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# TRADE-OFFS BETWEEN LOCAL AND REGIONAL SCALE MANAGEMENT OF METAPOPULATIONS

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## Abstract

*A model analysis of the extinction of metapopulations is presented, based on a general model which explicitly considers essential population dynamical factors, such as environmental fluctuations and dispersal of individuals. The model is used to evaluate the influences of three plausible management options on the viability of a metapopulation. These are the increase of the capacity and the number of patches and the improvement of their connectivity. We find that the effects of these management options depend on the specific environmental conditions, such as environmental variability and the patch capacities. We generate a set of scenarios which cover a wide range of different environmental situations. For each scenario the influences of the management options are evaluated. The results are used to compare local management of subpopulations with the establishment of a habitat network. © 1997 Published by Elsevier Science Ltd*

*Keywords:* metapopulation dynamics, population viability analysis, conservation management, fragmentation, stochasticity.

## INTRODUCTION

Fragmentation of habitat is one of the most important issues in the conservation of species (e.g. Wilcox, 1980; Norton, 1986; Shafer, 1990). Small populations in the remaining habitat patches are exposed to a stochastic environment and to demographic and genetic stochasticity (Goodman, 1987*a*,*b*; Hanski, 1991; Burgman *et al.*, 1993). This leads to stochastic fluctuations in the population sizes. The small populations therefore may be likely to become extinct in a short time. If there is dispersal between different patches, the small populations are subpopulations of a greater unit called a metapopulation (e.g. Levins, 1969; Hanski & Gilpin, 1991). One of the key processes in a metapopulation is the turnover of local extinctions and the recolonisation of empty patches. This may allow the metapopulation as a whole to persist for much longer than a single subpopulation. The existence of metapopulations has raised new questions in conservation biology, as the extinction of species no longer depends solely on the local dynamics within the subpopulations (discussed by Goodman, 1987*a*,*b*; Soulé, 1987; Burgman *et al.*, 1988; Lande, 1993; Wissel *et al.*, 1994), but also on additional factors, such as the number and the connectivity of the patches.

Management of an endangered metapopulation is improved when the manager knows which factors most strongly affect its extinction risk. Tools for discussing these questions are model analyses. In the past, many models of metapopulations have been presented in the literature. One may distinguish general models (Levins, 1969; Quinn & Hastings, 1987; Harrison & Quinn, 1989; Hanski & Gyllenberg, 1993) and model case studies, such as Verboom *et al.* (1991), Hanski (1994) and Grimm *et al.* (1994). While the neglect of details limits the practical applicability of general studies, the results of case studies are often difficult to generalise. In this paper we present an approach that is general, but explicitly considers details, such as environmental variability and dispersal. This will allow us to cover a wide range of different environmental situations.

As the model is general, the ranges of parameter values considered in the study have to be chosen by arguments of plausibility. This includes the determination of a critical subpopulation lifetime below which a metapopulation is never viable. Based on these plausible parameter ranges, representative parameter combinations ('scenarios') are formed. For each scenario we consider the typical situation in conservation biology that human impact has produced a metapopulation with low probability of survival and one wants to take action to increase this probability. In the context of our model a manager may have several options: to increase the capacities (size and habitat quality) of the patches, to increase the number of patches, and to improve their connectivity (e.g. by corridors). The effects of these options are evaluated for each scenario and the consequences for metapopulation management are discussed.

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## METHODS

### Outline of the model

The model combines a description of the local dynamics within the patches with a description of the regional dynamics of extinction and recolonisation. In particular, the regional parameters will be directly calculated from the parameters of the local dynamics (Drechsler & Wissel, 1997). We assume that demographic structure (sex, age and other stages) in the subpopulations can be neglected and describe the local dynamics in a general way by two rates $\lambda_n$ and $\mu_n$. These determine the change in the subpopulation size. In particular, $\lambda_n \Delta t$ and $\mu_n \Delta t$, respectively, give the probability of increase and decrease in the number of individuals during the time interval $\Delta t$. The complete derivation of the two rates, $\lambda_n$ and $\mu_n$, in the absence of emigration and immigration is found in Wissel and Stöcker (1991). Migration was included into the model equations by Drechsler and Wissel (1997). As the derivation of $\lambda_n$ and $\mu_n$ requires some non-trivial mathematical transformations (see also Goodman, 1987*a*,*b*), at this time we can provide only a short intuitive derivation.

First consider an isolated subpopulation. The mean change in its size in the time interval $\Delta t$ is given by the difference of increase, $\lambda_n \Delta t$, and decrease, $\mu_n \Delta t$. We assume logistic growth, i.e. the mean change is described by:

$$(\lambda_n - \mu_n)\Delta t = rn(1 - \frac{n}{K})\Delta t \qquad (1)$$

The parameter $r$ is the mean intrinsic growth rate and $K$ is the patch capacity which is a measure of the size and the habitat quality of the patch. The variance of the change in the subpopulation size can be written as the sum of increase, $\lambda_n \Delta t$, and decrease, $\mu_n \Delta t$ (Wissel *et al.*, 1994). We assume that it depends on the subpopulation size, $n$, and is given by

$$(\lambda_n + \mu_n)\Delta t = (\gamma n + \sigma^2 n^2)\Delta t \qquad (2)$$

The term linear in $n$ describes demographic fluctuations which arise from the chance nature of births and deaths (e.g. Goel & Richter-Dyn, 1974; Goodman, 1987*a*; Wissel *et al.*, 1994). The variance term quadratric in $n$ represents environmental fluctuations which may be caused by weather, interspecific competition, predation and other stochastic environmental factors (Goodman, 1987*b*; Lande, 1993; Wissel *et al.*, 1994). For further details about environmental and demographic fluctuations, see the Appendix.

Beside the birth and death events, local dynamics in a metapopulation are affected by the immigration and emigration of individuals. For the emigration we simply assume that each of the $n$ individuals leaves the subpopulation at a constant rate (probability per time), $e$. So emigration raises the death rate, $\mu_n$, by the rate $e \cdot n$. In contrast, immigrants increase the subpopulation size. This increase is assumed to be independent of the actual size of the target subpopulation. Thus the birth rate, $\lambda_n$, is raised by an immigration rate, $i$, which will depend on the occupancy of all other patches (see below).

Combining eqns (1) and (2) and adding the terms of migration, $e \cdot n$ and $i$, leads to

$$\lambda_n = 0 \cdot 5 \cdot [rn(1 - n/K) + \gamma n + \sigma^2 n^2] + i \qquad (3)$$

$$\mu_n = 0 \cdot 5 \cdot [-rn(1 - n/K) + \gamma n + \sigma^2 n^2] + e \cdot n \qquad (4)$$

A few remarks should be added here. Technically speaking, the modelled dynamics are a combination of two Poisson processes (one for the birth events and one for the death events; Goodman, 1987*a*,*b*). In such a combined process the variance, $(\lambda_n + \mu_n)\Delta t$ (eqn (2)), always exceeds the mean $(\lambda_n - \mu_n)\Delta t$ (eqn (1)). In the absence of environmental fluctuations and density-dependent regulation ($\sigma^2 = 0$ and $1/K = 0$), this implies that the demographic fluctuations exceed the mean growth rate: $\gamma > r$. This constraint will be used in the entire analysis (see the Appendix) and makes sure that the death rate, $\mu_n$ (eqn (4)), is always positive. Further, eqn (3) shows that if environmental fluctuations are weak ($\sigma^2/r < 1/K$) the birth rate, $\lambda_n$, can become negative when $n > 2K$. Analyses of the model (Wissel & Stöcker, 1991) show that in the case of weak environmental fluctuations ($\sigma^2/r < 1/K$) population numbers $n > 2K$ are very unlikely. Therefore negative $\lambda_n$ were set to zero without affecting the dynamics. Finally, because the dynamics are a Poisson process, the quantities $\sigma^2$ and $\gamma$ are variances per time unit and therefore have the physical dimension of an inverse time like the rates $r$, $i$ and $e$.

The stochastic sequence of birth and death events (including immigration and emigration) in a subpopulation can be described by a Monte Carlo simulation or with the help of a so-called Master equation with rates $\lambda_n$ and $\mu_n$ (Goel & Richter-Dyn, 1974; Wissel & Stöcker, 1991). Wissel *et al.* (1994) used eqn (3) and eqn (4) without the migration parameters (i.e. $e = i = 0$) to calculate the expected lifetime of a single population. The result agrees with Lande (1993) who used a different approach. Drechsler and Wissel (1997) included the migration rates in eqn (3) and eqn (4) to discuss the dynamics of a subpopulation with non-zero emigration and immigration. They showed that from these local dynamics, the regional quantities, extinction and recolonisation rate, can be derived if the following two conditions are fulfilled.

(a) The immigration rate must be small compared with the mean intrinsic growth rate: $i < 0 \cdot 1r$.

(b) Environmental fluctuations, $\sigma^2$, must not exceed the mean rate of change in the subpopulation size, $r - e$ (because of condition (a) the contribution of the immigration rate to the mean change can be neglected).

With eqn (8) below, conditions (a) and (b) imply that the emigration rate, too, has to be small compared with the mean intrinsic growth rate: $e < 0 \cdot 1r$ (Appendix: Parameter ranges).

If condition (b) is fulfilled the probability, $P_{sub}$, of finding a patch occupied decreases exponentially with time at a constant extinction rate, $x$ (Drechsler & Wissel, 1997):

$$P_{sub} = \exp(-xt) \tag{5}$$

This rate of local extinction, $x$, is the inverse of the expected life time, $T_{sub}$, of a subpopulation and can be calculated from the rates, $\lambda_n$ and $\mu_n$ (Goel & Richter-Dyn, 1974; Wissel & Stöcker, 1991; Drechsler & Wissel, 1997). The expected subpopulation life time, $T_{sub}$, depends on the immigration rate, $i$, and increases with increasing immigration. With this we have explicitly modelled the rescue effect (Brown & Kodric-Brown, 1977). If condition (a) is fulfilled, an empty patch becomes occupied at a constant rate

$$c = i \cdot E \tag{6}$$

(Appendix). Here $E$ is the probability that a single immigrant (the model is asexual) establishes a subpopulation. It can be calculated from the rates $\lambda_n$ and $\mu_n$ (Appendix).

For the regional dynamics, we assume spatial homogeneity such that all patches are identical, except that the fluctuating sizes of the subpopulations may be different. Then with eqn (5), the probability per time that one of $s$ existing subpopulations becomes extinct is

$$\mu_s = xs = \frac{s}{T_{sub}} \tag{7}$$

We further assume that the connectivity between any two patches is identical for all pairs of patches. Then we can model the immigration rate as the product of the total number of emigrants produced per time unit and the proportion of dispersers that immigrate into a particular patch. The total number of emigrants is given by the per capita emigration rate, $e$, the expected size of a subpopulation, $<n>$ (Appendix), and the number of occupied patches, $s$. Each patch receives a proportion of $d/S$ dispersers, where $d$ is the chance that a disperser reaches some patch, and $1/S$ is the proportion of all immigration events which fall on a single one of the $S$ patches:

$$i = e \cdot <n> \cdot s \cdot d \cdot 1/S \tag{8}$$

The factor $d$ increases with increasing patch connectivity and is called 'connectivity factor'.

The probability per time unit that one of the $S - s$ empty patches becomes occupied is

$$\begin{aligned}\lambda_s &= c \cdot (S - s) = i \cdot E \cdot (S - s) \\ &= \{e \cdot <n> \cdot d \cdot E\} \cdot s \cdot \left(1 - \frac{s}{S}\right)\end{aligned} \tag{9}$$

(we used eqns (6) and (8)). On the right hand side of eqn (9) we have ordered the parameters such that the 'subpopulation birth rate', $\lambda_s$, is written as the product of three quantities: the colonisation rate (probability per time that a particular subpopulation colonises a patch)

$$m = e \cdot <n> \cdot d \cdot E, \tag{10}$$

the number $s$ of subpopulations, and the probability $1 - s/S$ that a colonised patch was empty. The colonisation rate, $m$, as defined here is identical to the one used by Levins (1969). Its expression by eqn (10) equals the phenomenological assumptions of other models (Verboom *et al.*, 1991; Hanski & Zhang, 1993) which assume that the colonisation rate, $m$, is the product of the emigration rate, the expected subpopulation size, the probability that an emigrant reaches a patch and the probability that an immigration event leads to the establishment of a subpopulation.

The stochastic sequence of local extinctions and recolonisations can be regarded as a sequence of births and deaths of subpopulations (Hanski, 1991). The rate $\lambda_s$ (eqn (9)) represents the 'birth rate' of subpopulations and $\mu_s$ (eqn (7)) is the subpopulation 'death rate'. Therefore, the regional dynamics of local extinctions and recolonisations can be described by a Master equation with rates, $\lambda_s$ and $\mu_s$ (Wissel & Stöcker, 1991, cf. above). In the Appendix we briefly analyse the turnover dynamics with rates $\lambda_s$ and $\mu_s$. If the turnover ratio of colonisation and extinction rates, $m/x$, is not too small we find a simple relation between the probability $P_{meta}(t)$ that the metapopulation survives a given time $t$, and its expected life-time, $T_{meta}$:

$$P_{meta} \approx \exp\left(-\frac{t}{T_{meta}}\right), \tag{11}$$

which is the regional counterpart of eqn (5). It means that the metapopulation becomes extinct approximately at a rate $1/T_{meta}$. Therefore, except for the cases of small turnover ratios, we can use $T_{meta}$ as a measure for the viability of a metapopulation. It can be calculated from the rates, eqns (7) and (9) (Goel & Richter-Dyn, 1974; Wissel & Stöcker, 1991) by

$$T_{meta} = \sum_{s=1}^{S} \sum_{u=s}^{S} \frac{1}{\mu_u} \prod_{v=s}^{u-1} \frac{\lambda_v}{\mu_v} \tag{12}$$

### Sensitivity analysis of selected model parameters

In this subsection we outline how to compare the influences of the patch capacity, $K$, the patch number, $S$, and the connectivity factor, $d$, on the lifetime, $T_{meta}$, of a metapopulation. Assume that $T_{meta}$ is to be increased by a factor $F_t$. This can be achieved by increasing the patch capacity, $K$, by a particular factor $F_k$. Alternatively one might keep the patch capacity fixed and instead increase the patch number, $S$, by a particular factor, $F_s$, or the connectivity factor, $d$, by a factor $F_d$. We form the three sensitivity coefficients

$$I_k = \frac{\ln(F_t)}{\ln(F_k)}, \quad I_s = \frac{\ln(F_t)}{\ln(F_s)}, \quad \text{and} \quad I_d = \frac{\ln(F_t)}{\ln(F_d)} \tag{13}$$

It can be shown that these sensitivity coefficients are mathematically equivalent to those defined by de Kroon *et al.* (1986; eqn (2)). They give the proportional change in $T_{meta}$ from a proportional change in $K$, $S$ and $d$, respectively. By numerical tests we further found that the sensitivity coefficients in eqn (13) are nearly independent of the factor $F_t$ by which the metapopulation lifetime shall be increased. Therefore, they provide general measures for the influences of the three parameters, $K$, $S$ and $d$. Their interpretation is simple. A ratio of $I_k/I_s > 1$, for instance, means that the patch capacity, $K$, has a stronger influence on the expected lifetime of the metapopulation than the patch number, $S$. To provide a quantitative example, a ratio of $I_k/I_s = 2$ is equivalent to $F_k = F_s^2$ (eqn (13)). This means that increasing the patch capacity, $K$, by a factor 1·5 has the same effect as increasing the patch number, $S$, by a factor of $1{\cdot}5^2 = 2{\cdot}25$. The three sensitivity coefficients, eqn (13), can be combined to a triple ratio, $I_k{:}I_s{:}I_d$, which represents the relative influences of the parameters, $K$, $S$ and $d$.

## RESULTS

### 'Non-trivial metapopulations'

In this section we derive plausible ranges for the turnover ratio, $m/x$, the patch capacity, $K$, and the subpopulation lifetime, $T_{sub}$, where a discussion of the viability of a metapopulation is non-trivial. First consider a metapopulation with a low turnover ratio of $m/x < 1$. For these turnover ratios, a numerical analysis of eqn (12) leads to an expected metapopulation lifetime which is of the order of

$$T_{meta} = T_{sub} \cdot (1 + m/x) \cdot \ln S \tag{14}$$

A metapopulation with a low turnover ratio of $m/x < 1$ therefore is rather unlikely to survive for longer than the expected lifetime of a subpopulation, $T_{sub}$, unless the number of patches, $S$, is very large. Even though $T_{meta}$ is not a very good measure for the viability of a metapopulation with low turnover rate (Methods), this result is plausible. At turnover ratios below unity the equilibrium number of occupied patches is zero (Levins, 1969) and such a metapopulation will rapidly become extinct on a time scale given by the lifetimes of its subpopulations. So in general, the conservation of a metapopulation with a low turnover ratio will have to focus on the management of the subpopulations in order to increase their viability. We call these metapopulations 'trivial', as the discussion of their viability is similar to the discussion of single populations. In this paper we consider only non-trivial metapopulations whose turnover ratio, $m/x$, exceeds unity.

In order to find the smallest plausible patch capacity, we ask for the minimum patch capacity, $K_{min}$, which is required to obtain a large metapopulation lifetime of $T_{meta} = 2000/r$ (2000 years if $r = 1$/year). The result is shown in Fig. 1 for four different parameter combinations. Each of the four curves represents a combination of strong or weak environmental fluctuations ($\sigma^2 = 0 \cdot 1r$; $\sigma^2 = 0 \cdot 95r$) and large or small connectivity factor ($d = 0{\cdot}95$; $d = 0{\cdot}05$). In each curve the minimum patch capacity, $K_{min}$, decreases asymptotically with increasing number of patches, and beyond a patch number of 20 it is more or less constant. In the case of optimal connectivity, where almost all dispersers reach some patch ($d = 0{\cdot}95$) this minimum patch capacity is between 10 (weak environmental fluctuations) and 35 (strong environmental fluctuations). Metapopulations on smaller patches, therefore, are not viable, regardless of the number and the connectivity of the patches.

We calculated the subpopulation lifetimes, $T_{sub}$, which correspond to the minimum patch capacities of 10 in the case of weak environmental fluctuations and 35 in the case of strong environmental fluctuations. In both cases the corresponding subpopulation lifetimes were found to be of the order of $10/r$. Patch capacities below the minimum values of 10 and 35 (weak and strong environmental fluctuations, respectively) led to subpopulation lifetimes below $10/r$. As we found metapopulations with such small patch capacities not to be viable, so are metapopulations whose subpopulations have expected lifetimes below $10/r$.

An upper plausible limit for the lifetime of a subpopulation should be $1000/r$, because here the subpopulations are long-lived themselves and a discussion of metapopulation viability would be redundant. The corresponding patch capacities that are needed to obtain a subpopulation lifetime of $1000/r$ are 35 and 600 for weak and strong environmental fluctuations, respectively.

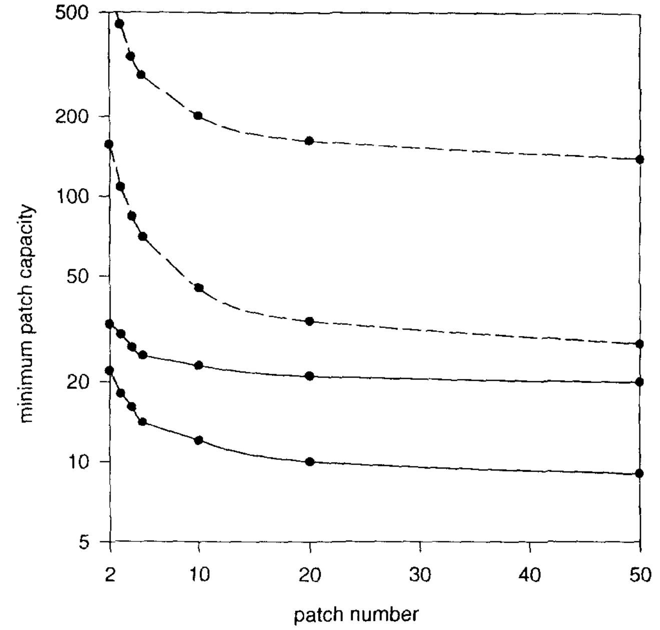

**Fig. 1.** Minimum patch capacities which are necessary to obtain a metapopulation lifetime of $T_{meta} = 2000/r$ as a function of the patch number. Solid lines: strong environmental fluctuations ($\sigma 2 = 0{\cdot}95r$); dashed lines: weak environmental fluctuations ($\sigma^2 = 0{\cdot}1r$). Upper curve of each pair: small connectivity factor ($d = 0{\cdot}05$); lower curve: large connectivity factor ($d = 0{\cdot}95$).

Figure 1 shows that these are the minimum patch capacities that are required in a long-lived metapopulation if there are only two poorly connected patches ($d = 0{\cdot}05$). As two poorly connected patches is the worst case considered in this study, patch capacities above 35 and 600 (weak and strong environmental fluctuations, respectively) should always lead to viable metapopulations. The discussion of metapopulation viability is therefore non-trivial only if the patch capacities are below these values. Plausible ranges for the other model parameters are derived in the Appendix.

## Evaluation of management options

We assume that a metapopulation is in danger of extinction and there is a choice between three different management options which are the increase of the capacities, the number and the connectivity of the patches. We expect their influences on the lifetime of the metapopulation to depend on the specific environmental conditions. In order to keep the discussion simple we divide the large variety of different environmental situations into 16 classes which we call 'scenarios'. We define a scenario by whether each of the four parameters, environmental fluctuations, patch capacity, immigration rate and patch number, is large or small (Table 1). The values of Table 1 represent large and small values with respect to the plausible ranges of the model parameters. For the derivation of these ranges, see above and the Appendix. Demographic fluctuations, $\gamma$, and emigration rate, $e$, are not considered in the table. Demographic fluctuations are kept fixed at a value of $\gamma = 3r$ and deviating values are discussed separately in the Appendix. As we consider only small emigration rates (Methods), emigration affects the metapopulation dynamics only via the immigration rate (Appendix: Parameter Ranges) which is already considered in Table 1.

For each of the 16 scenarios we have calculated the triple ratio, $I_k : I_d : I_s$ (see Methods), which represents the relative influences of the three 'management parameters', patch number, patch capacity and connectivity factor. We found that the triple ratios obtained for the scenarios with large patch capacities and low immigration are similar to the triple ratios obtained for small patch capacities and high immigration. These scenarios are intermediate cases lying between the 'extreme' scenarios, where both patch capacity and immigration rate are large or small. Therefore, the results for the intermediate scenarios can be obtained by an interpolation between the extreme scenarios and need not be considered separately. Further, the triple ratio turned out to be independent of the environmental fluctuations and the patch number when both the patch capacity and the immigration rate were small. With this only five different scenarios have to be distinguished (Fig. 2).

### *Metapopulations with small and poorly connected patches (Scenario 1)*

Here both the patch number and the connectivity factor have a rather small influence, whereas the influence of the patch capacity is very large ($I_k : I_d : I_s = 10{:}1{:}1$). This is because small and short-lived subpopulations are not able to recolonise empty patches — regardless of the connectivity factor. So the metapopulation lifetime can best be increased by increasing the patch capacity.

### *Metapopulations with few large and well connected patches and weak environmental fluctuations (Scenario 2)*

Here the influence of the patch capacity is large compared with the influences of patch number and connectivity factor ($I_k : I_d : I_s = 5{:}1{:}2$). The reason is that in a weakly fluctuating environment, the influence of the habitat capacity on the lifetimes of small (sub) populations is large (Goodman, 1987*a*,*b*; Shafer, 1990; Lande, 1993; Wissel *et al.*, 1994).

### *Metapopulations with few large and well connected patches and strong environmental fluctuations (Scenario 3)*

Here the influence of the patch capacity is smaller than in Scenario 2 ($I_k : I_d : I_s = 2{:}1{:}2$). The reason is that increasing environmental fluctuations reduce the influence of the habitat capacity on the lifetimes of small populations (Goodman, 1987*a*,*b*; Shafer, 1990; Lande, 1993; Wissel *et al.*, 1994). Therefore, it may also be reasonable to reduce the extinction risk of the metapopulation by

**Table 1. Large and small values with respect to the plausible ranges of four model parameters, including environmental fluctuations, patch capacity, immigration rate and patch number** Environmental fluctuations, $\sigma^2$, and immigration rate, $i$, are scaled in units of the mean intrinsic growth rate, $r$. Note that the question whether a patch capacity is regarded as large or as small, depends on the environmental fluctuations, $\sigma^2$.

| Model parameter | Small | Large |
|---|---|---|
| Environmental fluctuations, $\sigma^2$ | $0{\cdot}1r$ | $0{\cdot}95r$ |
| Patch capacity, $K$ ($\sigma^2 = 0{\cdot}1r$) | 15 | 30 |
| ($\sigma^2 = 0{\cdot}95r$) | 100 | 500 |
| Immigration rate, $i$ | $0{\cdot}01r$ | $0{\cdot}1r$ |
| Patch number, $S$ | 3 | 15 |

increasing the patch number. The influence of the connectivity factor is comparatively small.

*Metapopulations with many large well connected patches (Scenarios 2a and 3a)*

The difference between Scenarios 2 and 2a and Scenarios 3 and 3a is that the influence of the patch number on the metapopulation lifetime is comparatively low, if the patch number is already large. With this, Scenarios 2a and 3a are qualitatively similar to Scenario 1, but with a weaker influence of the patch capacity.

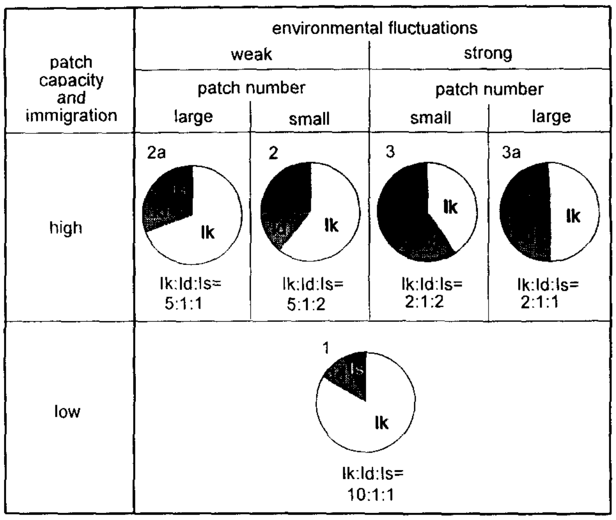

**Fig. 2.** Direct comparison of the sensitivity coefficients $I_k$, $I_d$ and $I_s$, of the three quantities, patch capacity $K$, connectivity factor $d$, and patch number $S$. The relative influences of these three parameters depend on the particular scenario (numbered as 1, 2, 2a, 3 and 3a), i.e. on the number of patches $S$, the immigration rate $i$, environmental fluctuations $\sigma^2$, and the patch capacity, $K$.

## DISCUSSION

With a general model which explicitly considers important aspects of metapopulation dynamics such as dispersal and environmental and demographic stochasticity, we evaluated the influences of three plausible management options. These are the increase of the capacities, the number and the connectivity of the patches. We analysed a systematic array of parameter combinations, 'scenarios', and found that the sensitivity of a particular management option depends on the scenario. We identified five representative scenarios which encompass all of the variability (Fig. 2). From Fig. 2 a few well-known conclusions can be drawn.

1. The patch capacity has always a considerable influence on the viability of a metapopulation. This agrees with the results of other studies, for instance Lindenmayer and Lacy (1995), and it can also be seen from the analytical formula derived by Nisbet and Gurney (1982).
2. The stronger the environmental fluctuations, the weaker the influence of the patch capacity on the life time of a subpopulation (Goodman, 1987*a*,*b*; Shafer, 1990; Lande, 1993; Wissel *et al.*, 1994) and the larger the patch capacities that are needed in a viable metapopulation (Results: Non-trivial metapopulations). Provided that the patch capacities are large enough to sustain fairly viable subpopulations ('large' patch capacities; Table 1), an increase of the patch number may be an effective option when environmental fluctuations are strong and the patch number is small.
3. The effect of the demographic fluctuations on the subpopulation life times is converse to that of the patch capacity (Appendix), i.e. an increase in the demographic fluctuations has a similar effect as a decrease in the patch capacity. This means that with increasing demographic fluctuations larger patch capacities are needed (McCarthy *et al.*, 1994).

Figure 2 also provides some new results which are discussed in detail below.

(a) Within the considered parameter range, the patch capacity always has a stronger influence on the lifetime of a metapopulation than patch number and connectivity.
(b) If the subpopulations are small, an increase of the patch capacity is much more promising than an increase in patch number or connectivity.
(c) The same is true if dispersal between the patches is very low.

The main reason behind these results is that the viability (extinction rate) of a subpopulation and its ability to colonise other patches (colonisation rate) are not independent quantities, and both depend on the local parameters, such as the patch capacity (an aspect that has been ignored in all general models we have found in the literature). Consequently, habitat management that increases the patch capacity will not only increase the lifetime of a subpopulation but also its size and (assuming that this will not decrease the per capita emigration rate) hence the number of dispersers and the colonisation rate. This contributes to the special role of the patch capacity ((a) above).

Conversely, a reduction in patch capacity will destabilise the subpopulations and reduce the number of dispersers. Eventually the patch capacity may become so small that even under perfect dispersal conditions, the turnover ratio of colonisation and extinction rates may fall below the critical threshold of one (see Results). In such a case the viability of the metapopulation can only be increased by increasing the turnover ratio and this can be only achieved by increasing size and persistence of the subpopulations. An increase in patch number and connectivity has almost no effect, which agrees with results by Lindenmayer and Lacy (1995). Such a scenario may sound extreme, but it explains why the patch capacity becomes more and more important as the subpopulations become critically small ((b) above). Similarly, if dispersal is weak, even a substantial improvement of connectivity is likely to have a smaller effect than an increase in size and persistence of subpopulations ((c) above). Conversely, the stronger the dispersal, the greater the relative importance of patch connectivity.

The study was based on a number of assumptions which are likely to affect the results.

1. Spatial heterogeneity in the metapopulation was ignored. In particular, all patches were assumed to be equal in size and quality and their spatial arrangement was ignored. Dispersal mortality was assumed to be distance-independent. The results of this study cannot be directly applied to a spatial heterogeneous metapopulation, mainly because it cannot assess the importance of a particular patch or the connectivity between two particular patches. Whether spatial heterogeneity increases the importance of patch number and connectivity relative to the importance of the patch capacity remains to be seen. However, we believe that there will still be a relationship between subpopulation viability and the importance of habitat networks such that the benefit from habitat networks is reduced when subpopulations become critically small.
2. Environmental correlations have been ignored. Gilpin (1990), Akçakaya and Ginzburg (1991) and Frank *et al.* (1994) showed that long-range environmental correlations reduce the benefit to a metapopulation from the recolonisation of empty patches. This reduces the effectiveness of corridors as a means to improve recolonisation. Ignoring long-range environmental correlation, therefore, is likely to lead to an overestimation of the value of habitat networks. In contrast, if environmental correlations have a short correlation-length so that dispersers have a chance to escape from unfavourable conditions, habitat networks can play an important role (e.g. Lindenmayer & Possingham, 1996).
3. Emigration and immigration rates are small compared to the growth rate of the subpopulations. In particular, the rescue effect (Brown & Kodric-Brown, 1977) is weak in this case (Drechsler, unpublished data). Therefore, in cases of higher dispersal rates, the role of habitat networks is likely to be more important than indicated in this study (see Discussion of Point (c) above).
4. The chance that an individual emigrates was assumed to be independent of subpopulation size. This type of dispersal has been observed in goldenrod beetles *Trirhabda virgata* (Herzig, 1995). Other types of dispersal will change the influence of the subpopulation size on the total number of dispersers and hence on the colonisation rate.
5. Very strong environmental fluctuations ($\sigma^2 > r$) were not considered. This excludes those species that are dominated by environmental fluctuations ('$r$-selected' species; see Appendix). As this study shows, with increasing environmental fluctuations ('moving into the $r$-selected regime') the importance of the number of patches increases (den Boer, 1968).

Demography, such as age-dependence in birth, death and dispersal rates, was ignored. This may result in an underestimation of demographic fluctuations (McCarthy *et al.*, 1994) and is also likely to reduce the viability of the subpopulations and the recolonisation of empty patches (Lindenmayer & Lacy, 1995).

## CONCLUSION

The study confirmed that subpopulation viability is the key to metapopulation stability and suggests that its role may have been underestimated in previous studies. There is no general answer to the question whether it is better to focus on local or regional scale management. Although the numerical results downplay the importance of patch connectivity, this study does not argue against corridors and habitat networks in general. It rather demonstrates that their effect is likely to depend on a number of factors, including the viability of the subpopulations. In metapopulations with viable subpopulations, the number and connectivity of patches can be of considerable importance. However, if the overall viability of the subpopulations is critically low the potential of the subpopulations to colonise empty patches is likely to be small and the stabilising effect of corridors is limited. In this case, local management to increase the viability of the subpopulations may be the only promising management option.

Apart from these general considerations, the practical applicability of this model study is limited. It made a number of simplifying assumptions, especially regarding spatial aspects. Therefore, in conservation problems, the results should be applied only as general guidelines. Practical considerations, local constraints and the particular attributes of the species in hand and its habitat will govern the best decisions in any single instance.

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## APPENDIX

### Calculation of the rate, $c$ (eqn (6))

The rate, $c$, by which an empty patch is recolonised, is the inverse of the average time needed for the recolonisation process (Drechsler & Wissel, 1997). The recolonisation process is regarded as complete when the patch has reached a large individual number $N$ close to the expected individual number of an occupied patch, $<n>$ (see below). After Goel and Richter-Dyn (1974), the average time that it takes for an empty patch to reach an individual number, $N$, is given by

$$T_{N0} = \sum_{n=0}^{N}\sum_{u=0}^{n}\frac{1}{\lambda_u}\prod_{v=u+1}^{n}\frac{\mu_v}{\lambda_v} \qquad \text{(A1)}$$

where $\lambda_j$ and $\mu_j$ are given by eqn (3) and eqn (4). This sum can be re-ordered to

$$T_{N0} = \frac{1}{i \cdot E} + T_{N1} \qquad \text{(A2)}$$

Here $E$ is the probability that the immigration of an individual leads to the establishment of a subpopulation of size $N$:

$$E = \left(\sum_{n=1}^{N}\prod_{v=1}^{n-1}\frac{\mu_v}{\lambda_v}\right)^{-1} \qquad \text{(A3)}$$

(Goel & Richter-Dyn, 1974; Wissel *et al.*, 1994) and $T_{N1}$ is the average time that it takes for a single immigrant to establish a subpopulation of size $N$:

$$T_{N1} = \sum_{n=1}^{N}\sum_{u=0}^{n}\frac{1}{\lambda_u}\prod_{v=u+1}^{n}\frac{\mu_v}{\lambda_v} \qquad \text{(A4)}$$

(Goel & Richter-Dyn, 1974). By a numerical analysis we found that $T_{N1}$ is small compared with $1/(i \cdot E)$ if $i < 0 \cdot 1r$. As we consider such small immigration rates only (Methods), we can neglect $T_{N1}$ in eqn (16) and obtain

$$c = \frac{1}{T_{N0}} \approx i \cdot E \qquad \text{(A5)}$$

### Calculation of the expected subpopulation size, $<n>$

Drechsler and Wissel (1997) calculated the probability, $P_n^{quasi}$, of observing a particular individual number, $n$, in a subpopulation. The probabilities, $P_n^{quasi}$, form a so-called 'quasistationary distribution' and can be expressed by the birth and death rates, eqns (3) and (4) (Goel & Richter-Dyn, 1974; Nisbet & Gurney, 1982; Wissel & Stöcker, 1991). From this probability distribution we calculate the expected size of the subpopulation by

$$<n> = \sum_{n \geq 1} n P_n^{quasi} \qquad \text{(A6)}$$

As we consider small immigration rates only (Methods), their effect on the local dynamics and the expected subpopulation size is weak.

### Discussion of the turnover dynamics and eqn (11)

We analysed the turnover dynamics of local extinctions and recolonisations with rates, eqns (7) and (9), and calculated the probability, $P_{meta}$, of finding at least one patch occupied (Wissel & Stöcker, 1991). The result is shown in Fig. A1 for $S = 10$ patches and three different turnover ratios, $m/x$. At a large turnover ratio, $m/x = 10$, we find an exponential decrease of $P_{meta}$ at a rate of $1/T_{meta}$ (solid line) and the approximation, eqn (11), is valid. A very small turnover ratio, $m/x = 0{\cdot}1$, leads to strong deviations from the exponential decay (dash-dotted line). We exclude those metapopulations with very small turnover ratios from our viability analysis, because they lead to trivial results (Results). With increasing turnover ratio, the exponential approximation of $P_{meta}$ improves. The dashed curve ($m/x = 1{\cdot}5$) still shows deviations from the exponential shape of the solid curve, but a qualitative similarity between both curves can be observed. We conclude that in metapopulations with 'trivial' turnover ratios, $m/x < 1$, the exponential approximation of $P_{meta}$, eqn (11), is not valid. In metapopulations with 'non-trivial' turnover ratios, $m/x > 1$, the exponential approximation is not always perfect in a quantitative sense, but qualitatively it well describes the decay of $P_{meta}$ with time $t$. The rate

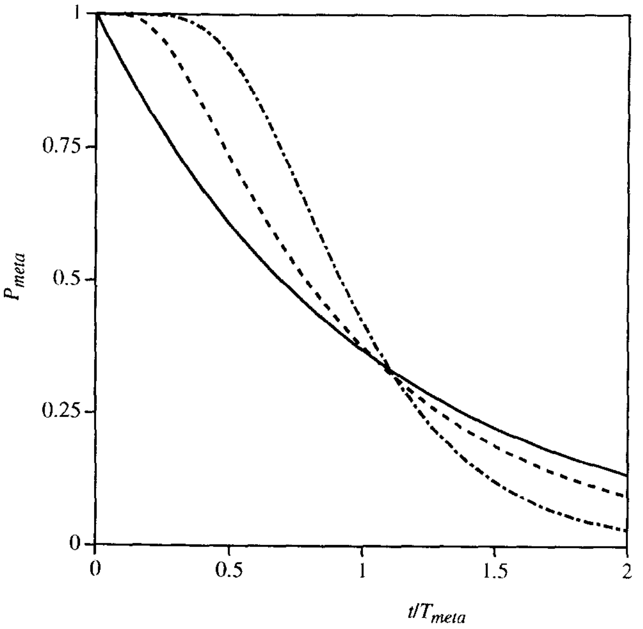

**Fig. A1.** Probability of metapopulation survival, $P_{meta}$, as a function of time, $t$, in units of the expected lifetime of the metapopulation, $T_{meta}$. The number of patches is $S = 10$ and the turnover ratios are $m/x = 0{\cdot}1$ (dash-dotted line), $1{\cdot}5$ (dashed line), and 10 (solid line).

of this decay is in good approximation given by $T_{meta}$, which therefore represents a suitable measure for the viability of a 'non-trivial' metapopulation.

### Suitable ranges for the model parameters

As described in the Methods section, the model is valid only if $i < 0{\cdot}1r$ and $\sigma^2 \leq r$. According to the latter inequality, we can consider a range of environmental fluctuations of $\sigma^2 \leq r$. When we choose a large value of $\sigma^2 = 0{\cdot}95r$ we can consider emigration rates up to $0{\cdot}1r$. When we choose a small value for $\sigma^2$ larger emigration rates can be considered. However, as the immigration rate depends on the emigration rate (eqn (8)), emigration rates above $0{\cdot}1r$ are likely to violate the upper bound for the immigration rate of $i < 0{\cdot}1r$ set above. Therefore the study is restricted to small emigration rates, $e < 0{\cdot}1r$. Consequently, such small emigration rates have little impact on the subpopulation growth and the local dynamics. They affect the metapopulation dynamics only via the immigration rate (eqn (8)).

A lower bound for the immigration rate, $i > 10^{-3}r$, has to be set to exclude trivial turnover ratios, $m/x < 1$ (see above and Results). Further, Fig. 1 suggests that one may restrict the range of considered patch numbers to $S < 20$, as it shows that the size of the patch capacities required in a viable metapopulation does not strongly change when the patch number is increased from 20 to higher values (Results). Finally, the plausible range of demographic fluctuations is $r < \gamma < 5r$ (see below). In the model analysis we choose a median value of $\gamma = 3r$ and discuss variations from this value below.

### The role of the demographic fluctuations

Below, a biologically plausible range for the demographic fluctuations, $\gamma$, will be derived, followed by a discussion of their impact on the dynamics. To translate $\gamma$ into a more intuitive quantity, we take up some unpublished considerations by Wissel and Zaschke and consider the reproductivity, $R_0$, of an individual, which we define as the total number of offspring produced by the individual during its expected lifetime, $L$. The expected lifetime of an individual is the inverse of its death rate. The rate at which an individual produces its offspring, may be denoted as $f$. During its entire expected lifetime, $L$, an individual will then produce a number of $R_0 = f \cdot L$ offspring.

For the special case where environmental fluctuations and density-dependent effects play no role ($\sigma^2 = 0$ and $1/K = 0$), the quantities $f$ and $L$ can be calculated very easily. In that case the death rate of $n$ individuals is $\mu_n = 0{\cdot}5n(\gamma - r)$ (eqn (4)), and $n$ individuals produce offspring at a rate of $\lambda_n = 0{\cdot}5n(\gamma + r)$ (eqn (3); note that the migration rates, $e$ and $i$, which contribute to subpopulation growth, do not contribute to the actual births and deaths of individuals). With this, the expected lifetime of one individual and the rate by which it produces its offspring are

$$L = \frac{1}{\mu_n/n} = \frac{2}{\gamma - r} \quad \text{and} \tag{A7}$$

$$f = \lambda_n/n = 0.5(\gamma + r) \tag{A8}$$

With eqns (A7) and (A8), the reproductivity of an individual becomes $R_0 = f \cdot L = (\gamma + r)/(\gamma - r)$. This can be re-ordered to

$$\frac{\gamma}{r} = \frac{R_0 + 1}{R_0 - 1} \tag{A9}$$

Equation (A9) implies that a high reproductivity, $R_0 >> 1$, results in weak demographic fluctuations, $\gamma \approx r$, and that $\gamma$ always exceeds the mean intrinsic growth rate, $r$ (cf. remarks following eqns (3) and (4)). A lower limit for the reproductivity may be given by $R_0 > 1{\cdot}5$. According to the definition of $R_0$ above, this means that two individuals will produce at least three offspring during their expected lifetime. In the case where environmental fluctuations and density dependence play no role, thus that eqn (23) is valid, a value of $R_0 = 1{\cdot}5$ is equivalent to $\gamma = 5r$, and we obtain an upper limit for the demographic fluctuations of $\gamma < 5r$. For simplicity these two bounds, $\gamma > r$ and $\gamma < 5r$, are applied in the entire study, regardless of environmental fluctuations and density-dependent regulation.

The role of the demographic fluctuations in the metapopulation dynamics is rather simple. Wissel and Stöcker (1991) found that in the absence of emigration and immigration, the expected lifetime of a single population does not depend on the single quantities, patch capacity and demographic fluctuations, $K$ and $\gamma$, but solely on their ratio $K/\gamma$. We found the same for the expected lifetime, $T_{sub}$, of a subpopulation, as long as dispersal is low. So the demographic fluctuations have an effect on the lifetime of a subpopulation converse to that of the patch capacity. For instance, an increase in the demographic fluctuations from $\gamma = 3r$ to a value of $\gamma = 5r$, would have the same effect on the subpopulation lifetime as a decrease in the patch capacity, $K$, by a reciprocal factor of 3/5.

### Classification of the environmental fluctuations

In Table 1, environmental fluctuations were classified by comparing $\sigma^2$ to the mean subpopulation growth rate, $r - e$. In particular, the cases with $\sigma^2 << r - e$ were called 'weak environmental fluctuations' and $\sigma^2 \leq r - e$ was called 'strong environmental fluctuations'. The range $\sigma^2 > r - e$ may be denoted as 'very strong environmental fluctuations'. To provide a rough biological feel for this classification, consider the following. One can show that in the region of 'very strong environmental fluctuations' the expected subpopulation size is nearly independent of the patch capacity. This indicates that density-dependent regulation is not effective in this region, which may be typical for a so-called $r$-selected species (MacArthur & Wilson, 1967; Stearns, 1992). In the cases of 'weak environmental fluctuations' one finds that the expected subpopulation size is close to the patch capacity which indicates strong density-dependent regulation ('K-selected' species). In the cases of 'strong environmental fluctuations' one finds the expected subpopulation sizes to be much lower than, but still proportional to, the patch capacity, which indicates weak density-dependent regulation.