# Effects of patch connectivity and arrangement on animal metapopulation dynamics: a simulation study

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ABSTRACT

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We constructed a simulation model of metapopulation dynamics consisting of two or three habitat patches using STELLA. our simulations show that, given the assumptions of the deterministic model, the metapopulation is doomed to global extinction with or without interpatch immigration when all local populations are below minimum viable population (MVP) size. This suggests that for a cluster of scattered small populations, it is preferable to focus on augmenting individual population sizes rather than enhancing interpatch immigration. In the case when at least one of the subpopulations is above the MVP size, there is a critical size for that subpopulation above which the metapopulation persists and otherwise collapses. Also, when a metapopulation system is composed of more than two patches, the spatial configuration in terms of patch connection and the relative position of the above-MVP subpopulation will have significant effects on metapopulation dynamics and persistence. All simulation results from the three-patch animal metapopulation model suggest that both the number of interpatch connections and the magnitude represented by them are crucial for overall patch connectivity. The magnitude of interpatch immigration is positively related to the minimum size of the above-MVP subpopulation in both the two- and three-patch metapopulation systems due to population sink effect. The phenomenon is especially significant when subpopulations in sink patches are well below MVP. Appropriate introduction of stochastic components into the model may increase its realism especially for the cases where all subpopulations are well below MVP. Although the current version of the model involves no more than three patches, it may serve as a general conceptual framework and a specific simulator for modeling metapopulation dynamics incorporating a variety of spatial arrangements of habitat patches.

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INTRODUCTION

Most if not all species live in patchy environments. This has become increasingly true because of landscape fragmentation throughout the world. Nature reserves, national parks, wildlife refuges, and fragments of natural landscapes isolated to varying degrees are all examples of patchy or mosaic habitats. The set of local (patch) populations of a species in spatially discrete habitats may be called a metapopulation. The term metapopulation, describing "a population of populations", was first coined by Levins (1970) in a now-classical paper on group selection and extinction, although the idea that spatially heterogeneous populations experience local extinctions and recolonizations had been expressed in the context of population genetics (Wright, 1940), population dynamics (Andrewartha and Birch, 1954; Ehrlich, 1965; den Boer, 1968; Ehrlich and Raven, 1969), and species diversity on isolated habitats (MacArthur and Wilson, 1963, 1967; see Simberloff, 1988 and Hanski and Gilpin, 1991 for reviews). However, it was not until the late 1980s that the concept of metapopulation was rediscovered and spurred greatly by interests in population dynamics in heterogeneous environments, conservation biology, and landscape ecology (e.g., Quinn and Hastings, 1987; Opdam, 1988, 1991; Harrison et al., 1988; Merriam, 1988; Hanski, 1989, 1991; Harrison and Quinn, 1989; Hastings and Wolin, 1989; Gilpin, 1990, 1991; Wu, 1989, 1990, 1992a,b; Wu et al., 1990; Wu and Vankat, 1991a,b; Merriam et al., 1991; Hanski and Gilpin, 1991).

"Modeling populations of plants and animals presents a greater challenge than finding good representations of molecular behavior" (Roberts, 1978). Models of population dynamics in heterogeneous environments have been developed during the past two decades. Most of them fall into two distinctive categories: patch-occupancy and diffusion-reaction models (Levin, 1976a,b, 1978; DeAngelis et al., 1986). Patch-occupancy models deal with a large number of patches and involve both single-species dynamics and multi-species coexistence (e.g., interspecific competition and predator–prey interactions). The state variables are usually the proportions of patches occupied and unoccupied by a species' populations or by different species. A simple and widely used patch-occupancy model is Levins' (1969, 1970) original model which describes the dynamics of a single species metapopulation in a heterogeneous environment composed of homogeneous (identical) patches:

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp(1 - p) - ep$$

where $p$ is the proportion of patches occupied by the species and $m$ and $e$

are constants that are related to the colonizing ability and extinction rate of the species, respectively. Patch-occupancy models have been widely used in studies on the dynamics of patchy populations (e.g., Levins, 1970; Levins and Culver, 1971; Hanski, 1983, 1991).

The framework of the diffusion-reaction models takes the following general form:

$$dY(i)^u/dt = f(i)^u(\mathbf{Y}^u, \mathbf{X}^u) + (\text{net exchange with other patches})$$
$$+ (\text{net exchange with matrix})$$

in which $\mathbf{Y}^u$ is the vector $(Y1^u, Y2^u, \ldots, Yn^u)$ of state variables for a given patch $u$, $\mathbf{X}^u$ the vector $(X1^u, X2^u, \ldots, Xn^u)$ of parameters accounting for the same patch, and $f^u$ the specific functional relationship (Levin, 1976b; also see Levin, 1976a; Okubo, 1980; Hastings, 1982; Allen, 1983a,b, 1987). These models take into account both temporal and spatial heterogeneity for given state variables, such as population densities, with the aid of analytical power of mathematical diffusion theory. These models can further be divided into continuous and discrete types according to their different conceptualization and mathematical details. A simple, yet representative, example of the continuous diffusion-reaction model may be in the partial differential equation form of

$$\frac{\partial N(x,t)}{\partial t} = Nf(N) + \frac{\partial[D\ \partial N(x,t)]}{\partial x}$$

where $N(x, t)$ is the population density relative to the spatial position $x$, $D$ is the diffusion rate of individuals of the population, and $f(N)$ is the population growth rate (Hastings, 1990). The corresponding discrete model may be written as

$$\frac{dN_i}{dt} = N_i f(N_i) + \sum_{j \neq i} \left[ d_{ij}(N_j - N_i) \right]$$

where $d_{ij}$ is the exchange rate of individuals between patch $i$ and patch $j$ and $N_i$ and $N_j$ are population sizes in the two patches, respectively (cf. Levin, 1974). Patch-occupancy and diffusion-reaction models have made significant contributions to our current understanding of patch dynamics from a populational perspective.

The interactions between patches in a fragmented landscape may play an important role in the dynamics and persistence of metapopulations. The persistence of species may be related to matrix characteristics and the number, area, spatial arrangement, and disturbance regime of patches. These subject matters are also central concerns of the emerging field – landscape ecology (Forman, 1981; Forman and Godron, 1986; Vankat et

al., 1991; Wu and Vankat, 1991a,b) and conservation biology (Soule, 1986, 1987; Wu, 1990, 1992a,b). On the other hand, metapopulation dynamics may, to a large extent, affect or determine the spatial-temporal heterogeneity and pattern-process relationships of landscapes.

The studies of the dynamics and persistence of such animal metapopulations may not only have great theoretical values for landscape ecology and conservation biology, but also may provide important practical implications for nature conservation and resources management. Studies of metapopulation dynamics and stability have become an important and integral part of both conservation biology and landscape ecology (e.g., Fahrig et al., 1983; Fahrig and Merriam, 1985; Urban and Shugart, 1986; Gilpin, 1987, 1990; Henein and Merriam, 1990; May and Southwood, 1990; Smith and Peacock, 1990; Wu, 1990, 1992a,b; Opdam, 1991).

The dynamics of a metapopulation are products of interactions of local and regional processes. Interpatch immigration plays a pivotal role in these dynamics, with animal populations differing significantly from plants in that the dispersals of seeds and other propagules do not directly affect the plant population size of the source patch but emigration of animals reduces the population size in the source patch (see Wu et al., 1990). This difference in dispersal between plants and animals may have significant consequences for the general behavioral pattern and specific dynamic properties of metapopulations. In this study, metapopulation models are developed with incorporation of the above-mentioned characteristics of animal dispersal. Effects of subpopulation sizes, interpatch immigration, and patch configurations on metapopulation dynamics and persistence are examined through a series of simulations.

MODEL STRUCTURE AND FORMULATION

The metapopulation models are composed of two and three single-patch population models. The structural diagrams of the two-patch and three-patch animal population models are presented in Figs. 1 and 2, depicting the model variables and their relationships. It is assumed that local populations are subject to density-dependent regulation and that there exists a threshold population size below which local extinction would occur immediately. We define this critical population level as the minimum viable population (MVP) size which is basically a deterministic version of the concept defined by Shaffer (1981, 1987). Each habitat patch has a certain carrying capacity which might in turn be determined by its area and habitat diversity. For simplicity and convenience, however, this version of the model does not take account of the relationships between the carrying capacity and its potential determinants. A MVP value of 50 and a carrying
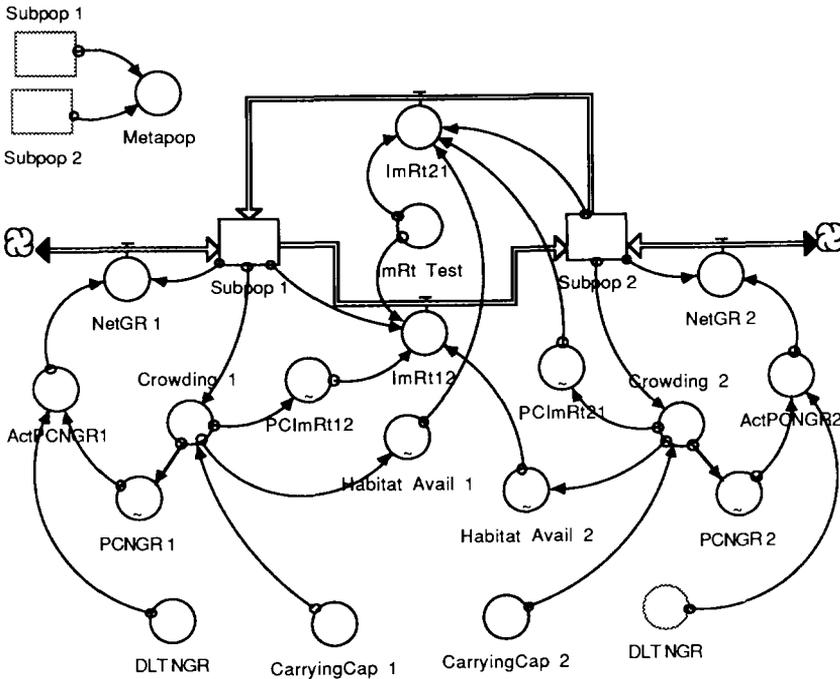
Fig. 1. Structural diagram of the two-patch animal population model.

capacity of 500 are used in the simulations. These values can be easily modified to fit a particular species when relevant data are available. The use of a MVP value of 50 is arbitrary and will not fit all species.

The degree of local crowding is modeled as the ratio of population size to the carrying capacity, which in turn determines per capita net growth rate. The relationship between crowding and per capita net growth rate is treated as a graphical function (Fig. 3), which can easily be modified to fit a particular density-dependently regulated species population. The general shape of the curve is agreeable with those reported for some field and experimental populations, including the ring-necked pheasant, the fruit-fly, and Antarctic fin whales (see Begon et al., 1986). Time delays in populational regulation, reflecting time-lagged populational responses in per capita net growth rate to crowding effect, are also incorporated in the model.

Local populations interact with each other through interpatch immigration and emigration and, consequently, constitute a metapopulation in the given patchy habitat setting. The existence of interpatch immigration does not necessarily mean that there are physical conduits (i.e., dispersal corridors) present between patches. The emphasis here is the consequences of
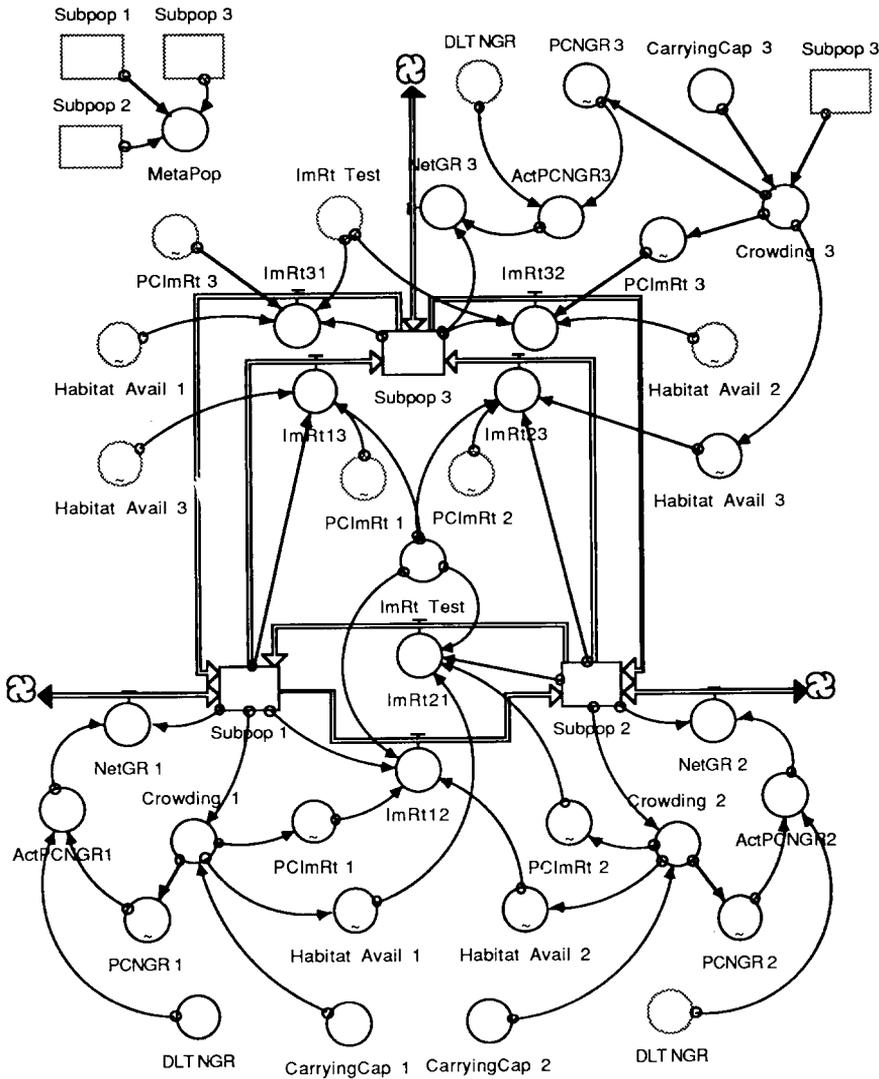
Fig. 2. Structural diagram of the three-patch animal population model.

interpatch immigration, not the means or mechanism of the process. We assume that the individuals moving out of a subpopulation go directly into other connected patches. Therefore, the metapopulation system is a conserved one in terms of immigration and emigration. In addition, the per capita (or percent) emigration rate in these models is assumed density-dependent; specifically, it has a positive relationship with crowding (Fig. 4). The immigration rate of a recipient patch is determined by its habitat availability for immigrants and the per capita emigration rate and popula-

| Input | Output |
|-------|--------|
| 0.00 | −0.15 |
| 0.1 | 0.00 |
| 0.2 | 0.076 |
| 0.3 | 0.088 |
| 0.4 | 0.088 |
| 0.5 | 0.088 |
| 0.6 | 0.086 |
| 0.7 | 0.082 |
| 0.8 | 0.062 |
| 0.9 | 0.032 |
| 1.00 | 0.00 |
| 1.10 | −0.032 |
| 1.20 | −0.072 |

PCNGR · 0.2 · −0.2 · Crowding · 0.00 · 1.20 · 0.00 · 1.50 · Data Points: 16 · Edit Output: · To equation · Delete graph · Cancel · OK
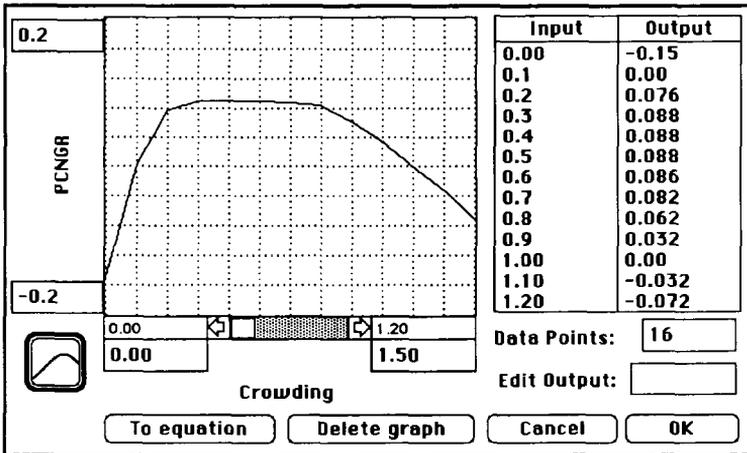
Fig. 3. Assumed relationship between crowding (population-size/carrying-capacity ratio) and per capita net growth rate in the two and three-patch animal population models.

tion size of the source patches. The habitat availability of a patch is negatively related to the degree of crowding, which is input as a graphical function (Fig. 5).

The dynamics of a metapopulation are the totality of changes in its component subpopulations. The size of each subpopulation at any moment is determined by its net growth rate and net interpatch immigration rate. In this particular model, the sources for immigration are the subpopulations

| Input | Output |
|-------|--------|
| 0.00 | 0.0525 |
| 0.1 | 0.0775 |
| 0.2 | 0.117 |
| 0.3 | 0.175 |
| 0.4 | 0.26 |
| 0.5 | 0.32 |
| 0.6 | 0.362 |
| 0.7 | 0.39 |
| 0.8 | 0.412 |
| 0.9 | 0.43 |
| 1.00 | 0.442 |
| 1.10 | 0.455 |
| 1.20 | 0.465 |

PCImRt · 0.5 · 0.00 · Crowding · 0.00 · 1.20 · 0.00 · 1.50 · Data Points: 16 · Edit Output: · To equation · Delete graph · Cancel · OK
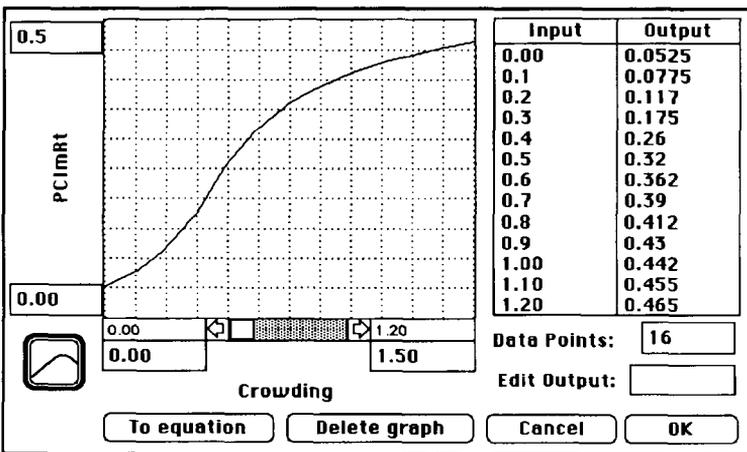
Fig. 4. Assumed relationship between crowding and per capita interpatch emigration rate in the two- and three-patch animal population models.
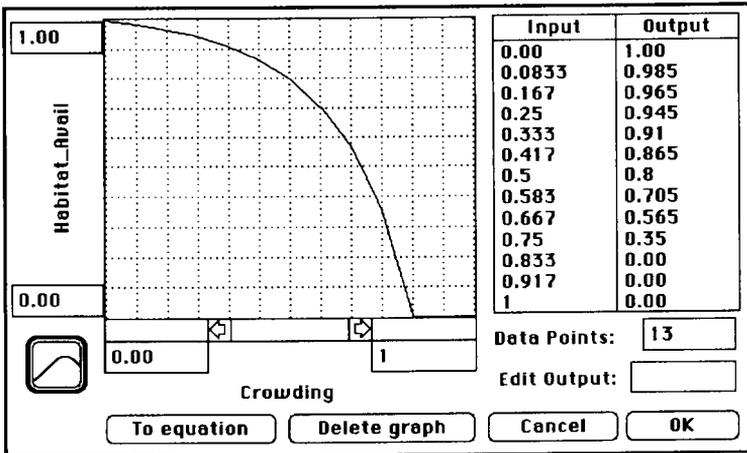
Fig. 5. Assumed relationship between crowding and habitat availability for interpatch immigrations in the two and three-patch animal population models.

themselves, as no outside dispersal pool is considered. This is much the case for today's fragmented landscapes (Burgess and Sharpe, 1981; Gilpin, 1987; Opdam, 1991). However, external immigration sources could be incorporated in the model when needed. For such a closed system, emigration and immigration are modeled in a combined term, as they are only relative terms for interactive habitat patches (i.e., interpatch emigration for one patch is interpatch immigration for the other). The relationships of which-influences-which type among all variables are explicitly depicted in structural diagrams (Figs. 1 and 2). All model equations, constants and table functions (corresponding to graphical inputs) are provided in the Appendix for both the two-patch and three-patch animal metapopulation models, respectively.

MODEL SIMULATION AND ANALYSIS OF RESULTS

*1. Population dynamics without interpatch immigration*

Both the two-patch and three-patch animal population models are simulated with all interpatch immigration rates being set zero (i.e., ImRt_Test = 0 in the STELLA equations) for the purpose of verification and understanding the fundamental behavior of the basic unit model – the one-patch module.

As shown in Fig. 6, the behavior of local populations exhibits complete agreement with the model assumptions. When the initial sizes are 50 (the assumed MVP value), the isolated populations remain unchanged, demon-

Initial pop:  Curve 1: 50     Curve 2: 49      Curve 3: 51       Curve 4: 100       Curve 5: 800



Initial pop:        Curve 1: 100      Curve 2: 100      Curve 3: 100      Curve 4: 70
Delay time:         Curve 1: 3        Curve 2: 5        Curve 3: 10       Curve 4: 99999
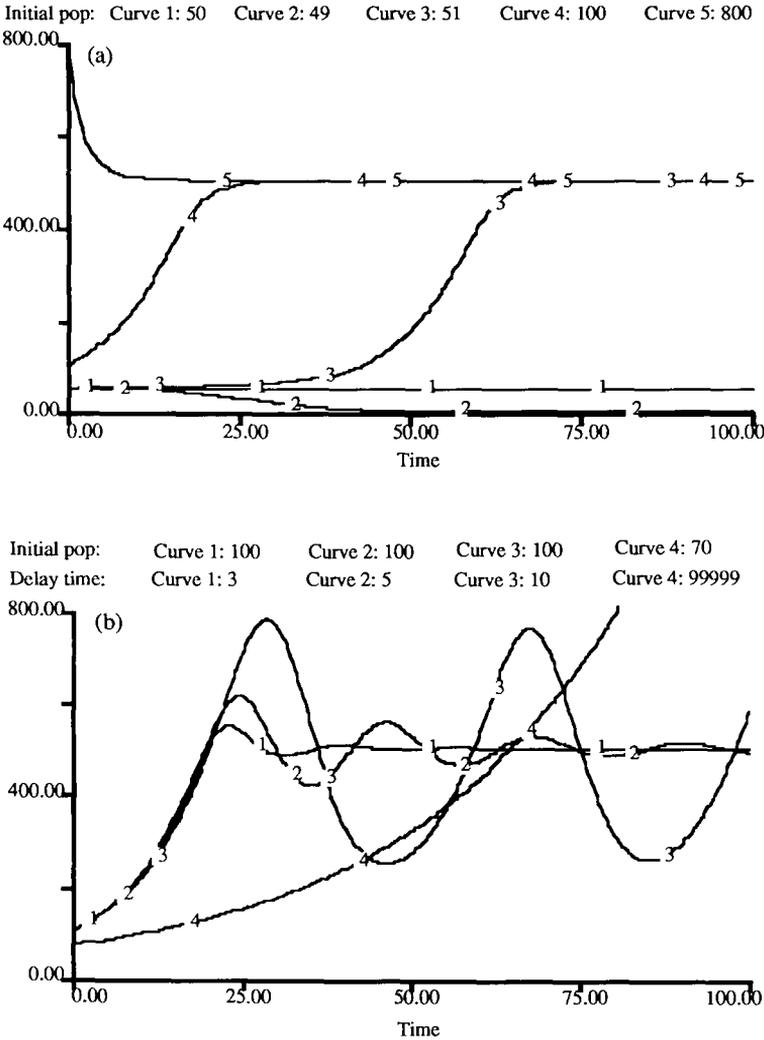


Fig. 6. Simulated dynamics of patch populations without interpatch immigration: (a) effects of different initial population sizes; (b) effects of different delay times engaged in density-dependent population regulation.

strating an unstable equilibrium point due to the deterministic nature of the model (curve 1 in Fig. 6a). The populations achieve the patch carrying capacity when they start with initial sizes larger than the MVP value (curves 3 and 4 in Fig. 6a). Local extinction occurs when the populations are below MVP (curve 2 in Fig. 6a). If the populations are larger than the carrying capacity, they decrease to and persist at the carrying capacity level (curve 5 in Fig. 6a). Therefore, the dynamics and persistence of the local

populations are deterministically dependent upon their initial sizes. The time delay engaged in the density-dependent regulation of growth rate introduces fluctuations in local population dynamics and the altitude of oscillations increases with delay time (Fig. 6b). In fact, the model behaves much like its density-independent (exponential) counterpart when the delay time is large enough to incapacitate the negative feedback control of population growth (see curve 4 in Fig. 6b).

When immigrations exist among all patches, the dynamics of a metapopulation composed of two or more such subpopulations is necessarily more complicated. In this study, metapopulation systems consisting of two and three patches are simulated for a variety of scenarios with different interpatch immigration rates, initial subpopulation sizes, and spatial configurations of patches. We first discuss the results from the two-patch model.

## 2. Dynamics and persistence of the two-patch animal metapopulation system

### 2.1 With both subpopulations below the minimum viable population size

With the assumed density-dependent per capita interpatch immigration rate, the two subpopulations remain unchanged in size when they both start with the MVP size, an unstable equilibrium point (curve set 1 in Fig. 7a). In reality, these populations would be highly subject to local extinction due to environmental, genetic, and demographic stochasticities that are markedly manifested in small populations (Goodman, 1987a,b; Shaffer, 1987; Wu, 1992b).

In contrast, when the initial sizes of the two subpopulations are below MVP or when one is below and the other at MVP, both go extinct. For example, when subpopulation 1 is 49 and subpopulation 2 is 50, both go extinct monotonically (curve set 2 in Fig. 7a). Even when the per capita emigration rate is increased by 10 times, the same result is obtained (Fig. 7b). Therefore, the two-patch metapopulation system is subject to both local and regional (or global) extinctions when no subpopulation is larger than the MVP size. These results for animals are fundamentally different from those for plants where persistence is possible in such situations (see Wu et al., 1990).

### 2.2 With one subpopulation below and the other above the minimum viable population size

Because the two-patch metapopulation system will obviously persist if both local populations are above the MVP size, a more interesting simulation scenario is to consider the situations where one subpopulation is below but the other is above MVP. Can the metapopulation system persist when only one local population is above the MVP value?
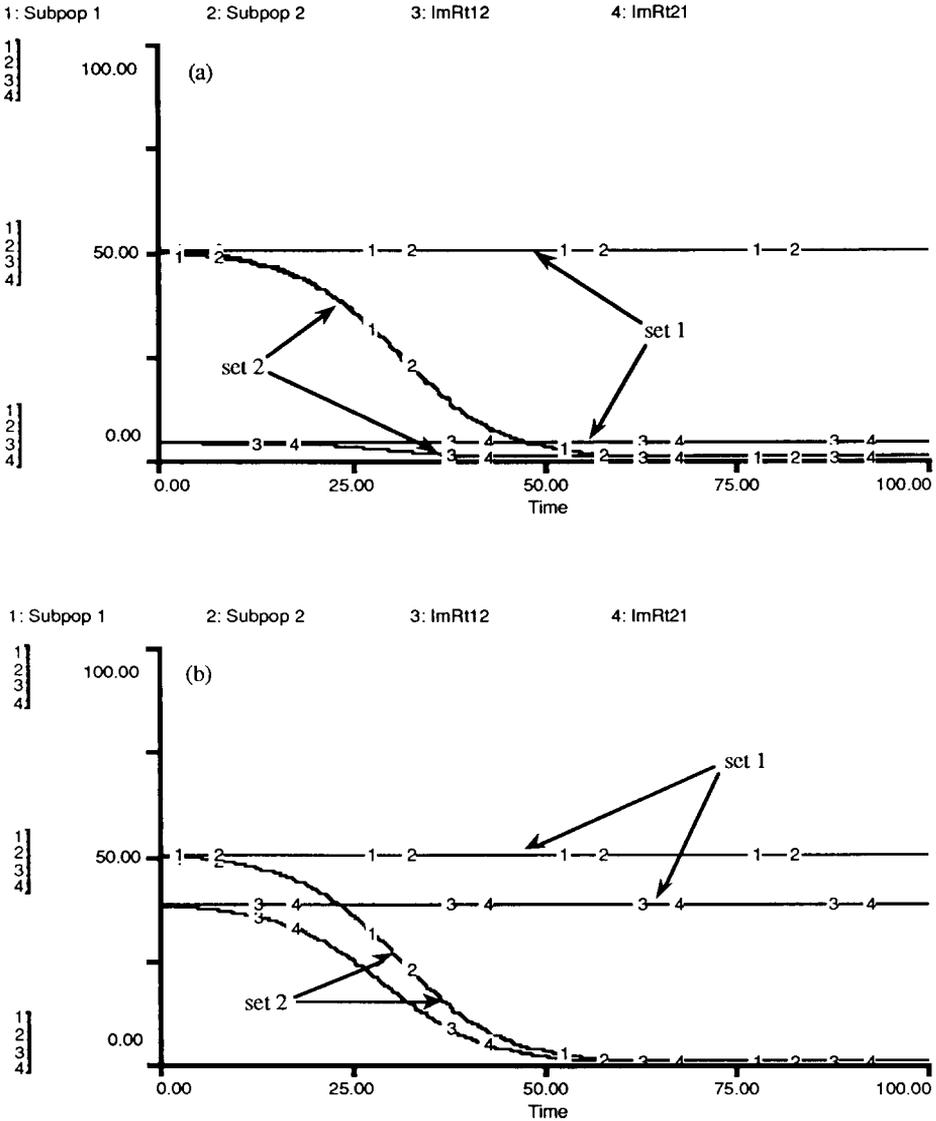
Fig. 7. Dynamics of the two-patch population system when both subpopulations are no larger than the MVP size: (a) with the per capita emigration rate in Fig. 4; (b) with a per capita emigration rate 10 times higher than the original one. The initial sizes for the subpopulations are both 50 for set 1 and 49 and 50 for set 2 in both (a) and (b).

The simulations show that both the subpopulations can persist at the patch carrying capacity level when the above-MVP subpopulation passes a threshold level whose magnitude varies with the below-MVP subpopulation size. As examples, for both subpopulations to persist, when the below-MVP
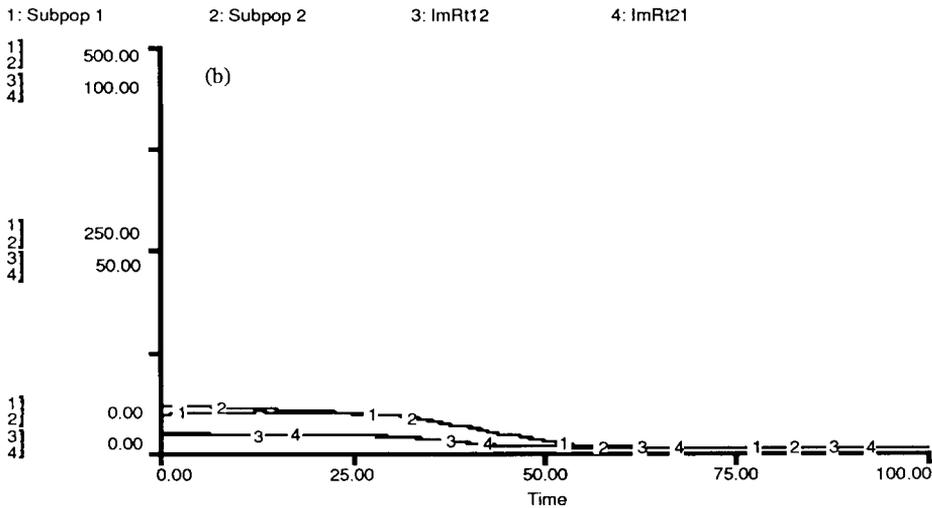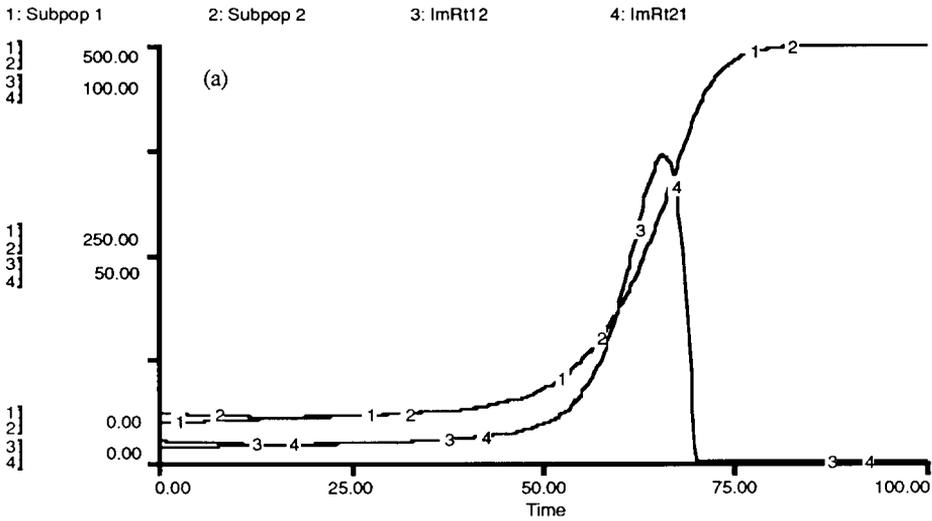
Fig. 8. Dynamics of two patchy populations linked through immigrations: (a) both persist at the carrying capacity when the initial size is 45 for the first subpopulation and 57 for the second; (b) both go extinct when the initial size is 45 for the first subpopulation and 56 for the second.

subpopulation size is 45, the minimum size of the above-MVP subpopulation is 57 (Fig. 8); when the below-MVP subpopulation is 25, the minimum size of the above-MVP subpopulation becomes 76 (Fig. 9); and when the below-MVP subpopulation is 0 (i.e., the patch is empty), the minimum
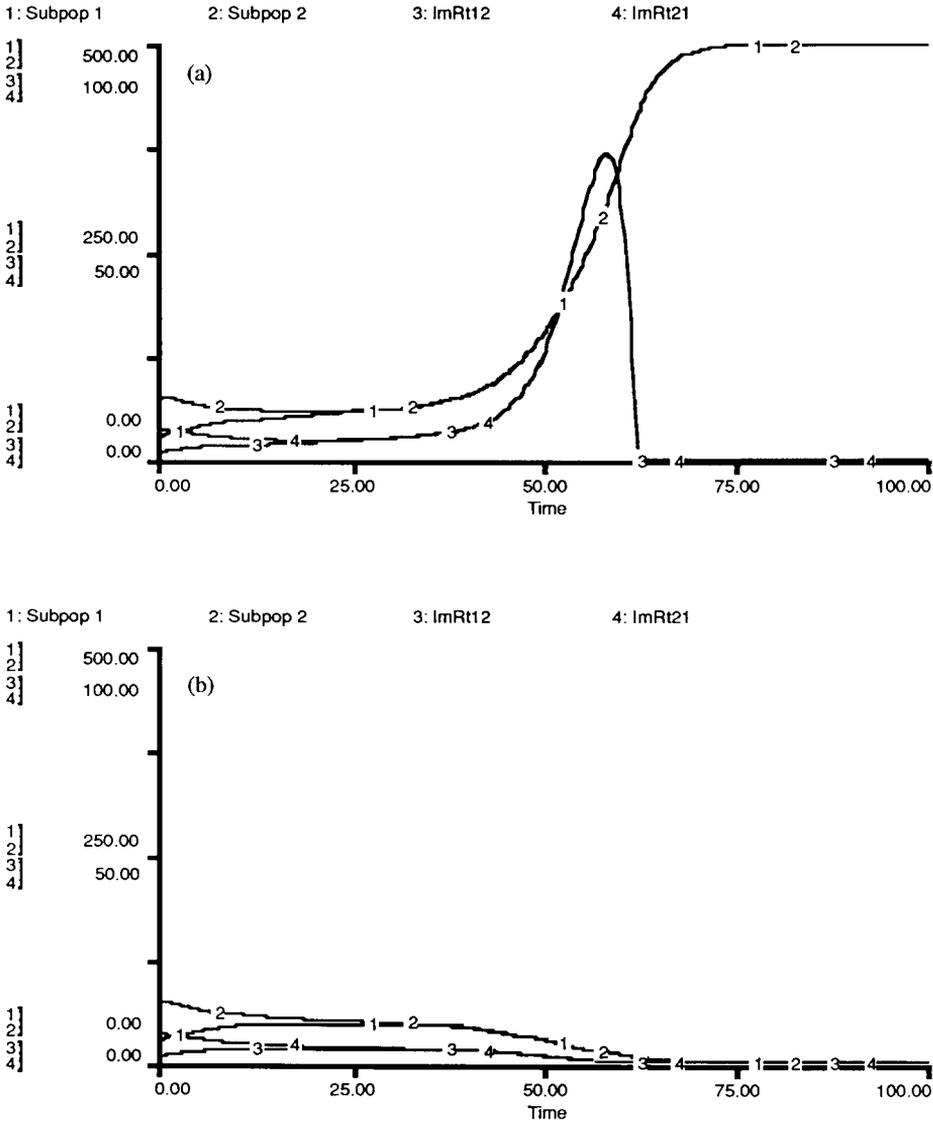
Fig. 9. Dynamics of two patchy populations linked through immigrations: (a) both persist at the carrying capacity when the initial size is 25 for the first subpopulation and 76 for the second; (b) both go extinct when the initial size is 25 for the first subpopulation and 75 for the second.

population size of the the occupied patch is 90 (Fig. 10). The rapid declines of immigration rates in Figs. 8a, 9a, and 10a result primarily from the drastic reduction in habitat availability for incoming immigrants when a subpopulation is approaching the carrying capacity of its inhabited patch.
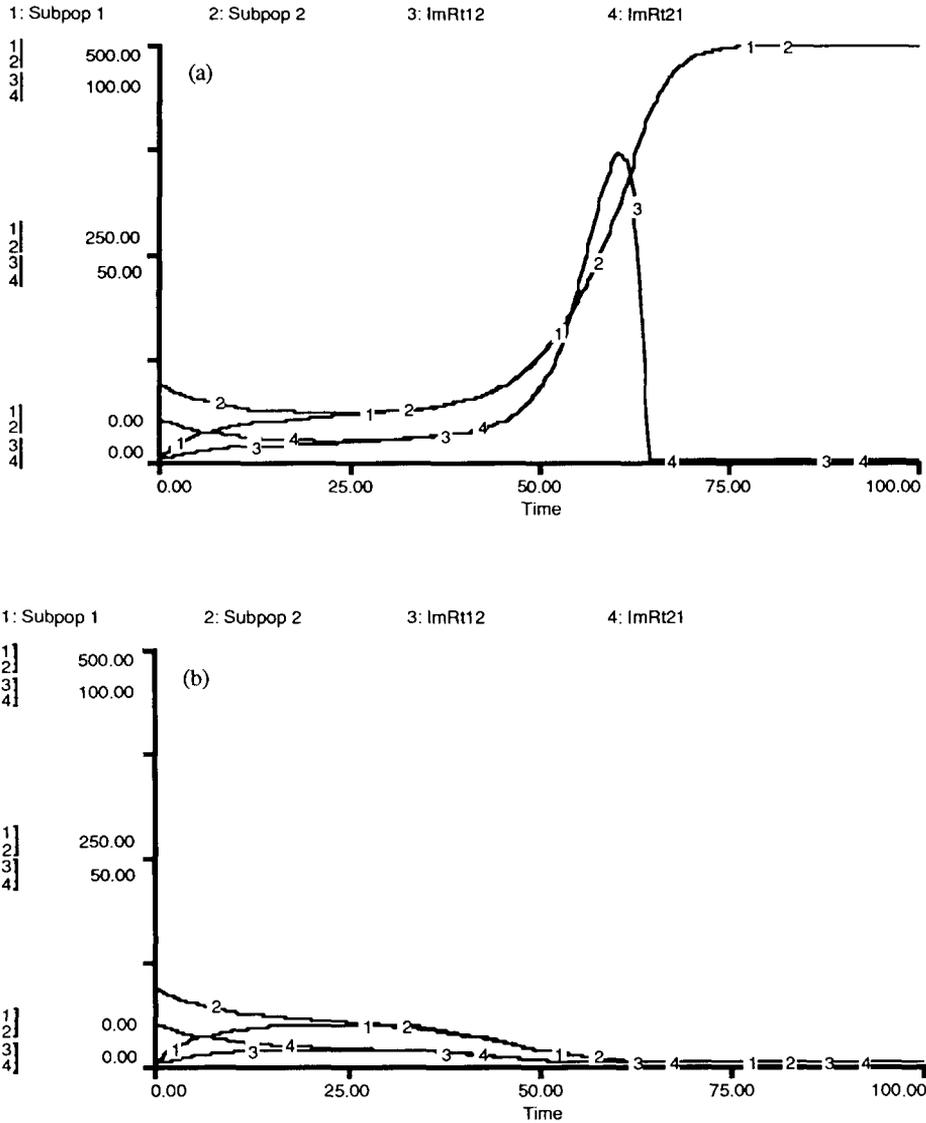
Fig. 10. Dynamics of two patchy populations linked through immigrations: (a) both persist at the carrying capacity when the initial size is 0 for the first subpopulation and 90 for the second; (b) both go extinct when the initial size is 0 for the first subpopulation and 89 for the second.

For each size of one subpopulation, there is always a minimum size of the other above which the immigrant flow from the source patch (with the larger subpopulation) to the sink patch (with the smaller) is large enough to counteract the dieback of the initially-below-MVP population. However,
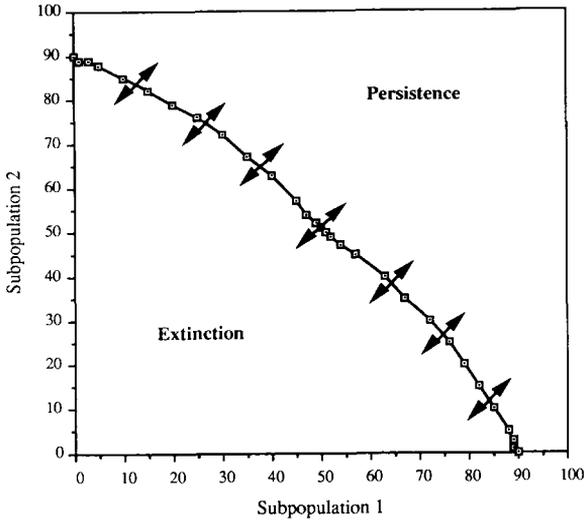
Fig. 11. A phase-plane presentation of the minimum persistent population size for the two-patch population system, showing the domains of persistence and extinction.

when either of the subpopulations is below a critical size, both subpopulations will go extinct (see Figs. 8b, 9b, and 10b). This is because the larger subpopulation drops below the MVP level as a result of its individuals flowing to the sink patch before being able to bring the second subpopulation up to the MVP size – an example of failed rescue effect.

Therefore, there are only two possibilities for the metapopulation system in which one is below and the other is above the MVP size: either both go extinct or both persist at the carrying capacity. However, if a constant (i.e., density-independent) per capita emigration rate is used to replace the density-dependent rate in Fig. 4, the two subpopulations can reach different new steady states other than the carrying capacity. For example, when per capita emigration rate is 0.0025 and the initial size is 55 for subpopulation 1 and 20 for subpopulation 2, the two subpopulations will reach two different new equilibria (496 and 10), respectively. This is primarily a result of the interplay of the constant percent immigration rate and the initial sizes of the subpopulations. This constant per capita emigration rate case is not considered further here and all the results presented in this paper are based on the density-dependent per capita emigration rate.

The domains of persistence and extinction for the two-patch metapopulation system, separated by a "persistence isocline," are depicted in Fig. 11. Because the same carrying capacity (500) is used for the two patches, the persistence isocline is necessarily symmetric relative to the diagonal axis.
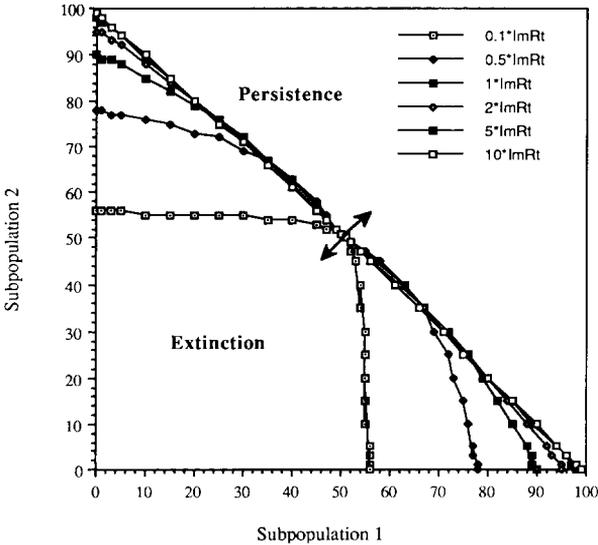
Fig. 12. Effects of the magnitude of interpatch immigration on the dynamics and persistence of the two-patch metapopulation, with subpopulation 1 starting from below and subpopulation 2 starting from above MVP. 0.1, 0.5, 1, 2, 5, and 10 times the values of the original density-dependent per capita emigration rate are used for different runs, respectively.

The minimum size of one subpopulation increases with the decrease in size of the other in a nearly linear fashion (Fig. 11).

*2.3 Effects of the magnitude of interpatch immigration rate on metapopulation dynamics and persistence*

We conducted many simulation runs to investigate the effects of immigration rates of different magnitudes on the dynamics and the minimum persistent population sizes when only one subpopulation is above MVP. The different simulation scenarios used values of 0.1, 0.5, 1, 2, 5, and 10 times the original per capita emigration rate (see Fig. 4). Figure 12 graphically summarizes the simulation results. Again, the symmetry of the persistence isoclines reflect the assumption that the two habitat patches are identical except for population sizes.

The effects of interpatch immigration rate on the dynamics and persistence of the two-patch metapopulation system are dependent on both the magnitude of the per capita emigration rate and the initial sizes of the subpopulations (Fig. 12). Several trends emerge out of these simulation results. When one subpopulation is below MVP, the minimum size of the other subpopulation required for persistence appears directly related to per capita emigration rate. More specifically, the minimum persistent

population is overall the smallest for the lowest per capita emigration rate (0.1 times the original), intermediate for the one of 0.5 times the original, and largest for the one of 10 times the original. This increase in minimum population size decreases with greater per capita emigration rate and becomes trivial when per capita emigration rate is larger than 5 times the original (Fig. 12).

The effects of these different immigration rates are population size-dependent, as much larger impacts are found at smaller below-MVP subpopulation sizes. In other words, differences in the minimum persistent population size caused by the immigration rates of different magnitudes increase with decreasing initial size of the below-MVP subpopulation. In addition, the general relationship of the minimum persistent sizes (reflected by the shape of persistence isocline) for the two subpopulations varies with the magnitude of per capita emigration rate. A linear or nearly linear relationship is found when per capita emigration rate is 5 or 10 times the original, suggesting that the minimum size of the above-MVP subpopulation required for persistence increases linearly when the below-MVP subpopulation decreases (Fig. 12). When per capita emigration rate is 0.1 times the original, the minimum size of the above-MVP subpopulation changes only slightly with the decreasing below-MVP subpopulation. The above two cases represent the situations where interpatch immigration rate is very large and very small, respectively. In contrast, when per capita emigration rate is the original or 0.5 times the original, the minimum size of the above-MVP subpopulation increases almost linearly and then tends to level off as the initial size of the below-MVP subpopulation decreases.

Based on the simulation results of the two-patch model, it is clear that the role of interpatch immigration in metapopulation dynamics is rather complex. With the interpatch emigration rate in Fig. 4, two small subpopulations (e.g., 20 and 79) are both able to persist at the carrying capacity level (Fig. 11). But only the above-MVP population can persist without interpatch immigration. The stabilizing role of immigration in metapopulation dynamics is convincingly demonstrated in such cases (see Figs. 8 to 12). However, it is not necessarily true that the larger the immigration rate, the better chance for persistence. On the contrary, large interpatch immigration rates require appreciably larger sizes of the above-MVP subpopulation in order for the metapopulation to persist when the below-MVP subpopulation is very small (e.g., below 30; see Fig. 12). What are the mechanisms behind these phenomena?

A patch with a below-MVP population is in effect a "population sink" in that its local population growth rate is negative, creating a drain on the overall metapopulation system. This "population sink effect" becomes stronger when the population gets even smaller (Fig. 3). Therefore, when
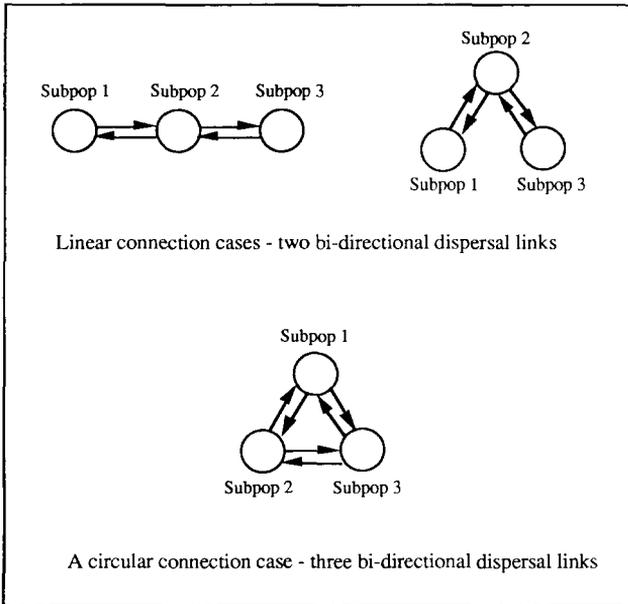
Fig. 13. Two types of configuration simulated with the three-patch animal population model.

an above-MVP patch and a below-MVP patch are connected by interpatch immigration, there are two processes taking place in the same time: augmentation of the below-MVP subpopulation and the depletion of the above-MVP subpopulation. Obviously, the immigrant flux from the sink patch to the source patch is trivial as compared to the flow in the opposite direction as the population size of the sink patch is small. Consequently, whether the metapopulation can persist depends on the relative rate of the two processes. That is, both subpopulations persist if the sink patch is brought up to the MVP size before the source patch being drained below the MVP size. Otherwise, both subpopulations go extinct.

## 3. Dynamics and persistence of the three-patch animal metapopulation system

The three-patch animal metapopulation model is simulated to examine two types of questions: how does interpatch immigration affect the dynamics of a metapopulation composed of three patches? Does spatial configurations alter these effects and, if so, how? Two types of configurations of the three-patch system are simulated: linear connection and circular connection (Fig. 13). While there are two pairs of dispersal links in the linear configuration, three pairs are present in the circular configuration. As in

the two-patch model, patches are "connected" in the sense of there being effective interpatch immigration either through dispersal corridors or due to proximity of patches. For both configurations, simulations are conducted for the situations where only one of the three subpopulations is above the MVP size. Within each configuration, different cases relative to the placement of the above-MVP subpopulation in the patchy system are considered. In addition, the effects of immigration rates of different magnitudes on the three-patch metapopulation dynamics and persistence are also examined.

### 3.1 Simulations of a linearly linked three-patch metapopulation system

The first simulation scenario in the linear connection cases assumes that the two below-MVP subpopulations are equal. The above-MVP subpopulation can either be in one of the end patches or in the middle patch (see Fig. 13). Ten combinations of patch placements with five different sizes of the below-MVP subpopulations are simulated and the results are summarized in Fig. 14.

These simulations show that there exists a critical size of the above-MVP subpopulation above which all three subpopulations persist at the carrying capacity and below which all of them go extinct. This is consistent with the result from the two-patch model. However, the minimum size for persistence of the three-patch metapopulation system is determined not only by the initial size of the two below-MVP subpopulations but also by the spatial placement of the above-MVP subpopulation. For instance, if the above-MVP subpopulation is at the end of the linkage, its minimum size for persistence is 58 when the other two are 45 (Fig. 14a) and increases to 65 when the other two decrease to 5 (Fig. 14e). However, if the above-MVP subpopulation is located in the middle, its minimum size for persistence is 64 when the other two are 45 (Fig. 14a') and 94 when the other two are 5 (Fig. 14e').

In general, the simulations of ten combinations show that the minimum sizes for persistence are much smaller when the above-MVP subpopulation is in an end patch than in the middle patch (compare a, b, c, d and e to a', b', c', d' and e' in Fig. 14). The differences in the minimum persistent population sizes due to the changes in the position of the above-MVP increase with the decrease in the size of below-MVP subpopulations. For instance, when the below-MVP subpopulations are 45, 40, 20, 10 and 5, the differences in the minimum persistent sizes are 6, 12, 25, 28, and 29, respectively (see the left column of Fig. 14). Therefore, the relative position of the above-MVP subpopulation in such a linearly linked metapopulation system seems to play a significant role in metapopulation dynamics and persistence. These results reflect interactions between the population sink

Linear connection cases - two bi-directional dispersal links
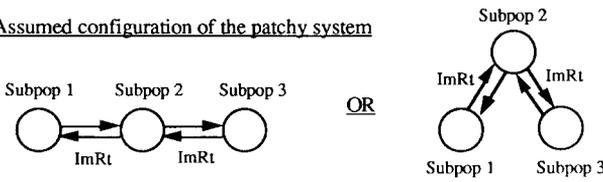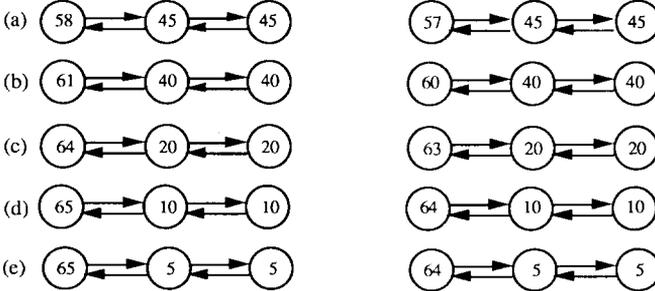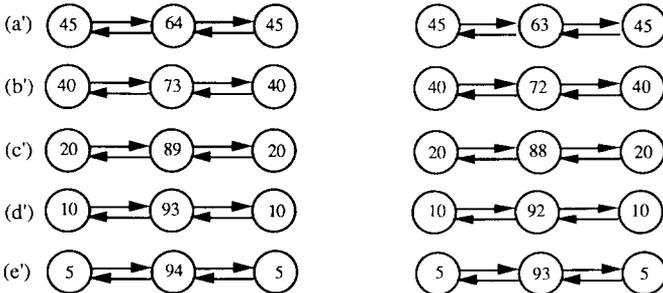


Fig. 14. Simulated minimum persistent populations for a linearly linked, three-patch population system with two subpopulations starting from below and one from above the MVP value.

effect and the relative positions of patches. It is more effective for the only viable subpopulation, when it is not well above the MVP size, to be in a position where it rescues one of the two dying subpopulations first and then jointly rescues the other, rather than saves both below-MVP subpopulations simultaneously. In other words, it is more effective for a source patch to convert a sink patch to a second source patch rather than act as the only source patch for two sink patches.

The second simulation scenario is designed to examine if immigration rates of different magnitudes will change the results discussed above. The

Linear connection cases - two bi-directional dispersal links:
0.5-times the original per capita immigration rate
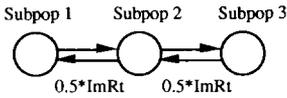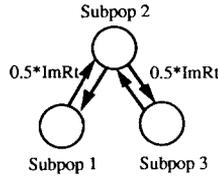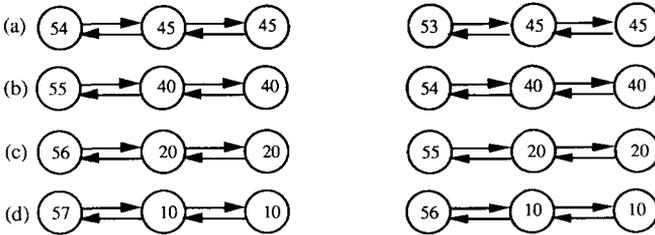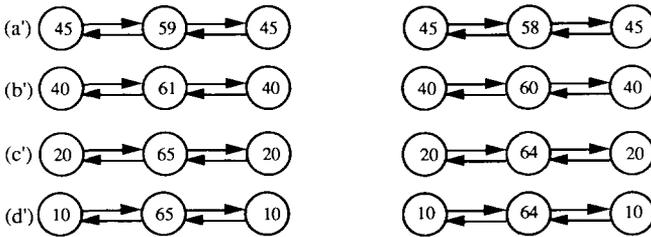


Fig. 15. Simulated minimum persistent populations for a linearly linked, three-patch population system with 0.5 times the original per capita emigration rate, two subpopulations starting from below and one from above the MVP value.

results for immigration rates of 0.5 and 5 times the original are graphically summarized in Figs. 15 and 16, respectively. In both cases, it is generally true that the minimum sizes for persistence are smaller when the above-MVP subpopulation is placed in an end patch than in the middle. However, the differences in the minimum persistent population sizes due to the changes in the relative position of the above-MVP are overall reduced for each case. Yet, as in the original per capita emigration rate case, the differences tend to increase with the decrease in the size of the below-MVP subpopulations (compare set 1 with set 2 in both Fig. 15 and Fig. 16).

In addition, for a given size of the two below-MVP subpopulations, the minimum size of the above-MVP subpopulation for the persistence of the

Linear connection cases - two bi-directional dispersal links:
with 5-times the original per capita immigration rate
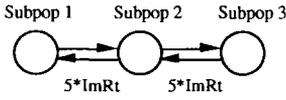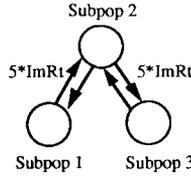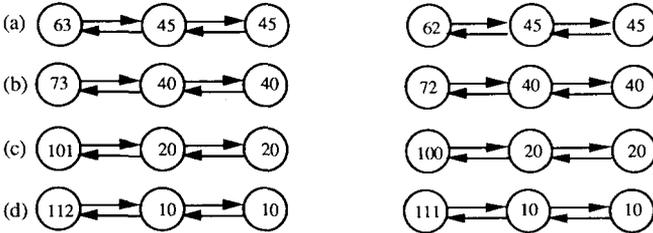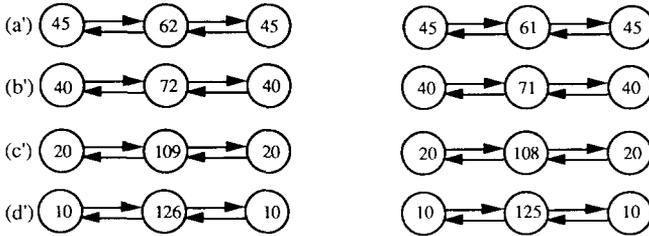


Fig. 16. Simulated minimum persistent populations for a linearly linked, three-patch population system with 5 times the original per capita emigration rate, two subpopulations starting from below and one from above the MVP value.

metapopulation system is smaller for low than for high interpatch immigration rates. In the case of the above-MVP subpopulation being at the end patch, for example when the below-MVP subpopulations are 40, the minimum persistence size increases from 55 to 61 to 73 as the per capita emigration rate increases from 0.5 to 1 to 5 times the original value (compare Figs. 15b, 14b and 19b). When the below-MVP subpopulations are 10, the minimum persist size increases from 57 to 65 to 112 with the same change in per capita emigration rate (see Figs. 15d, 14d and 19d). These findings result from higher interpatch immigration rates increasing the loss of individuals (drain effect) from the source patch, so that larger

minimum sizes for the above-MVP subpopulation are required in order to rescue the below-MVP subpopulations.

The third simulation scenario also assumes that only one of the subpopulations is above MVP and that the other two are below MVP; however, in contrast with the first scenario, the two below-MVP subpopulations are unequal. In this case, not only can the above-MVP subpopulation either be in an end patch or in the middle, but also the two below-MVP subpopulations can be in one of the two positions: being connected or disconnected with the above-MVP subpopulation (cf. Fig. 13). For each pair of below-MVP subpopulations, there are three different combinations. Nine combinations are simulated to examine the effects of interpatch immigration on
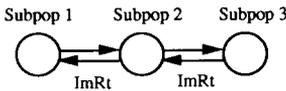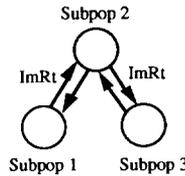


Fig. 17. Simulated minimum persistent populations for a linearly linked, three-patch population system when all three subpopulations are different in size and only one is above the MVP value.

metapopulation dynamics and persistence. All numerical results are graphically summarized in Fig. 17.

For a given pair of below-MVP subpopulations, the minimum size of the above-MVP subpopulation for persistence is lowest when the three patches are linked in an ascending or descending order of their population sizes (a2, b2, and c2 in Fig. 17) and highest when the above-MVP subpopulation is in the middle (a3, b3, and c3 in Fig. 17). The differences in the minimum persistent population size due to the position switch of the two below-MVP subpopulations, with the above-MVP subpopulation being at the end, are much smaller than those due to the changes in the relative location of the above-MVP subpopulation (compare a$i$, b$i$, and c$i$ in Fig. 17, where $i = 1$, 2, 3). These results reflect the population sink effect mentioned earlier. The configuration in which the larger below-MVP subpopulation is in
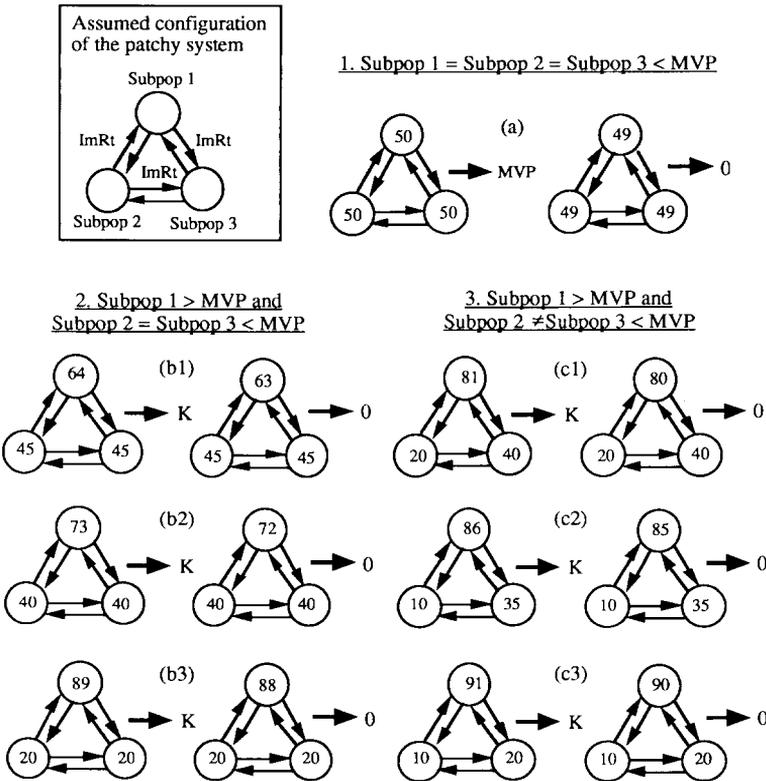


Fig. 18. Simulated minimum persistent populations for a circularly linked, three-patch population system when two of the three subpopulations are below and only one is above the MVP value.

between the above-MVP and the smaller below-MVP subpopulation, seems to reduce the magnitude of the sink effect rather effectively. More to the point, the direct connection between the above-MVP subpopulation and the smallest below-MVP subpopulation gives rise to the greatest "sinking gradient" and, consequently, results in the largest drain on the system.

### 3.2 Simulations of a circularly linked three-patch metapopulation system

Two general simulation scenarios based on different system configurations are adopted for the circularly linked three-patch system: homogeneous versus heterogeneous immigration rates among patches (Figs. 18 and 19, respectively). The homogeneous-immigration-rate scenario considers three situations in terms of population size: (1) three subpopulations are all at or below the MVP size (Fig. 18a); (2) two of the three are below MVP and equal (Fig. 18b); and (3) two are below MVP and unequal (Fig. 18c). The heterogeneous-rate case is divided into two different situations based on the relative position of the two different immigration rates (Fig. 19).
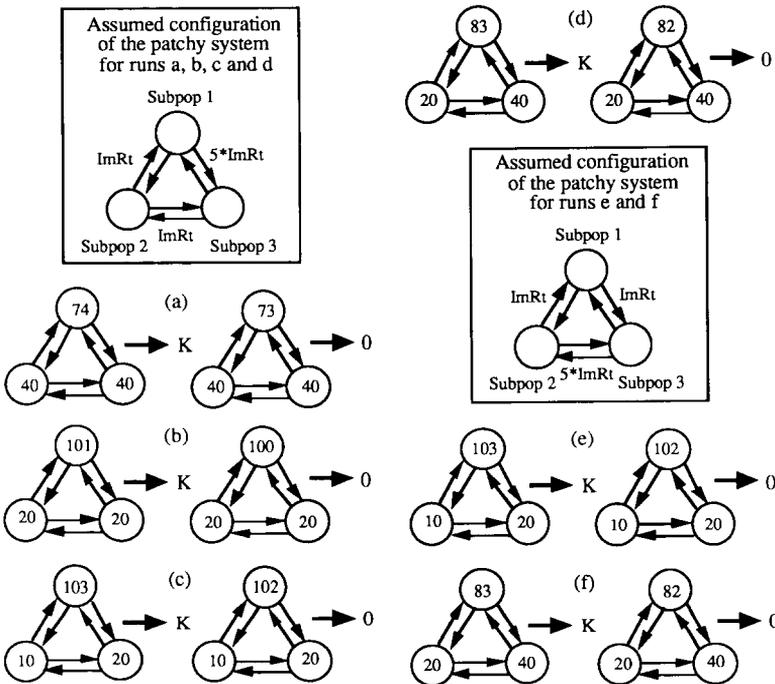


Fig. 19. Simulated minimum persistent populations for a circularly linked, three-patch population system with two different immigration rates assigned for the three interpatch links, with subpopulation 1 being above and the other two below the MVP size.

Although more combinations in terms of different immigration rates, spatial configurations, and different subpopulation sizes are possible, only a limited number of cases are arbitrarily selected here to examine the general nature of the dynamics of such a metapopulation system. While the original per capita emigration rate in Fig. 4 is used in the homogeneous case, an additional immigration rate of 5 times the original is assigned to one of the three links for the heterogeneous situations.

When the three subpopulations are all smaller than the MVP size (Fig. 18a), the metapopulation cannot avoid extinction. The circular connection case with one above-MVP subpopulation and two equal-sized below-MVP subpopulations (Fig. 18b) is parallel to the linear connection case with the same population size conditions (both set 1 and set 2 in Fig. 16). The only difference between them is that the interpatch immigration link between patch 1 and patch 3 in the circular connection case is absent in the linear case. in terms of the minimum size of the above-MVP subpopulation for persistence, this particular circular connection situation is equivalent to the corresponding linear connection case where the above-MVP subpopulation is placed in the middle (compare Fig. 18 with Fig. 16). The circular connection case with one above-MVP subpopulation and two unequal-sized below-MVP subpopulations (Fig. 18c) is parallel to the linear case with the same population size conditions (Fig. 17). The only difference between these two is again the addition of an interpatch immigration link between patch 1 and patch 3 in the circular connection case. The addition of this link seems to have, to varying degrees depending on the below-MVP subpopulation sizes, a negative effect on the minimum persistent population size. Overall, the circular situations with three subpopulations all different in size have similar metapopulation dynamics to the corresponding linear situations when the above-MVP subpopulation is in the middle (compare Fig. 18c with Fig. 17).

When one subpopulation is above MVP and the other two below MVP, the minimum size of the above-MVP subpopulation required for metapopulation persistence increases appreciably when the interpatch immigration link between patch 1 and 3 is increased to 5 times the original with the other two links being held unchanged (compare Fig. 19a,b,c,d with Fig. 18b2,b3,c3,c1, respectively). These results again reflect a positive relationship between interpatch immigration and draining rate for small subpopulations as discussed earlier. With the same conditions, the alternation of the relative position of the higher interpatch immigration link does not appear to affect the minimum persistent population size (compare Fig. 19e,f with Fig. 19c,d).

## DISCUSSION AND CONCLUSIONS

A system dynamics model of metapopulations consisting of two or three habitat patches was constructed and simulated using STELLA. Although having considered only two- and three-patch cases, this approach can be used to model metapopulation systems composed of more patches. In reality, the local birth and death rates of organisms of the same species are very likely to be different in spatially discrete habitats (Pulliam, 1988). This metapopulation model incorporates such patch-specific demographic differences. When quantitative or qualitative data are available, interpatch distance and species dispersal distance, along with physical characteristics of dispersal corridors, can also be easily incorporated in the model to elaborate the emigration and immigration processes (see Wu et al., 1990). Patch area may be included by further specifying the patch carrying capacity and/or introducing population density-related variables. With these additions, the model will also be able to examine possible effects of isolation and area on metapopulation dynamics. The deterministic nature of the model keeps its simulation simple, but stochastic modifications (e.g., relative to MVP) may make the model more realistic.

The simulations of the model following numerous different scenarios have produced interesting results concerning the dynamics and persistence of metapopulations. Of course, it is crucial to remember the assumptions behind the model when interpreting results. Therefore, it is important to emphasize the characteristics of the model metapopulation. First, the local populations have density-dependent net growth rates, although the specific relationship does not seems critical to the general behavior of the model. Second, the species modeled has a deterministic minimum viable population size. Although in reality it may not be a unique deterministic value, its typical or representative magnitude should possibly be estimated through population viability analysis (Shaffer, 1981, 1987; Gilpin and Soule, 1986; Gilpin, 1987). Third, there is no outside dispersal pool existing for the metapopulation; therefore, the only immigrations are among patches.

Several general relationships regarding effects of local population sizes, interpatch immigration flux, and spatial patch configuration on metapopulation dynamics have emerged out of this simulation study. With the determinism in MVP and the model as a whole, the animal metapopulation is doomed to global extinction with or without interpatch immigration when all local populations are below MVP. In such cases, the magnitude of immigration within the metapopulation system only affects the transient dynamics (trajectory or time to extinction) but not the ultimate outcome of system persistence. This suggests that for a cluster of scattered small populations, it may be preferable to focus efforts on augmenting individual

population sizes (through, for example, artificial introduction and breeding programs) rather than enhancing interpatch immigration (e.g., placement of dispersal corridors).

When at least one of the subpopulations is above the MVP size, interpatch immigration may play an important role in metapopulation dynamics and persistence. In such cases, there is a critical size for the above-MVP subpopulation above which the metapopulation persists and otherwise collapses. When a metapopulation system is composed of more than two patches, the spatial configuration in terms of patch connection and the relative position of the above-MVP subpopulation has significant effects on metapopulation dynamics and persistence. All simulation results from the three-patch animal metapopulation model suggest that both the number of interpatch connections and the magnitude represented by them are crucial for overall patch connectivity (see Merriam, 1984; Hansson, 1991; and Merriam et al., 1991 for reviews on connectivity). The importance of spatial arrangement of patches in metapopulation persistence has been reported in several studies (Fahrig et al., 1983; Lefkowitch and Fahrig, 1985; Hansson, 1991). These results obviously have implications for landscape ecology and nature conservation. Also, although the current version of the model involves no more than three patches, it may serve as a general conceptual framework and a specific simulator for modeling metapopulation dynamics incorporating a variety of spatial arrangements of habitat patches.

In general, connected patches are better than isolated ones in that interpatch dispersal provides opportunities for the below-MVP subpopulations to overcome their negative growth tendency and to stabilize at the carrying capacity. However, this is true only in a qualitative but not quantitative sense. The magnitude of interpatch immigration is actually found positively related to the minimum size of the above-MVP subpopulation in both the two- and three-patch metapopulation systems due to what can be called population sink or drain effect. This effect interacts with patch connectivity, generating complex patterns. The phenomenon is especially significant when subpopulations in sink patches are well below MVP. In addition, the simulation results suggest that drain effect has a more profound influence on metapopulation dynamics and persistence for animals than for plants. Given that recent literature in conservation biology and landscape ecology emphasizes primarily the positive effects of dispersal or immigration on the dynamics and stability of metapopulations, it is important to recognize that interpatch immigration may have a negative impact.

Pulliam (1988), in his discussion of single species population dynamics and regulation in spatially heterogeneous environments, used the term

"sink habitats" to refer to patches where local reproduction is insufficient to balance local mortality. Pulliam argued that for many plant or animal species, a large proportion of their populations may frequently occur in sink habitats and may persist there due to continuous immigration from neighboring source patches. A sink patch behaves as "a net importer of individuals" while a source patch serves as "a net exporter of individuals" (Pulliam, 1988). The source–sink dispersal characteristics may be a result of natural selection and, therefore, evolutionarily stable (cf. Roff, 1974; Comins et al., 1980; Pulliam, 1988; Hanski, 1991). This simulation study connects Pulliam's source–sink idea with the MVP concept and elaborates the relationship between source–sink dynamics and interpatch immigration. It has demonstrated that a sink patch may, when a large enough immigration flow is available, turn into a source patch to other smaller populations. Thus, source and sink are relative terms in metapopulation systems.

The population sink effect is related primarily to two assumptions in the model: (1) interpatch immigration flux is conserved and no outside or global immigration pool is available to these patches; (2) without immigration, local populations exhibit nonlinearly accelerating decay when their sizes fall below MVP while they have a logistic type of growth when their sizes are above MVP. Changes in these two model assumptions may alter the results presented here (Wu et al., 1990). In general, the dynamics and stability of metapopulations are the system-level manifestation of the interactions and interdependence among individual patches of a lower organizational level. They are ultimately determined by the nonlinear interactions between within-patch population growth and interpatch immigration flux.

## APPENDIX

## *A STELLA program listing of the two-patch animal metapopulation model*

```
Subpop_1(t) = Subpop_1(t - dt) + (NetGR_1 + ImRt21 - ImRt12) * dt
    INIT Subpop_1 = 0
INFLOWS:
NetGR_1 = ActPCNGR1*Subpop_1
ImRt21 = IF (ImRt_Test*PCImRt21≤ 1) THEN ImRt_Test * PCImRt21 * Subpop_2 *      Habitat_Avail_1
ELSE Subpop_2 * Habitat_Avail_1
OUTFLOWS:
ImRt12 = IF (ImRt_Test * PCImRt12 ≤ 1) THEN ImRt_Test * PCImRt12* Subpop_1
    *Habitat_Avail_2 ELSE Subpop_1 *Habitat_Avail_2
Subpop_2(t) = Subpop_2(t - dt) + (ImRt12 + NetGR_2 - ImRt21) * dt
    INIT Subpop_2 = 77
INFLOWS:
ImRt12 = IF (ImRt_Test * PCImRt12 ≤ 1) THEN ImRt_Test * PCImRt12* Subpop_1
    *Habitat_Avail_2 ELSE Subpop_1 *Habitat_Avail_2
NetGR_2 = ActPCNGR2*Subpop_2
OUTFLOWS:
ImRt21 = IF (ImRt_Test*PCImRt21≤ 1) THEN ImRt_Test * PCImRt21 * Subpop_2 *      Habitat_Avail_1
ELSE Subpop_2 * Habitat_Avail_1
ActPCNGR1 = IF DLT_NGR>0 THEN SMTH3(PCNGR_1, DLT_NGR) ELSE PCNGR_1
ActPCNGR2 = IF DLT_NGR>0 THEN SMTH3(PCNGR_2, DLT_NGR) ELSE PCNGR_2
CarryingCap_1 = 500
CarryingCap_2 = 500
Crowding_1 = Subpop_1/CarryingCap_1
Crowding_2 = Subpop_2/CarryingCap_2
DLT_NGR = 0
ImRt_Test = 1
Metapop = Subpop_1+Subpop_2
Habitat_Avail_1 = GRAPH(Crowding_1)
    (0.00, 1.00), (0.0833, 0.985), (0.167, 0.965), (0.25, 0.945), (0.333, 0.91), (0.417,        0.865),
(0.5, 0.8), (0.583, 0.705), (0.667, 0.565), (0.75, 0.35), (0.833, 0.00), (0.917,        0.00), (1, 0.00)
Habitat_Avail_2 = GRAPH(Crowding_2)
    (0.00, 1.00), (0.0833, 0.985), (0.167, 0.965), (0.25, 0.945), (0.333, 0.91), (0.417,        0.865),
(0.5, 0.8), (0.583, 0.705), (0.667, 0.565), (0.75, 0.35), (0.833, 0.00), (0.917,        0.00), (1, 0.00)
PCImRt12 = GRAPH(Crowding_1)
    (0.00, 0.0525), (0.1, 0.0775), (0.2, 0.117), (0.3, 0.175), (0.4, 0.26), (0.5, 0.32), (0.6,        0.362),
(0.7, 0.39), (0.8, 0.412), (0.9, 0.43), (1.00, 0.442), (1.10, 0.455), (1.20, 0.465),        (1.30, 0.477),
(1.40, 0.487), (1.50, 0.5)
PCImRt21 = GRAPH(Crowding_2)
    (0.00, 0.0525), (0.1, 0.0775), (0.2, 0.117), (0.3, 0.175), (0.4, 0.26), (0.5, 0.32), (0.6,        0.362),
(0.7, 0.39), (0.8, 0.412), (0.9, 0.43), (1.00, 0.442), (1.10, 0.455), (1.20, 0.465),        (1.30, 0.477),
(1.40, 0.487), (1.50, 0.5)
PCNGR_1 = GRAPH(Crowding_1)
    (0.00, -0.15), (0.1, 0.00), (0.2, 0.076), (0.3, 0.088), (0.4, 0.088), (0.5, 0.088), (0.6,        0.086),
(0.7, 0.082), (0.8, 0.062), (0.9, 0.032), (1.00, 0.00), (1.10, -0.032), (1.20, -   0.072), (1.30, -0.102),
(1.40, -0.132), (1.50, -0.156)
PCNGR_2 = GRAPH(Crowding_2)
    (0.00, -0.15), (0.1, 0.00), (0.2, 0.076), (0.3, 0.088), (0.4, 0.088), (0.5, 0.088), (0.6,        0.086),
(0.7, 0.082), (0.8, 0.062), (0.9, 0.032), (1.00, 0.00), (1.10, -0.032), (1.20, -   0.072), (1.30, -0.102),
(1.40, -0.132), (1.50, -0.156)
```

## *A STELLA program listing of the three-patch animal metapopulation model*

```
Subpop_1(t) = Subpop_1(t - dt) + (NetGR_1 + ImRt21 + ImRt31 - ImRt13 - ImRt12) * dt
    INIT Subpop_1 = 82
INFLOWS:
NetGR_1 = ActPCNGR1*Subpop_1
ImRt21 = if (ImRt_Test * PCImRt_2 ≤ 1) then ImRt_Test * PCImRt_2* Subpop_2
    *Habitat_Avail_1 else Subpop_2 *Habitat_Avail_1
ImRt31 = IF (ImRt_Test * PCImRt_3 ≤ 1) THEN ImRt_Test * PCImRt_3* Subpop_3
    *Habitat_Avail_1 ELSE Subpop_3 *Habitat_Avail_1
OUTFLOWS:
ImRt13 = IF (ImRt_Test * PCImRt_1 ≤ 1) THEN ImRt_Test * PCImRt_1* Subpop_1
    *Habitat_Avail_3 ELSE Subpop_1 *Habitat_Avail_3
ImRt12 = if (ImRt_Test * PCImRt_1 ≤ 1) then ImRt_Test * PCImRt_1* Subpop_1
    *Habitat_Avail_2 else Subpop_1 *Habitat_Avail_2
Subpop_2(t) = Subpop_2(t - dt) + (NetGR_2 + ImRt12 + ImRt32 - ImRt21 - ImRt23) * dt
    INIT Subpop_2 = 20
INFLOWS:
NetGR_2 = ActPCNGR2*Subpop_2
ImRt12 = if (ImRt_Test * PCImRt_1 ≤ 1) then ImRt_Test * PCImRt_1* Subpop_1
    *Habitat_Avail_2 else Subpop_1 *Habitat_Avail_2
```

ImRt32 = IF (ImRt_Test * PCImRt_3 ≤ 1) THEN ImRt_Test * PCImRt_3* Subpop_3
   *Habitat_Avail_2 ELSE Subpop_3 *Habitat_Avail_2
OUTFLOWS:
ImRt21 = if (ImRt_Test * PCImRt_2 ≤ 1) then ImRt_Test * PCImRt_2* Subpop_2
   *Habitat_Avail_1 else Subpop_2 *Habitat_Avail_1
ImRt23 = if (ImRt_Test * PCImRt_2 ≤ 1) then ImRt_Test * PCImRt_2* Subpop_2
   *Habitat_Avail_3 else Subpop_2 *Habitat_Avail_3
Subpop_3(t) = Subpop_3(t - dt) + (ImRt13 + ImRt23 + NetGR_3 - ImRt31 - ImRt32) * dt
   INIT Subpop_3 = 40
INFLOWS:
ImRt13 = IF (ImRt_Test * PCImRt_1 ≤ 1) THEN ImRt_Test * PCImRt_1* Subpop_1
   *Habitat_Avail_3 ELSE Subpop_1 *Habitat_Avail_3
ImRt23 = if (ImRt_Test * PCImRt_2 ≤ 1) then ImRt_Test * PCImRt_2* Subpop_2
   *Habitat_Avail_3 else Subpop_2 *Habitat_Avail_3
NetGR_3 = ActPCNGR3*Subpop_3
OUTFLOWS:
ImRt31 = IF (ImRt_Test * PCImRt_3 ≤ 1) THEN ImRt_Test * PCImRt_3* Subpop_3
   *Habitat_Avail_1 ELSE Subpop_3 *Habitat_Avail_1
ImRt32 = IF (ImRt_Test * PCImRt_3 ≤ 1) THEN ImRt_Test * PCImRt_3* Subpop_3
   *Habitat_Avail_2 ELSE Subpop_3 *Habitat_Avail_2
ActPCNGR1 = if DLT_NGR>0 then SMTH3(PCNGR_1, DLT_NGR) else PCNGR_1
ActPCNGR2 = if DLT_NGR>0 then SMTH3(PCNGR_2, DLT_NGR) else PCNGR_2
ActPCNGR3 = if DLT_NGR>0 then SMTH3(PCNGR_3, DLT_NGR) else PCNGR_3
CarryingCap_1 = 500
CarryingCap_2 = 500
CarryingCap_3 = 500
Crowding_1 = Subpop_1/CarryingCap_1
Crowding_2 = Subpop_2/CarryingCap_2
Crowding_3 = Subpop_3/CarryingCap_3
DLT_NGR = 0
ImRt_Test = 1

MetaPop = Subpop_1+Subpop_2+Subpop_3
Habitat_Avail_1 = GRAPH(Crowding_1)
   (0.00, 1.00), (0.0833, 0.985), (0.167, 0.965), (0.25, 0.945), (0.333, 0.91), (0.417,        0.865),
(0.5, 0.8), (0.583, 0.705), (0.667, 0.565), (0.75, 0.35), (0.833, 0.00), (0.917,        0.00), (1, 0.00)
Habitat_Avail_2 = GRAPH(Crowding_2)
   (0.00, 1.00), (0.0833, 0.985), (0.167, 0.965), (0.25, 0.945), (0.333, 0.91), (0.417,        0.865),
(0.5, 0.8), (0.583, 0.705), (0.667, 0.565), (0.75, 0.35), (0.833, 0.00), (0.917,        0.00), (1, 0.00)
Habitat_Avail_3 = GRAPH(Crowding_3)
   (0.00, 1.00), (0.0833, 0.985), (0.167, 0.965), (0.25, 0.945), (0.333, 0.91), (0.417,        0.865),
(0.5, 0.8), (0.583, 0.705), (0.667, 0.565), (0.75, 0.35), (0.833, 0.00), (0.917,        0.00), (1, 0.00)
PCImRt_1 = GRAPH(Crowding_1)
   (0.00, 0.001), (0.1, 0.016), (0.2, 0.039), (0.3, 0.078), (0.4, 0.13), (0.5, 0.17), (0.6,        0.203),
(0.7, 0.224), (0.8, 0.242), (0.9, 0.255), (1.00, 0.266), (1.10, 0.275), (1.20,     0.282), (1.30, 0.288),
(1.40, 0.296), (1.50, 0.3)
PCImRt_2 = GRAPH(Crowding_2)
   (0.00, 0.001), (0.1, 0.016), (0.2, 0.039), (0.3, 0.078), (0.4, 0.13), (0.5, 0.17), (0.6,        0.203),
(0.7, 0.224), (0.8, 0.242), (0.9, 0.255), (1.00, 0.266), (1.10, 0.275), (1.20,     0.282), (1.30, 0.288),
(1.40, 0.296), (1.50, 0.3)
PCImRt_3 = GRAPH(Crowding_3)
   (0.00, 0.001), (0.1, 0.016), (0.2, 0.039), (0.3, 0.078), (0.4, 0.13), (0.5, 0.17), (0.6,        0.203),
(0.7, 0.224), (0.8, 0.242), (0.9, 0.255), (1.00, 0.266), (1.10, 0.275), (1.20,     0.282), (1.30, 0.288),
(1.40, 0.296), (1.50, 0.3)
PCNGR_1 = GRAPH(Crowding_1)
   (0.00, -0.15), (0.1, 0.00), (0.2, 0.076), (0.3, 0.088), (0.4, 0.088), (0.5, 0.088), (0.6,        0.086),
(0.7, 0.082), (0.8, 0.062), (0.9, 0.032), (1.00, 0.00), (1.10, -0.032), (1.20, -     0.072), (1.30, -0.102),
(1.40, -0.132), (1.50, -0.156)
PCNGR_2 = GRAPH(Crowding_2)
   (0.00, -0.15), (0.1, 0.00), (0.2, 0.076), (0.3, 0.088), (0.4, 0.088), (0.5, 0.088), (0.6,        0.086),
(0.7, 0.082), (0.8, 0.062), (0.9, 0.032), (1.00, 0.00), (1.10, -0.032), (1.20, -     0.072), (1.30, -0.102),
(1.40, -0.132), (1.50, -0.156)
PCNGR_3 = GRAPH(Crowding_3)
   (0.00, -0.15), (0.1, 0.00), (0.2, 0.076), (0.3, 0.088), (0.4, 0.088), (0.5, 0.088), (0.6,        0.086),
(0.7, 0.082), (0.8, 0.062), (0.9, 0.032), (1.00, 0.00), (1.10, -0.032), (1.20, -     0.072), (1.30, -0.102),
(1.40, -0.132), (1.50, -0.156)

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