits of these conditional probabilities is known as the quasi-stationary distribution (Darroch and Seneta, 1965; Gilpin and Taylor, 1994).

Consider the transition matrix of the truncated Markov process, limited to the transient states. In our case, this is a reduced matrix,  $R$ , of dimension  $(2^n - 1) \times (2^n - 1)$ , obtained from matrix  $T$  by deleting the first row and first column. Darroch and Seneta (1965) show that the left eigenvector corresponding to the maximal eigenvalue,  $p_1$ , of matrix  $R$  is a quasi-stationary measure and hence normalisation of this eigenvector gives the quasi-stationary distribution.

The quasi-stationary distribution is useful only if movement from any initial state towards the quasi-stationary distribution is much more rapid than the movement of the process towards absorption, and also if the movement towards absorption is slow. It is possible to find the decay parameter, which indicates the rate of movement of the process from the quasi-stationary state towards absorption. This parameter is a long-term rate, describing movement of the process from this "averaged" quasi-stationary state, where there are particular probabilities of being in each of the states, towards extinction. The probability of extinction from any particular state is best found from the  $k$ -step transition matrix,  $T^k$ , as indicated above.

The decay parameter,  $p_1$ , is the maximal eigenvalue of the matrix  $R$ , and it can be shown that  $p_1$  is always strictly less than one. The transition probabilities between any two states over a time interval,  $t$ , will decay at a rate proportional to  $\exp((p_1 - 1) t)$ . The decay parameter cannot be compared directly to the probability of extinction, as the constant of proportionality will change with different systems and for different initial conditions. However, the closer  $p_1$  is to one, the longer the process is likely to continue before reaching absorption.

Darroch and Seneta (1965) show that the rate at which the process approaches the quasi-stationary state will depend on the ratio  $|p_2|/p_1$ , where  $p_2$  is the second largest eigenvalue, in absolute size, of matrix  $R$ . Convergence to the quasi-stationary distribution will be fast if this ratio is small.

Gyllenberg and Silvestrov (1994) also formulate a transition matrix giving probabilities of transitions between states based on local extinction and colonisation probabilities. In their model, both local extinctions and colonisations occur between each time step, but the order of these events is not specified. In contrast, in our model the two processes of local extinction and colonisation occur at different phases of the breeding cycle and hence cannot occur simultaneously. This leads to differences in the two formulations.

Gyllenberg and Silvestrov (1994) calculate conditional stationary distributions for their transition matrix. These conditional stationary distributions appear not to correspond to the quasi-stationary distribution described above. Accordingly, Gyllenberg and Silvestrov (1994) use different techniques to find the conditional stationary distributions, compared to the methods we use to calculate the quasi-stationary distribution. In this paper, we detail a straightforward procedure for obtaining the quasi-stationary distributions and extinction probabilities, using established techniques (Darroch and Seneta, 1965; Gilpin and Taylor, 1994).

#### 4. APPLICATION

To illustrate the use of the model, we explore the metapopulation dynamics of malleefowl (*Leipoa ocellata*) in a 40,000 hectare region. This allows us to answer various questions about the viability of this population, and patch occupancy probabilities, under different management scenarios.

We also look at some theoretical questions, exploring the effects of explicit spatial structure and variation of patch sizes. This allows us to assess the relative importance of some of the key assumptions of our model.

In the Bakara region of South Australia there is an area of eight isolated patches of mallee, see Figure 1. These patches of suitable habitat are separated by cleared agricultural land which is not suitable for malleefowl to live and breed. The patches range in size from 100 to 2700 hectares.

Measuring patch extinction probabilities in the field would require many years of data collection. We initially used the population viability analysis package ALEX (Possingham *et al.*, 1992) to estimate the annual patch extinction probabilities for each patch in isolation. ALEX tracks the number of individuals in a patch, and, with appropriate life history parameters, enables estimation of the per patch extinction probability as a function of patch area, through Monte Carlo simulation.

Such simulation produces some variability in the estimates of extinction. To avoid spurious results which may result from slight errors in these estimates of the extinction probabilities for a patch of a given area, we smoothed out these extinction probabilities, assuming that the extinction probability was only a function of patch area. Using a simple extinction function is useful to illustrate the model and also to explore the effects of variation of patch size on metapopulation extinction and patch occupancy. Any alternative method to estimate these extinction probabilities could be used.

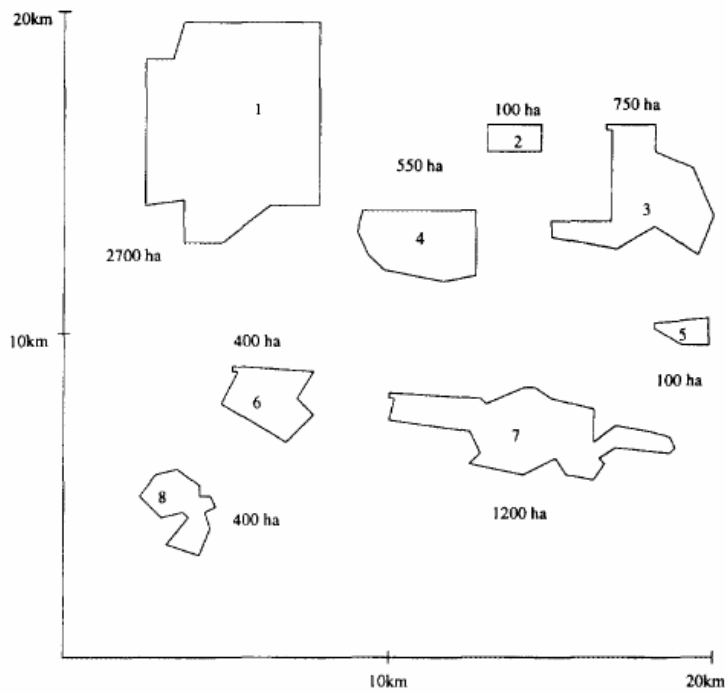


Figure 1. Size and position of suitable habitat patches for malleefowl in the Bakara region.

TABLE I.  
Size, coordinates, and annual extinction probabilities for each of the eight patches.

Patch no. <i>i</i>	Area (km) <sup>2</sup>	x-coordinate (km)	y-coordinate (km)	Extinction probability <i>a<sub>i</sub></i>
1	2700	6	17	0.0048
2	100	14	16	0.1300
3	750	18	14	0.0173
4	550	11	13	0.0236
5	100	19	10	0.1300
6	400	6	8	0.0325
7	1200	14	7	0.0108
8	400	3	5	0.0325

To calculate the annual extinction probabilities  $a_i$ , for patch  $i$  with area  $A_i$ , we use

$$a_i = 13/A_i.$$

This function gives patch extinction probabilities which closely match those obtained using ALEX and is a form similar to that used by Hanski (1994b). Table 1 summarises information about the size and position of the patches and lists the extinction probabilities used.

The probability that an empty patch is colonised from any particular occupied patch is not well known empirically for this species, so we assume a colonisation function based on the distance,  $d$ , between any two patches. Following Gilpin and Diamond (1976), we assume that the colonisation probability,  $b_{ij}$  between patches  $i$  and  $j$  is

$$b_{ij} = 0.005e^{-1/5\sqrt{d_{ij}}}$$

The factor of 0.005 is chosen arbitrarily for the purposes of illustrating this model. The distance,  $d_{ij}$ , is the distance from the centre of patch  $i$  to the centre of patch  $j$ .

Using this information, we constructed the 256 x 256 transition matrix,  $T$ , for this system of



eight patches and we calculated the quasi-stationary distribution. We used the NAG routine F02AGF, on the truncated matrix, to calculate the appropriate eigenvalues and eigenvector.

The quasi-stationary distribution gives a complete probability distribution for each of the 511 nonzero states for this particular example. This quasi-stationary distribution is somewhat unwieldy. However, in similar fashion to the summaries for the full probability distribution, the quasi-stationary distribution can be summarised by calculating the probability distribution of having any particular number of patches occupied, or, more usefully, the probability that any particular patch is occupied given that the metapopulation is not extinct.

## 5. RESULTS AND DISCUSSION

The same system can be analysed assuming that this particular region had been cleared differently, leaving the same total area of native vegetation, but with each patch having equal area, 775 hectares. As colonisation probabilities are expressed as functions only of the distance between pairs of patches and are independent of patch area in this formulation, this change alters only the extinction matrix,  $E$ . Redistributing the total area equally among all patches may change the minimum distance between pairs of patches. However, colonisation probabilities are functions of the distance between centres of patches, so this change in patch size does not alter the modelled explicit spatial arrangement of the patches.

To investigate the importance of explicit spatial structure, we constructed two more transition matrices, one each for the variable and the equal sized patch systems, with the extra assumption that colonisation from one patch to another was equally likely, regardless of the actual distance between patches. This is equivalent to the assumption that all patches are pairwise equidistant. This assumption is common to many metapopulation models, but is impossible to physically arrange in a two dimensional landscape. We chose the distance to maintain the same mean distance between pairs of patches as found in the system in Figure 1. This gives an interpatch distance of about 9.7 km.

By setting the recolonisation probabilities to zero, it is also possible to look at the effect of recolonisation on the metapopulation extinction probabilities of this system, both in the system where the patches have variable sizes, and for the case where all patches have equal area. This assumes that the eight patches are completely isolated from one another. Quasi-stationary distributions cannot be calculated in this case because some nonzero states are not accessible from others in this system. Extinction probabilities were calculated for this system and compared to systems with recolonisation.

### 5.1. Extinction Probabilities

Table II shows the 100-year extinction probabilities for six different scenarios, assuming that all patches are initially occupied. Patches can either be all the same size or vary according to the patch areas given in Table I. Recolonisation can vary according to the distance between patches, occur with equal probability between any two patches, or be non-existent.

For this particular arrangement of patches, variation in size of patches has a much larger effect on the extinction probability than the particular spatial structure of the system. In both cases with migration between patches, the extinction rate is marginally reduced by relaxing the assumption that all patches are equally accessible. There is a significant reduction in the metapopulation extinction probability in the system with equal-sized patches compared to the system with variable-sized patches.

This reduction in extinction rate with equal-sized patches will depend on the parameters and geometry of the particular system and will not hold in general. To illustrate this, consider the same systems with the additional restriction that no migration is allowed between patches. This gives two systems, each with eight independent patches. For this case with no migration, there is an increase in the 100-year extinction probability when the system with variable-sized patches is compared to the system with equal-sized patches.

This suggests that if patch extinction rates can be represented by a simple function of patch area, then with low colonisation rates, patch size variation reduces metapopulation extinction probabilities. In contrast, for high colonisation rates, patch size variation increases metapopulation extinction probabilities.

The difference in extinction probabilities between systems with and without migration gives an indication of the importance of the recolonisation of patches to the persistence of a metapopulation. For this example, positive colonisation probabilities result in a decrease of more than 50% in the 100-year extinction probability, compared to similar systems with no migration.

TABLE II  
100-Year Extinction Probabilities, Expressed as Percentages,  
for the Six Scenarios Analysed

	Variable patch size	Equal patch size
Spatial structure	10.98	7.27
Equal access	11.02	7.42
No migration	17.69	19.62

5.2. Patch Occupancy

Consider initially the system with variable-sized patches and variable distances between patches, with colonisation probabilities depending on the interpatch distances, Figure 1. The patch occupancy probabilities for this system are summarised in Figure 2, where the quasi-stationary probability of occupancy has been plotted against a log scale of the size of the patch. Clearly, large patches are more likely to be occupied than small patches in the quasi-stationary state.

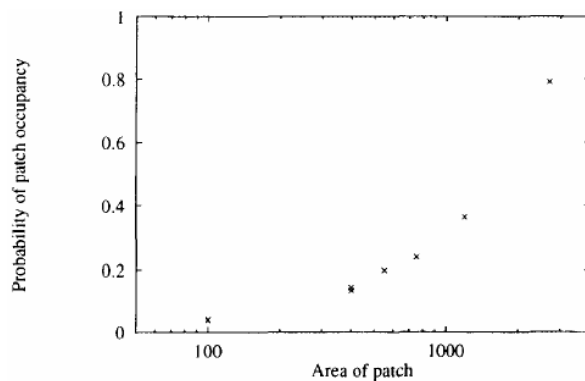


Figure 2. Patch occupation probabilities—quasi-stationary probability of patches of particular sizes being occupied. Scenario with variable-sized patches and variable interpatch distances.

The effects of spatial structure on patch occupancy can be seen in Figure 2. The differences in patch occupancy of the two pairs of equal-sized patches reflect the differing isolation of these pairs of patches. In each case, when two patches are the same size, the more isolated patch is less likely to be occupied, with the relative differences in patch occupancy being around 8% in each case. It would take a very large number of simulations to show a statistically significant difference between the occupancies of these equal-sized patch pairs using a Monte Carlo simulation model, especially for the 100-hectare patches which have patch occupancy probabilities less than 0.05.

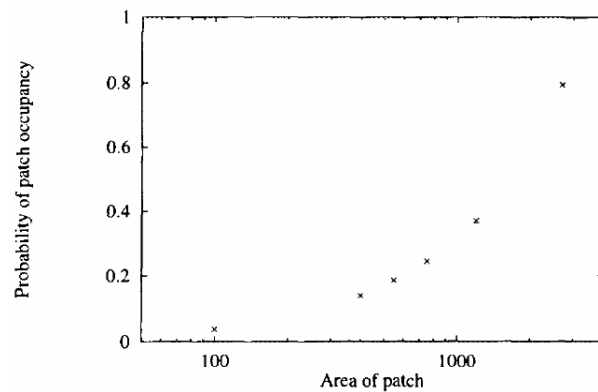


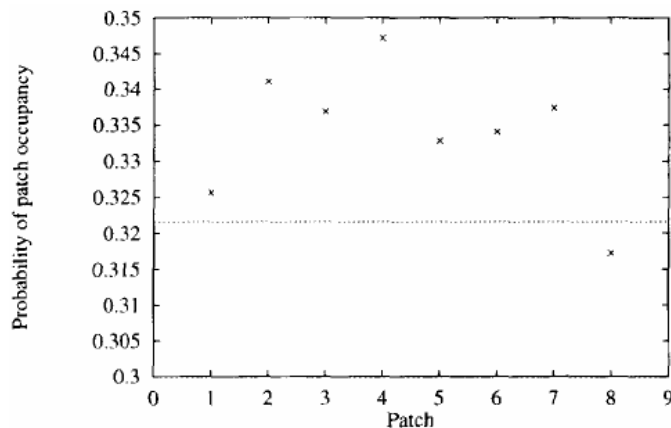
Figure 3. Patch occupation probabilities – quasi-stationary probability of patches of particular sizes being occupied. Scenario with variable-sized patches and all patches pairwise equidistant.

If the explicit spatial arrangement is removed, and the patches are all assumed to be pairwise equidistant, the quasi-stationary distribution gives patch occupancies that depend only on patch areas, Figure 3. A comparison of the patch occupancies under these two scenarios highlights the influence of the position of patches on the quasi-stationary patch occupancy.

The 550-hectare patch 4 has the largest decrease in patch occupancy, due to losing the favourable central location, with a relative decrease in patch occupancy of 7%. The 100-hectare patch 2 has the second smallest mean interpatch distance in Figure 1, and this is reflected in the second largest relative decrease in patch occupancy of around 6%. The 400-hectare patch 8 has a relative increase in patch occupancy of 5%, reflecting the isolation of this patch in the spatially structured system. All other patch occupancies change by less than 3%. Removing the explicit spatial structure alters the patch occupancy probabilities to line with the relative isolation of the patches.

Now consider the cases where all patches have the same size, 775-hectares. Figure 4 shows the quasi-stationary patch occupancy where each patch retains its position. The maximum relative variation in patch occupancy is approximately 10%, and this difference is solely due to the differences to isolation of these equal-sized patches

With equal sized patches, patch 4 has the highest patch occupancy. This is the most central patch, with the smallest mean distance to other patches. The most isolated patch, patch 8, has the lowest patch occupancy. The mean patch occupancy is higher in this system than in the variable patch size systems, which have a mean patch occupancy of around 0.25. In the spatially structured system, the 750-hectare patch 3, which has almost the same area as each of the 775-hectare equal-sized patches, has a quasi-stationary patch occupancy of 0.24. This probability of occupancy is significantly lower than the system with equal-sized patches.



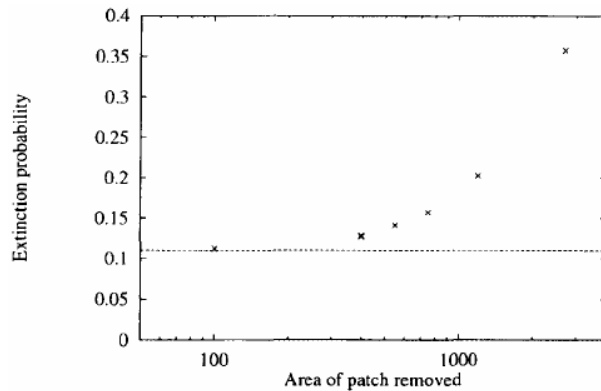
**Figure 4.** Patch occupation probabilities-quasi-stationary probability of patches of particular sizes being occupied. Scenarios with equal-sized patches.

If all patches have equal size and are pairwise equidistant, they all have the same quasi-stationary patch occupancy of 0.322. This patch occupancy is indicated in Figure 4 by the dotted line. For systems with equal sized patches, spatial structure appears to give higher mean probability of patch occupancy.

For a given total area, it seems that mean patch occupancy is higher in a system with equal-sized patches compared to a system with variable-sized patches. Most metapopulations do not have equal sized patches. These results suggest that it is important to explicitly model variation in patch size.

### 5.3. Patch Removal

For each of the scenarios, we now examine the effect of removal of patches from the system, reflecting the effect of habitat destruction on the probability of extinction. We remove each patch, in turn, and calculate the 100-year extinction probabilities for each of the remaining seven patch systems.



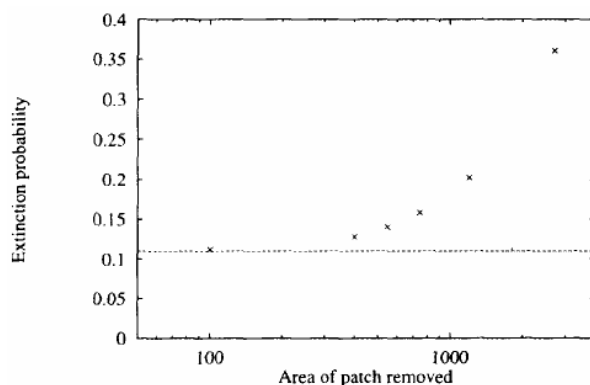
**Figure 5.** Extinction probabilities-effect of removing various patches. These extinction probabilities are calculated for a 100-year period with all patches initially occupied. Scenario with variable-sized patches and variable interpatch distances.

For the system with variable-sized patches and variable interpatch distances, these extinction probabilities are plotted against the area of the patch removed, again using a log scale for the area of each patch. Figure 5 shows these probabilities, with the dotted line enabling comparison to the extinction probability for the full eight patch system.

The differences in extinction probability from removing each patch, from a pair of equal-sized patches, illustrate the effects of isolation on the importance of a patch to the long-term viability of the metapopulation. The degree of isolation of the two 100-hectare patches has a very small impact on the change in the overall 100-year extinction probability. This reflects the fact that smaller patches have little influence on the overall extinction probability, due to their relatively low occupancy probabilities. Hence, for these particular patches, the effect of patch isolation is minimal in determining the contribution to metapopulation persistence. These comments also apply to the two 400-hectare patches, though to a somewhat lesser extent.

The spatial position of the patches has a very minor effect on changes to the metapopulation extinction probability due to the removal of individual patches from the system. Figure 6 shows the same information as shown in Figure 5, except that the probabilities plotted are for a system with pairwise equidistant patches. Once again, the dotted line indicates the 100-year extinction probability for the full eight patch system. The 100-year extinction probability for each of the seven patch systems is plotted against the area of the patch removed.

The relative differences in the metapopulation extinction probabilities, due to the removal of identical patches, between the spatially structured and unstructured systems are very small. The largest relative change is a 1 % decrease in extinction probability when patch 4 is removed from the equidistant patch system, compared to removal of the same patch from the spatially structured system. The 550-hectare patch 4 is the most central patch in the spatially structured system, so this result is not surprising. Both the probability of patch occupancy and the effect of removal of this patch on the extinction probability indicate the importance of central patch location in a spatially structured model. Note the similarities in the shape of the curves in Figs. 3 and 6.



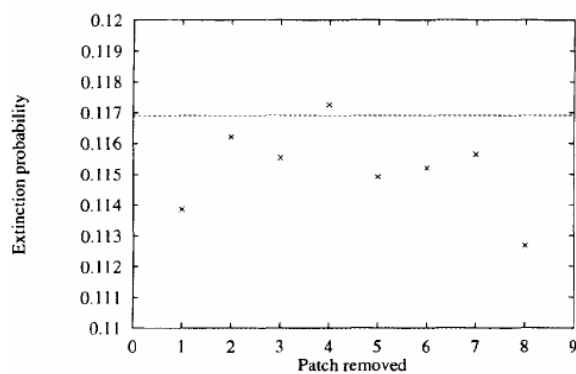
**Figure 6.** Extinction probabilities-effect of removing various patches. These extinction probabilities are calculated for a 100-year period with all patches initially occupied. Scenario with variable-sized patches and all patches pairwise equidistant.

For the systems where all patches have the same area, the 100-year extinction probability for a

seven patch system is increased by at least 50% compared to the similar eight patch system. For the spatially structured system with equal sized patches, the 100-year extinction probabilities, for the seven patch system, plotted against patch number of the patch removed, are shown in Figure 7. For comparison, the dotted line shows the extinction probability for a seven patch system with equal-sized patches which are pairwise equidistant.

In both these systems, removing one patch results in an increase in 100-year extinction probability of at least 50% compared to the 100-year extinction probability for an eight patch system. For a seven patch system with all patches pairwise equidistant, all patches of equal size and no migration, the 100-year extinction probability is 24.05%.

It is interesting to note that the quasi-stationary probability that a patch is occupied is closely related, in a relative sense, to the increase in metapopulation extinction probability from removing that patch. In these examples, a ranking of patches in terms of occupancy is identical to a ranking of patches in terms of the increase in metapopulation extinction probability from removing that patch. This result holds for systems with variable-sized patches and for systems with no variability in patch size. This suggests that, in some circumstances, the quasi-stationary probability of occupancy is a good measure of the importance of a patch for metapopulation persistence.



**Figure 7.** Extinction probabilities-effect of removing various patches. These extinction probabilities are calculated for a 100-year period with all patches initially occupied. Scenario with equal-sized patches.

The decay parameter for the full eight patch system is  $\rho_1 = 0.99625$ , suggesting that we can expect the time until extinction of the metapopulation to be large. Hence the quasi-stationary distribution is of great interest.

#### 5.4. Comparison with other Patch Occupancy Models

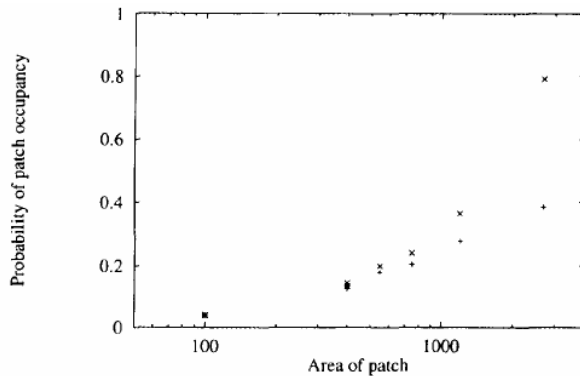
Hanski (1994b) uses patch occupancy data to estimate extinction and recolonisation rates for a metapopulation. This "incidence function" approach depends on the metapopulation being at a quasi-stationary equilibrium, at the time when data is collected on patch occupancy, and is suitable only for systems with large numbers of patches. Hanski does allow variation in patch size and, to some extent, allows patch dynamics to depend on isolation. He suggests that recolonisation rates may vary, depending on occupancy of adjacent patches, and also assumes that isolation of a given patch is independent of the occupancy of neighbouring patches. This work is based on the assumption that each patch will have fixed extinction and colonisation rates.

Acknowledging these modelling differences, it is possible to incorporate our extinction rates and colonisation rates into Hanski's model, to see if his incidence function will predict the same patch occupancy as we obtained.

As colonisation probabilities in our model are state dependent, we weighted them according to the quasi-stationary probability that each patch providing migrants was occupied and summed these weighted patch colonisation probabilities. For patch  $i$ , this gives an averaged colonisation probability,  $r_i$ . According to Hanski's incidence function, the probability of patch  $i$  being occupied,  $j_i$ , is given by

$$j_i = \frac{r_i}{r_i + a_i},$$

where  $a_i$  is the extinction probability for patch  $i$ .



**Figure 8.** Patch occupancy comparison of predictions from two models. The quasi-stationary patch occupancy probabilities ( $\times$ ) and patch occupancy probabilities predicted by Hanski's model ( $+$ ) are plotted against the area of the patches.

The quasi-stationary patch occupancy probabilities are shown in Figure 2. To compare these probabilities with Hanski's incidence function approach, both sets of patch occupancy probabilities are plotted on the same axes in Figure 8.

The predicted patch occupancies from Hanski's model are all lower than the true quasi-stationary patch occupancies. The biggest relative difference is a 50% reduction in the patch occupancy prediction for patch 1, the largest patch. For the other patches, the relative differences in predicted patch occupancy between the two models decreases with area, ranging from a decrease of 24% for the 1200-hectare patch 7 to less than 1% for the two 100-hectare patches.

Hanski's model excludes the possibility of metapopulation extinction and assumes there is no variation in patch colonisation rate, because his patch colonisation rate does not depend on the state of the system. Constant colonisation rates have two consequences for our model, preventing extinction and reducing patch occupancy probabilities when large numbers of patches are occupied. In our model, if the patch colonisation rate is low, due to a small number of patches being occupied, it is likely that the metapopulation will become extinct in the near future. If there are a large number of patches occupied, colonisation rates will be higher than the averaged colonisation rates used above.

The quasi-stationary patch occupancies are calculated with the assumption that the metapopulation has not yet become extinct and hence are biased against small numbers of patches being occupied. Hence, we believe that in general the quasi-stationary patch occupancies will be higher than the patch occupancies predicted by Hanski's model, especially for large patches. Hanski's model underestimates patch occupancy for the malleefowl metapopulation in the Bakara region.

Hanski (1994b) incorporates a rescue effect into his patch occupancy function. This variation on the previous incidence function gives a probability of patch occupancy,

$$j_i = \frac{r_i}{r_i + a_i - r_i a_i},$$

for patch  $i$ . With the same values for  $r_i$  and  $a_i$ , the patch occupancy probabilities obtained from this new incidence function all changed by less than 1% compared to the patch occupancy probabilities given by the previous incidence function. Using Hanski's models for the Bakara malleefowl metapopulation, the rescue effect makes very little difference to patch occupancy predictions.

## 6. CONCLUSION

We present a metapopulation model which can demonstrate analytically the effects of different patch sizes and various spatial arrangements of patches. We use this model to calculate metapopulation extinction probabilities. We also use the model to predict the probability that a particular patch is occupied, either directly from the state probability vector at some given time, or by using the quasi-stationary probability distribution. This distribution can be tested empirically. Most other stochastic models predict only the expected time to extinction, which is difficult to test empirically given the large number of populations which would have to be

followed to extinction.

For a particular patch structure, once the transition probabilities have been found, our model gives exact analytical results. Rather than having to run Monte Carlo simulations many times to estimate probabilities of extinction and patch occupancy, these probabilities can be calculated exactly (Gilpin and Taylor, 1994). Estimating accurate probabilities for rare events using simulation requires a very large number of simulations and can be subject to significant error. The exact results obtained from our model enable direct comparison between the effects of removing different patches. Hence we can rank the various patches in order of their significance for the likely survival of the metapopulation. This ranking appears to be strongly correlated with the probability of patch occupancy.

For the malleefowl metapopulation in the Bakara region, modelling variation in patch sizes appears to have more impact on the metapopulation dynamics than modelling the explicit spatial position of each patch. Using the same colonisation and extinction rates, our model produces different patch occupancy predictions than Hanski (1994b), especially for large patch sizes.

Other authors (Akçakaya and Ginzburg, 1991; Gyllenberg and Silvestrov, 1994) also recognise the importance of using a stochastic model with a discrete state space. Gyllenberg and Silvestrov (1994) calculate conditional stationary distributions for three different systems, each consisting of three patches, and concentrate on searching for a bimodal distribution of the number of patches occupied.

The assumption that local populations dynamics are not important and can be modelled as being either present or absent is the weakest feature of the model we present here. However, ignoring the internal patch dynamics does reduce the number of parameters required and restricts the state space to a size which is manageable.

A further limitation of these models is that they cannot be used to explore systems with large numbers of patches. As the number of patches increases, computer storage requirements for the transition matrix,  $T_n$ , increase geometrically, as does the computer time required for matrix multiplication. Finding the eigenvectors of high dimension matrices is more difficult computationally than matrix multiplication and requires large amounts of computer time and memory (Gilpin and Taylor, 1994). Hence, without writing special software, calculating quasi-stationary distributions for systems with more than nine patches is not feasible. Calculating extinction probabilities over  $k$  time periods is possible for slightly larger systems, however, although it becomes more expensive computationally as the dimension of the system increases. These problems may be reduced with continued improvements in the speed and memory capabilities of computer systems.

Accurately measuring or estimating the parameters for this model is one of the biggest challenges (Akçakaya and Ginzburg, 1991; Dennis *et al.*, 1991; Conroy *et al.*, 1995). Understanding the colonisation and local extinction processes for real situations can be difficult. A number of detailed simulation models are available which can be used to estimate these parameters, including ALEX (Possingham *et al.*, 1992), RAMAS/Space (Akçakaya and Ferson, 1992) and VORTEX (Lacy, 1993). If the local extinction and colonisation parameters can be estimated, or measured, and the parameters for our model obtained, the real distribution of organisms can be compared with the patch occupancy probabilities predicted by the model. Unlike existing metapopulation models, this model is useful for examining the combined effects of patch size and isolation, for examining the influence of particular patches, and for investigating how different spatial arrangements of suitable habitat patches will influence population viability.

**APPENDIX**

This Appendix gives the full transition matrix for a two patch metapopulation,  $T_2$ , in terms of the extinction and colonisation probabilities,  $a_i$  and  $b_{ij}$ .

$$T_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ a_1 & (1-a_1)(1-b_{12}) & 0 & (1-a_1)b_{12} \\ a_2 & 0 & (1-a_2)(1-b_{21}) & (1-a_2)b_{21} \\ a_1a_2 & (1-a_1)a_2(1-b_{12}) & (1-a_2)a_1(1-b_{21}) & (1-a_1)a_2b_{12} + (1-a_2)a_1b_{21} + (1-a_1)(1-a_2) \end{bmatrix}$$

The full colonisation matrix,  $C_3$ , is shown below for a three patch metapopulation. The entries of this matrix are given in terms of the entries of the intermediate matrix  $D_3$ , and also in terms of the extinction and colonisation probabilities,  $a_i$  and  $b_{ij}$ .

$$C_3 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & (1-d_{22})(1-d_{23}) & 0 & d_{22}(1-d_{23}) & 0 & d_{23}(1-d_{22}) & 0 & d_{22}d_{23} \\ 0 & 0 & (1-d_{31})(1-d_{33}) & d_{31}(1-d_{33}) & 0 & 0 & d_{33}(1-d_{31}) & d_{31}d_{33} \\ 0 & 0 & 0 & 1-d_{43} & 0 & 0 & 0 & d_{43} \\ 0 & 0 & 0 & 0 & (1-d_{51})(1-d_{52}) & d_{51}(1-d_{52}) & d_{52}(1-d_{51}) & d_{51}d_{52} \\ 0 & 0 & 0 & 0 & 0 & 1-d_{62} & 0 & d_{62} \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-d_{71} & d_{71} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$= \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & (1-b_{12})(1-b_{13}) & 0 & b_{12}(1-b_{13}) & 0 & b_{13}(1-b_{12}) & 0 & b_{12}b_{13} \\ 0 & 0 & (1-b_{23})(1-b_{21}) & b_{23}(1-b_{21}) & 0 & 0 & b_{21}(1-b_{23}) & b_{23}b_{21} \\ 0 & 0 & 0 & (1-b_{13})(1-b_{23}) & 0 & 0 & 0 & 1-(1-b_{13})(1-b_{23}) \\ 0 & 0 & 0 & 0 & (1-b_{31})(1-b_{32}) & b_{31}(1-b_{32}) & b_{32}(1-b_{31}) & b_{31}b_{32} \\ 0 & 0 & 0 & 0 & 0 & (1-b_{12})(1-b_{32}) & 0 & 1-(1-b_{12})(1-b_{32}) \\ 0 & 0 & 0 & 0 & 0 & 0 & (1-b_{21})(1-b_{31}) & 1-(1-b_{21})(1-b_{31}) \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

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