From Individual Behavior to Metapopulation Dynamics: Unifying the Patchy Population and Classic Metapopulation Models

Otso Ovaskainen* **and Ilkka Hanski†**

Metapopulation Research Group, Departments of Biological and Environmental Science, University of Helsinki, P.O. Box 65, Viikinkaari 1, FI-00014, Finland

Submitted January 9, 2004; Accepted May 13, 2004; Electronically published August XX, 2004

Online enhancement: appendix.

ABSTRACT: Spatially structured populations in patchy habitats show much variation in migration rate, from patchy populations in which individuals move repeatedly among habitat patches to classic metapopulations with infrequent migration among discrete populations. To establish a common framework for population dynamics in patchy habitats, we describe an individual-based model (IBM) involving a diffusion approximation of correlated random walk of individual movements. As an example, we apply the model to the Glanville fritillary butterfly (*Melitaea cinxia*) inhabiting a highly fragmented landscape. We derive stochastic patch occupancy model (SPOM) approximations for the IBMs assuming pure demographic stochasticity, uncorrelated environmental stochasticity, or completely correlated environmental stochasticity in local dynamics. Using realistic parameter values for the Glanville fritillary, we show that the SPOMs mimic the behavior of the IBMs well. The SPOMs derived from IBMs have parameters that relate directly to the life history and behavior of individuals, which is an advantage for model interpretation and parameter estimation. The modeling approach that we describe here provides a unified framework for patchy populations with much movements among habitat patches and classic metapopulations with infrequent movements.

Keywords: patchy population, metapopulation, individual-based model, stochastic patch occupancy model, Glanville fritillary butterfly, SPOMSIM.

* E-mail: otso.ovaskainen@helsinki.fi.

† E-mail: ilkka.hanski@helsinki.fi.

Am. Nat. 2004. Vol. 164, pp. 000–000. © 2004 by The University of Chicago. 0003-0147/2004/16403-40263$15.00. All rights reserved.

Populations and metapopulations inhabiting fragmented landscapes show much variation in migration rate among habitat patches. In one extreme, termed the patchy population model (Harrison 1991), individuals move frequently among habitat patches and may reproduce in several patches during their lifetime. In the other extreme, most individuals remain all their life in the natal population, and movements among populations are infrequent, though migration rate is high enough to allow eventual recolonization of habitat patches where a local population has gone extinct (the classic metapopulation model; Levins 1969). Clearly, it would be helpful to have a theoretical framework that allows the full range of migration rate to be modeled. One such modeling framework is called structured metapopulation models, which are structured by the distribution of local population sizes (Hastings and Wolin 1989; Gyllenberg and Hanski 1992; Lande et al. 1998, 1999; Casagrandi and Gatto 1999; Saether et al. 1999) or by a simple classification of population sizes (Hanski 1985; Hastings 1991; Hanski and Zhang 1993). Local dynamics and migration are modeled mechanistically, and there are no restrictions on the rate of migration; the consequences of emigration and immigration on local dynamics are fully accounted for. However, these models make the simplifying island model assumptions of global migration among infinitely many identical habitat patches (the assumption of identical patches was relaxed by Gyllenberg and Hanski [1997]). These assumptions greatly facilitate the mathematical analysis.

An important consideration in developing theory for populations and metapopulations is the possibility of generating testable quantitative predictions. The traditional island model in population ecology (Levins 1969) and population genetics (Wright 1931) was a step forward in introducing spatial population structure, but the island model provides a limited framework within which to study many important phenomena, such as the ecology and evolutionary biology of source-sink dynamics (Kawecki 2004), the effective population size (Whitlock 2004), and the evo-

lution of migration rate (Heino and Hanski 2001). The situation is worse when the focus is on quantitative questions, such as the viability of metapopulations in fragmented landscapes. In this case, it is clear that the assumption of identical habitat patches has to be relaxed and the influence of the spatial configuration of the habitat on population processes has to be accounted for. The models that do so are typically based on individuals (e.g., Gaona et al. 1998; Pettifor et al. 2000; Jager et al. 2001; King and With 2002) and quickly become so complex that they can be analyzed only through simulations (Schiegg et al. 2002). Although it is possible to incorporate biological realism into individual-based simulation models, the generality of the results is questionable; individual-based models (IBMs) are hard to develop, hard to communicate, and hard to analyze (Grimm et al. 1999; Lorek and Sonnenschein 1999).

Another modeling approach, termed the spatially realistic metapopulation theory (SMT; Hanski 1999, 2001; Hanski and Ovaskainen 2003), aims at merging a realistic landscape description with mathematically tractable population models. This combination is expected to facilitate the development of models that can be rigorously parameterized and hence used to generate quantitative predictions. The models developed so far in the context of SMT ignore local population dynamics and involve a phenomenological description of migration. The habitat patches are simply classified as occupied or empty, hence the name stochastic patch occupancy models (SPOMs) by Moilanen (1999). The SMT has turned out to provide an effective framework both for parameter estimation (Moilanen et al. 1998; Hanski 1999; Moilanen 1999, 2000, 2002; O'Hara et al. 2002; ter Braak and Etienne 2003) and mathematical analysis (Day and Possingham 1995; Hanski and Ovaskainen 2000; Ovaskainen and Hanski 2001, 2002, 2003; Frank and Wissel 2002; Ovaskainen 2002), and it has become a standard tool in quantitative metapopulation studies (Sjögren-Gulve and Hanski 2000; Hanski 2001).

What has been largely lacking is a link relating IBMs to SPOMs, though such integration has been called for by ecologists for a long time (Ims 1995). A pioneering work here is by Adler and Nuernberger (1994), who constructed an individual-based simulation model for a network of identical habitat patches. They assumed that migrants leave their natal patch in a random direction and move away along a straight path and that successful migration distances are exponentially distributed. Although Adler and Nuernberger (1994) did not explicitly construct a SPOM that would correspond to their IBM, they derived a sequence of analytical approximations for assessing the viability of the metapopulation in terms of the original model parameters. These approximations ignored spatial and temporal autocorrelations in patch occupancy (zero correlation assumption). Another analysis of metapopulation dynamics explicitly based on individual behavior is from Keeling (2002), who assumed an assemblage of identical and equally connected local populations with logistic dynamics. He calculated the extinction and recolonization rates from the IBM and compared them with the rates based on the simplest possible SPOM, the Levins model (Levins 1969). Keeling (2002) found that the single-species metapopulation dynamics predicted by the IBM agreed with the dynamics predicted by the Levins model, but there were deviations in multispecies models, which Keeling (2002) attributed to the zero correlation assumption.

The aim of this article is to continue to develop links between IBMs and SPOMs in a spatially realistic setting in which the actual spatial configuration of a highly fragmented landscape is taken into account. A novel part in the IBM is that we use a mechanistic description of the movement behavior of individuals that obey the rules of correlated random walk both within the habitat patches and while dispersing through the matrix and that show edge-mediated behavior at the habitat patch boundaries. With these ingredients, the movement model generates emigration and immigration events in a mechanistic manner and avoids the need for particular assumptions about how the areas and connectivities of the habitat patches influence migration (as in, e.g., Hanski et al. 2000). Using analytical formulas derived by Ovaskainen and Cornell (2003), we can calculate without any simulations the probabilities of migration and the times that individuals spend in the habitat patches. Because some specific assumptions have to be made about the life history and demography of the species for quantitative predictions, we apply the model to a well-studied species of butterfly, the Glanville fritillary, that lives in a highly fragmented landscape in the Åland Islands in southwest Finland (Hanski 1999). We consider three different models, assuming constant environment (pure demographic stochasticity), uncorrelated environmental stochasticity, and (completely) spatially correlated environmental stochasticity (an extreme version of regional stochasticity). Having constructed the IBMs, we derive the corresponding SPOMs on the basis of the assumption that once a habitat patch is occupied, the size of the local population can be replaced by a constant size. Using parameter values that are realistic for the Glanville fritillary, we demonstrate that the SPOMs thus derived mimic the behavior of the IBMs well.

The Individual-Based Model

We construct an IBM of local population dynamics and individual movement behavior. We make assumptions that are motivated by the biology of the Glanville fritillary butterfly (*Melitaea cinxia*), but these assumptions would be

applicable to a wide range of other insects as well. It would also be straightforward to modify specific assumptions to make the model applicable to species with other life histories. We start with a short description of the life cycle of the Glanville fritillary in the Åland Islands in southwest Finland (Hanski 1999; Nieminen et al. 2004).

The adult flight season lasts from early June until early July. Males tend to emerge earlier than females, as is usual in butterflies (protandry; Wiklund 1984), and females mate soon after hatching. Females typically mate only once, after which they lay several batches of 50–200 eggs at intervals of one or more days, usually starting 2–3 days after mating. Eggs are laid on two host plants, *Plantago lanceolata* and *Veronica spicata*, which grow on dry meadows ranging from dry rocky outcrops to grazed meadows on deeper soils. Eggs hatch in 10–14 days, and the newly hatched larvae spin a web around the host plant. During the summer, a larval group typically defoliates the host plant and moves as a group to another host plant individual. In the autumn, the larvae spin a dense "winter nest" in which they diapause as a group. Diapause is terminated soon after snow melts in April, and the larvae are ready to pupate in early May (Hanski 1999). Most meadows are located within a few hundred meters from the nearest other meadow, and a substantial fraction of adult butterflies moves once or several times among meadows (Hanski et al. 1994). Emigration rate decreases and immigration rate increases with the size of the meadow (Hanski et al. 2000).

While constructing the IBM, we split the life cycle into two parts: local population dynamics and migration. We ignore sex and thus consider only females. The suitable habitat, which consists of dry meadows containing either of the two host plants, occurs as a network of n habitat patches. In the Åland Islands, there are altogether about 4,000 meadows, which are clustered into semi-independent patch networks (Hanski et al. 1996). Figure 1 shows one of these networks that we use as an example throughout this article.

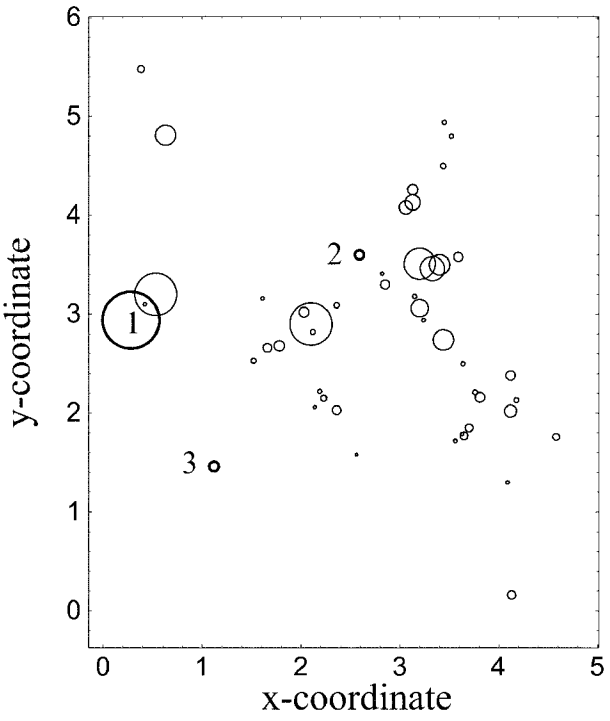


Figure 1: Habitat patch network inhabited by the Glanville fritillary butterfly (*Melitaea cinxia*) in the Åland Islands in southwest Finland and used as an example in this article. The areas of the circles are proportional to the sizes of the habitat patches (though not drawn to scale). The network consists of 51 patches, the sizes of which vary from 0.0025 to 2.7 ha. Patches 1, 2, and 3 are further analyzed in figure 4. The spatial unit is kilometers.

Local Population Dynamics

We let $a_i(t)$ denote the number of egg groups that are oviposited in patch i in year t, $\hat{a}_i(t+1)$ the number of larval groups that survive over winter in patch i, and $b_i(t+1)$ the number of female butterflies that hatch to patch i in year $t+1$. We assume that each group has the probability $e_i(t)$ to survive over winter (mortality at the group level is especially great for newly hatched larvae). Second, we assume that in the absence of density dependence, the number of females that would hatch from each surviving group follows the Poisson distribution with a fixed mean n_{h}^0. We assume that density dependence acts through scramble competition for food during the late larval instars such that the number of females that hatch has the mean $n_{\mathrm{h}} = n_{\mathrm{h}}^0 \exp[-\hat{a}_i(t+1)n_{\mathrm{h}}^0/(\exp(1)K_i)]$. With this assumption, the maximum mean number of individuals that may hatch in patch i is K_i, which is the case if the number of surviving groups is $\exp(1)K_i/n_{\mathrm{h}}^0$.

In reality, there is environmental stochasticity both at the level of groups and at the level of individuals, but for simplicity, we include environmental stochasticity only at the group level, where we expect it to be most important (Hanski 1999). The survival probability of groups, $e_i(t)$, is assumed to depend on the environmental conditions in patch i during the period from the end of the flight season in year t until the spring in year $t+1$ according to one of the following models.

Model A (constant environment). The environmental conditions $e_i(t)$ are fixed to a constant value, $e_i(t) = e_\mu$ for all i, t.

Model B (uncorrelated environmental stochasticity). The environmental conditions $e_i(t)$ are independent random variables that follow the gamma distribution with mean

e_μ and standard deviation e_σ. We denote by e_ζ the coefficient of variation, $e_\zeta = e_\sigma/e_\mu$. As the range of the gamma distribution is in $[0, \infty]$, $e_i(t)$ may become larger than 1, in which case we set $e_i(t) = 1$. The reason for using the gamma distribution instead of, for example, the beta distribution, which would have its range in [0, 1], is that the former turns out to have an advantage for the analysis. The exact shape of the distribution does not have a large effect on the behavior of the IBM.

Model C (correlated environmental stochasticity). The environmental conditions $e_i(t)$ are fixed for each year, $e_i(t) = e(t)$. The yearly values $e(t)$ are independent random variables that follow the truncated gamma distribution with mean e_μ and standard deviation e_σ.

Migration

We assume that once a female butterfly has eclosed in a particular patch, it mates with probability 1, after which it starts the migration phase. We assume that migrating females move according to the rules of correlated random walk both within habitat patches as well as in the surrounding matrix, though possibly with different parameter values in the habitat and the matrix. Correlated random walk models have been frequently used in butterfly studies (Odendaal et al. 1989; Turchin 1991; Schultz and Crone 2001; Fownes and Roland 2002). In addition to the correlated random walk, we assume that individuals show edge-mediated behavior and bias their movements toward the habitat patch when close to patch boundary. Butterflies have been observed to respond to edges by avoiding crossing them, by turning back once they have crossed an edge, or by recognizing a patch from some distance (Conradt et al. 2000; Ries and Debinski 2001; Schultz and Crone 2001).

We assume that the oviposition rate within habitat patches is constant and hence that the mean number of egg groups oviposited in a patch is directly proportional to the amount of time that females spend in the patch. Letting $q_i(t)$ be the total time spent by all female butterflies in patch i, we thus assume that $a_i(t)$ follows the Poisson distribution with mean $q_i(t)/t^*$, where t^* is the mean number of butterfly days needed to oviposit one egg group.

Although correlated random walk may easily be incorporated into a simulation model (Byers 2001), we aim at mathematical tractability by using the diffusion approximation, which aggregates the distributions of move lengths and durations, and the distribution of turning angles into habitat-specific diffusion coefficients D_i and mortality rates μ_i (Patlak 1953; Turchin 1998). The strength of edge-mediated behavior is quantified by habitat-specific multipliers k_i, with the ratio k_i/k_j measuring the individual's preference to move to habitat type i instead of to habitat type j (Ovaskainen and Cornell 2003; Ovaskainen 2004). Assuming a landscape consisting of circular patches, Ovaskainen and Cornell (2003) employed the diffusion approximation to derive analytical formulas for migration probabilities among habitat patches and for the times that an individual is expected to spend in any one patch. The formulas take into account not only the interpatch distances but also the actual spatial configuration of the patch network. For example, adding a new patch between two existing patches reduces the probability of migration between the two previous patches because the new patch "competes" for the migrants. Because the formulas have been previously published only in the mathematical literature, we reproduce them here in the appendix in the online edition of the *American Naturalist*.

To calculate the total time $q_i(t)$ that females spend in patch i, we proceed as follows. First, we use the probability R_{ij} (appendix) to determine whether an individual initially in patch i will visit patch j before it dies. Note that by definition, $R_{ii} = 1$, and thus all females visit their natal patch. We let $m_i(t)$ denote the number of females originating from the other patches that visit patch i in year t, while $n_i(t) = b_i(t) + m_i(t)$ is the total number of females that visit patch i in year t. If an individual visits patch i, we assume that the time it spends in that patch is exponentially distributed with mean T_i, which is the time that an individual presently in patch i is expected to spend in patch i during its lifetime (appendix). The exponential distribution is not exact, but it should be a good approximation because the individual has a constant death rate and a constant emigration rate following a short transient after immigration. Because the sum of exponential distributions follows the gamma distribution, the total time $q_i(t)$ that females spend in patch i is distributed according to the gamma distribution with parameters $n_i(t)$ and T_i.

The SPOM Approximation

A SPOM describes the dynamics of a metapopulation in which the state of each patch in each year is classified simply as occupied or empty. Because a patch may be occupied in one stage of the life cycle and empty in another, it is important to specify to which stage of the life cycle one refers. We will classify patch i in year t as occupied if $b_i(t) > 0$, that is, if any females emerge in the patch in year t, which indicates that the patch has been successfully used for reproduction. We denote by $O_i(t) \in \{0, 1\}$ the state of patch i in year t and by $\mathbf{o}(t) = \{O_i(t)\}_{i=1}^N$ the vector describing the state of the entire metapopulation. By the above reasoning, we let $O_i(t) = 1$ if $b_i(t) > 0$ and $O_i(t) = 0$ if $b_i(t) = 0$.

The major simplification of the SPOM approximation is that it ignores variation in local population sizes. We

do this by assuming that $b_i(t) = cr_iO_i(t)$, where c is a scaling constant and r_i is a suitable surrogate, such as the carrying capacity K_i, for the number of females that eclose in patch i conditioned on the patch being occupied. Note that cr_i is not necessarily the average population size in patch i, but it is such a constant population size that makes the SPOM behave in the same manner as the IBM.

Our aim is to derive the transition probabilities that are needed to move from the state $\mathbf{o}(t)$ to the state $\mathbf{o}(t+1)$. We will derive the transition probabilities by working backward in time, and we thus start by considering whether any females will eclose in the patch in year $t+1$. Ignoring the unlikely possibility of extinction due to a very high larval density (which may happen occasionally as a result of scramble competition), the risk of local extinction is greatest when the number of egg groups is smallest, in which case density dependence in larval mortality may be ignored. As the number of females produced by a larval group that has survived the winter is distributed according to the Poisson distribution, the probability that at least one female ecloses from a given surviving group is $p = 1 - \exp(-n_h^0)$. Thus, the probability that no females eclose from the $\hat{a}_i(t+1)$ groups that survived over winter is

$$P[O_i(t+1) = 0] = (1-p)^{\hat{a}_i(t+1)}. \tag{1}$$

Because $\hat{a}_i(t+1)$ is distributed as $\mathrm{Bin}(a_i(t), e_i(t))$, we obtain the probability that no individuals will eclose next year by summing over the binomial distribution, which gives

$$P[O_i(t+1) = 0] = (1 - e_i(t)p)^{a_i(t)}. \tag{2}$$

The number of egg groups $a_i(t)$ oviposited in patch i follows the Poisson distribution with parameter $q_i(t)/t^*$. Summing equation (2) over this distribution gives

$$P[O_i(t+1) = 0] = \exp\left(\frac{-e_i(t)pq_i(t)}{t^*}\right). \tag{3}$$

Because the time $q_i(t)$ follows the gamma distribution with parameters $n_i(t)$ and T_i, we may integrate equation (3) over the distribution for $q_i(t)$, which gives

$$P[O_i(t+1) = 0] = (1 + z_i(t))^{-n_i(t)}, \tag{4}$$

where $z_i(t) = e_i(t)pT_i/t^*$. Note that T_i/t^* is the mean number of egg groups produced in patch i by a female originally located in patch i and that $e_i(t)p$ is the probability that at least one female ecloses from a group. Thus, $z_i(t)$ is the mean number of egg groups that will produce at least one female in year $t+1$, laid in patch i by a female that was born in patch i in year t.

The number of females that originate from patches other than patch i and visit patch i at least once during their lifetime, $m_i(t)$, has the mean $\bar{m}_i(t) = \Sigma_{j\neq i} b_j(t)R_{ji} = c\Sigma_{j\neq i} r_j R_{ji} O_j$. Because $m_i(t)$ is the sum of a large number of independent Bernoulli random variables, each of which has a small probability to be 1, the distribution for $m_i(t)$ may be approximated by the Poisson distribution with mean $\bar{m}_i(t)$ (Grimmett and Stirzaker 2001). The total number of individuals visiting patch i is $n_i(t) = b_i(t) + m_i(t)$, and hence summing equation (4) over the Poisson distribution gives

$$\begin{aligned} P[O_i(t+1) = 0] &= \exp\left(\frac{-\bar{m}_i z_i(t)}{1 + z_i(t)}\right)(1 + z_i(t))^{-b_i(t)} \\ &\approx \exp(-\bar{n}_i z_i(t)), \end{aligned} \tag{5}$$

where $\bar{n}_i = \bar{m}_i + b_i(t)$ and the approximation is based on the assumption that $z_i(t) \ll 1$. Combining the above, we obtain

$$P[O_i(t+1) = 0] = \exp\left(-\frac{ce_i(t)p}{t^*}(\mathbf{Mo})_i\right), \tag{6}$$

where $\mathbf{M}$ is the matrix with elements $\mathbf{M}_{ij} = T_i R_{ji} r_j = T_{ji} r_j$. We are now ready to consider the three specific models.

Model A. If the environmental conditions $e_i(t)$ are constant, we may replace $e_i(t)$ in equation (6) with the mean value e_μ to obtain

$$P[O_i(t+1) = 0] = \exp\left(-\frac{(\mathbf{Mo}(t))_i}{\delta}\right), \tag{7}$$

where $\delta = t^*/(ce_\mu p)$.

Model B. If the environmental conditions vary independently between the years and the patches, we may integrate equation (6) over the assumed gamma distribution (assuming that the tail for which $e_i(t) > 1$ has a negligible effect) to obtain

$$P[O_i(t+1) = 0] = \left(1 + \frac{e_\xi^2(\mathbf{Mo}(t))_i}{\delta}\right)^{-1/e_\xi^2}. \tag{8}$$

Note that as $e_\xi \to 0$, equation (8) converges to equation (7) as expected.

Model C. Even if the environmental conditions are correlated, equation (8) still holds. However, equation (8) ignores the correlation structure, and a better description of the dynamics is obtained by simply replacing $e_i(t)$ with $e(t)$ in equation (6). This gives

$$P[O_i(t+1) = 0] = \exp\left(-\frac{e(t)(\mathbf{Mo}(t))_i}{e_\mu \delta}\right), \quad (9)$$

which is a SPOM with a temporally varying parameter.

Qualitative Behavior of the SPOMs

Before comparing the dynamics predicted by the SPOMs and the IBMs, we briefly examine the qualitative behavior of the SPOMs that we have just derived. We will ignore here the effects of stochasticity and consider only the deterministic drift in patch occupancy dynamics (Ovaskainen 2002). In the deterministic approximation, model C behaves as model B, and it hence suffices to consider models A and B only.

Elementary stability analysis shows that both models A and B possess a nontrivial equilibrium state $p^* > 0$ if and only if the trivial equilibrium state is unstable. Therefore, in the terminology of Ovaskainen and Hanski (2001), all the three models are Levins-type models. The threshold condition for persistence, in the sense of existence of a nontrivial equilibrium state, may be written as $\lambda_M > \delta$, where λ_M is the leading eigenvalue of matrix **M**, termed the metapopulation capacity of the patch network (Hanski and Ovaskainen 2000).

Although the threshold value δ in models B and C does not depend on the coefficient of variation e_ζ, the equilibrium occupancy state depends strongly on e_ζ. This is illustrated by figure 2, in which we consider the deterministic variants of the models defined by equations (7) and (8) in the case of homogeneous patch networks with identical and equally connected patches. In other words, we consider the solutions to the equations

$$p = 1 - \exp\left(-\frac{\lambda_M p}{\delta}\right), \quad (10)$$

$$p = 1 - \left(1 + \frac{e_\zeta^2 \lambda_M p}{\delta}\right)^{-1/e_\zeta^2}. \quad (11)$$

As expected, the equilibrium occupancy state decreases with e_ζ. It is interesting that the case $e_\zeta = 1$ corresponds to the Levins model (Levins 1969) because in this case the equilibrium state satisfies the equation $p = (1 - \delta)/\lambda_M$.

Results

Our aim is to compare the IBM and the SPOMs using parameter values that are realistic for the Glanville fritillary butterfly. We first describe the behavior of the IBM and then test to what extent this is matched by the dynamics predicted by the SPOM approximations.

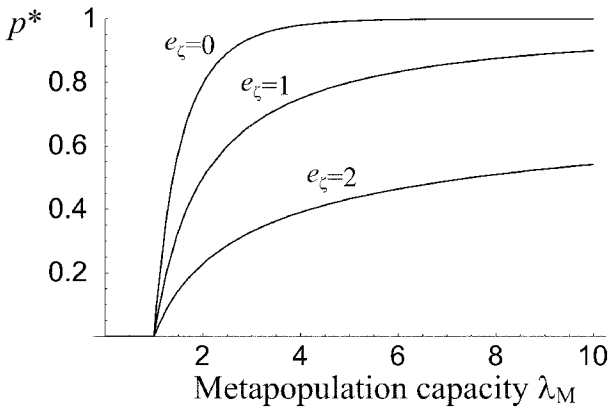


Figure 2: Qualitative behavior of the SPOMs given by equations (10) and (11). The figure shows the equilibrium fraction of occupied patches p^* as a function of the metapopulation capacity λ_M. The case $e_\zeta = 0$ corresponds to model A and the cases $e_\zeta = 1$ and $e_\zeta = 2$ to model B. Parameter $\delta = 1$.

The Behavior of the IBM

Let us first consider the migration phase. We use the parameter values estimated by Ovaskainen (2004) for *Melitaea diamina*, a close relative of the Glanville fritillary. Ovaskainen (2004) used mark-release-recapture data to estimate the diffusion coefficients, mortality rates, and the boundary multipliers for a landscape consisting of discrete habitat patches (h) and matrix (m). There were no statistically significant differences in the parameter values between different habitat types; hence, we use the maximum likelihood estimates $D = 94{,}000$ (m^2/day) and $\mu = 0.1$ (1/day) for both the habitat patches and the matrix. Because only the relative values of the boundary multipliers matter, we set $k_h = 1$, and hence the strength of the bias is measured by the value of $k = k_m$, which was estimated as $k = 1/115$ (Ovaskainen 2004).

Patterns of migration predicted by these parameter values in the patch network in figure 1 are shown in figure 3. Individuals spend roughly half of their expected lifetime of 10 days in the habitat patches. The time spent in patches increases with the area of the natal patch (fig. 3*A*). The likelihood that an individual will ever make a successful migration event varies between 0.14 and 0.97 and is greatest for the smallest patches (fig. 3*B*). This is to be expected because individuals born in small patches have a higher emigration rate than individuals born in large patches. The model generates a mechanistic rescue effect because it assumes that reproduction depends on the

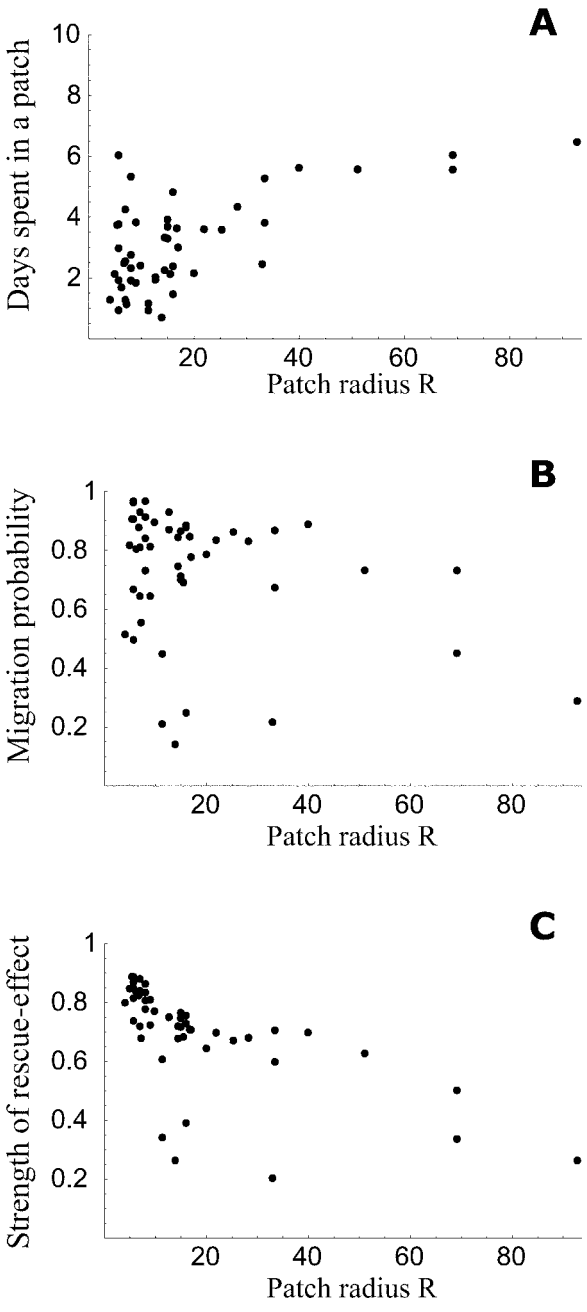


Figure 3: Summary statistics for the consequences of migration (based on the IBM) in the network shown in figure 1. *A*, Time that an individual born to a particular patch is expected to spend within any one of the habitat patches. *B*, Probability that an individual born to a particular patch will ever visit any other patch than the natal one. *C*, Maximal strength of the rescue effect, which is measured as the proportion of individuals originating from the other habitat patches out of all butterflies visiting the focal patch at least once.

pooled time that all butterflies spend in a habitat patch. Figure 3*C* indicates the strength of the rescue effect in terms of the proportion of butterfly days spent in a patch by individuals originating from the other patches. In our example, this proportion varies from 0.20 to 0.89 and is largest in the smallest patches, as expected. All the results in figure 3 show much variation, which means that the size of a habitat patch alone does not explain well the importance of a patch for migrating individuals. The remaining variance is explained by the position of the patch within the patch network.

We continue with the demographic parameters. If the habitat patches were of uniform quality, it would be natural to assume that the carrying capacity of a patch is proportional to its area. However, larger patches are typically of lower average quality. Hanski et al. (1994) found that the density of butterflies tends to be higher in smaller patches. We assume that the carrying capacity is proportional to the square root of patch area (in ha), $K_i = 150(A_i)^{1/2}$, which is consistent with the results of Hanski et al. (1994). Because the patch areas in figure 1 range from 0.005 to 2.7 ha, the carrying capacities range from 11 to 246 females. We will use $n_h^0 = 5$ as a reasonable mean number for females emerging per surviving egg group in the absence of density dependence. We assume $t^* = 5$, corresponding to a situation in which a female with an average lifetime of $1/\mu = 10$ days would oviposit two egg groups on average if it would spend all its life within the habitat patches.

Setting reasonable parameter values for the environmental conditions is a more difficult task. We chose to fix the mean environmental conditions to $e_\mu = 0.4$, which corresponds to a situation in which a female would produce on average at most $e_\mu n_h^0 t^*/\mu = 4$ new females. In other words, without density dependence, the population would on average grow at most as $N(t + 1) = R_0 N(t)$ with $R_0 = 4$. Quite arbitrarily, we set $e_\xi = 0.8$. With this assumption, and assuming that females would spend all their life within habitat patches, $P(R_0 < 1) \approx 0.13$, $P(R_0 < 0.5) \approx 0.05$, and $P(R_0 < 0.1) \approx 0.004$. In reality, many females will spend a substantial part of their lifetime in the matrix (fig. 3*A*), and hence the realized population growth rate will be somewhat lower.

Figure 4 shows the dynamics produced by the three versions of the IBM. This figure shows 50-year-long time series of local population sizes for three habitat patches. The three patches include one large patch (*1* in fig. 1), one small well-connected patch (*2*), and one small isolated patch (*3*). In model A, which includes only demographic stochasticity, the population size in the large patch fluctuates only mildly around the carrying capacity. Populations in the smaller patches seldom reach the carrying capacity because individuals born to these patches have a

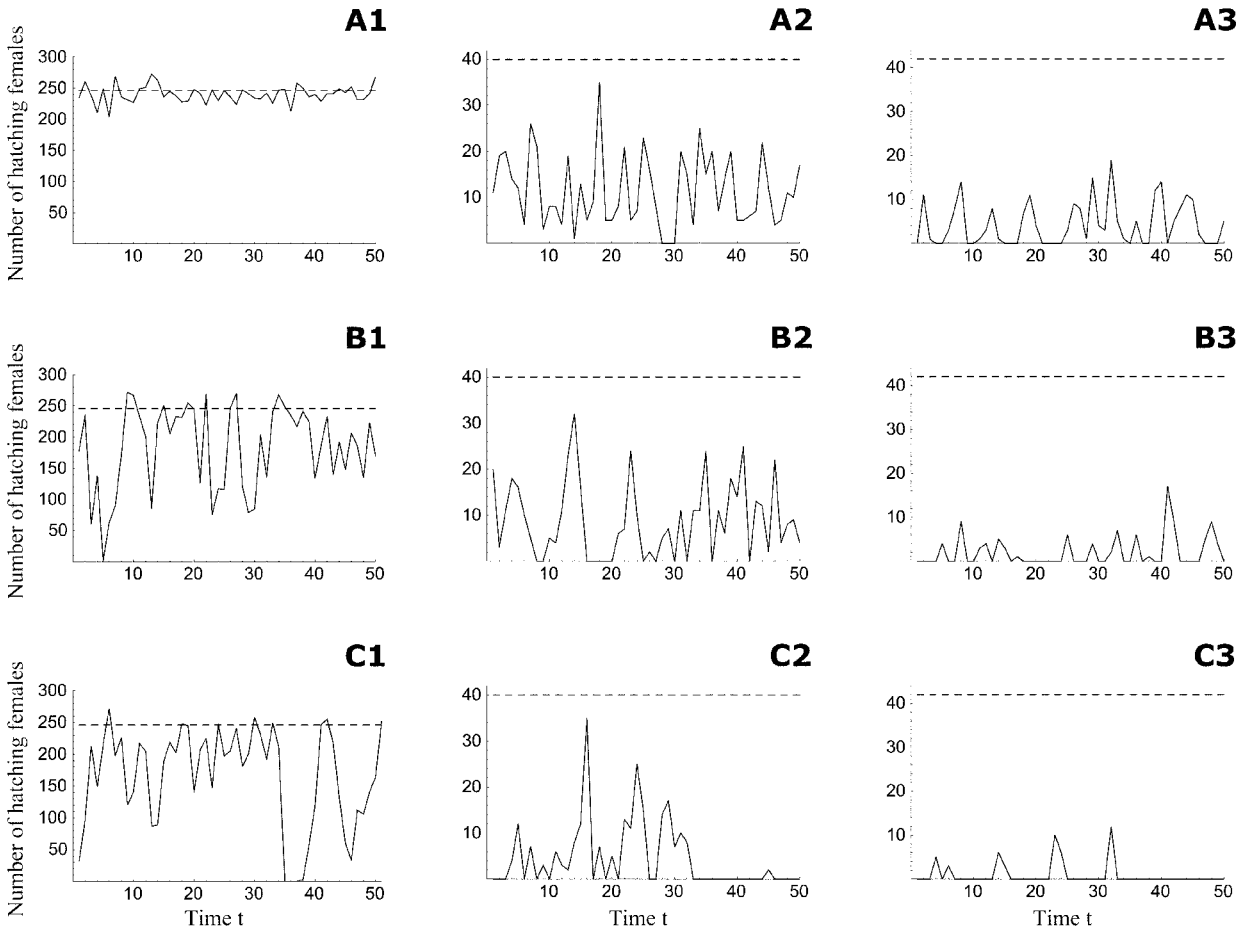


Figure 4: Local population dynamics (based on the IBM) in the three patches highlighted in figure 1. *A1–A3*, *B1–B3*, and *C1–C3* correspond to patches 1–3 and models A, B, and C, respectively. *B1* and *C1* represent nonrandom samples because we chose periods that included a local extinction. During the simulation run of 2,000 years, local extinction occurred four times in patch 1 in model B and seven times in model C.

high tendency to leave the patch; consequently, these patches would not support viable populations if they were isolated from the rest of the network. The population in the small isolated patch frequently goes extinct, whereas the small well-connected patch remains occupied most of the time because of the rescue effect. In model B with uncorrelated environmental stochasticity, local population sizes fluctuate greatly, and, as expected, environmental stochasticity increases the risk of local extinction in all three patches. Assuming that environmental stochasticity is completely spatially correlated (model C) does not change the local dynamics much in comparison with the previous case (model B) once a patch is occupied. This is so because within each patch, the environmental conditions vary in an identical manner in models B and C. However, if a population happens to become extinct, the recolonization of the respective patch is much delayed in model C in comparison with model B. This happens because the adverse environmental conditions that make the focal population become extinct are likely to simultaneously suppress the local populations in the neighboring patches, which reduces the numbers of potential immigrants to the focal patch in the following years.

Comparison between IBMs and SPOMs

We now turn to a comparison between the IBMs and the SPOMs. Using the SPOMs given by equations (7)–(9), we attempted to find parameter values that would make the SPOM behave as similarly as possible to the IBM. Throughout the comparisons, we kept the migration parameters (and thus the matrix **M**) fixed to the same values that were used in the IBMs. This leaves only one free parameter in model A, c, which was fitted by requiring

that the mean number of occupied patches was the same for the SPOM as it was for the IBM. In models B and C, there are two free parameters, c and e_s, which were fitted by requiring that in addition to the mean also the patch-specific occupancy probabilities should agree as closely as possible in the two models.

We used two choices for the surrogate r_i. In case 1, we set r_i to the mean value of $b_i(t)$ obtained from a 2,000-year-long simulation of the IBM. In case 2, we set r_i equal to the carrying capacity, $r_i = K_i$. Note that while we use information about the behavior of the IBM in case 1, this case is relevant for applications because it is often more feasible to determine the actual population sizes for the occupied patches than to determine the theoretical carrying capacity. Of course, in reality one will have information about the local population sizes only for a limited number of years and populations. With case 1, we test whether the behavior of the IBM could be approximated by a SPOM if knowledge about the mean population sizes would be available, while the estimation of the local population sizes is left as a separate problem and not considered here.

Figure 5 shows the ability of SPOMs to mimic the behavior of the IBMs. The left-hand panels compare the occupancy probabilities for individual habitat patches, whereas the right-hand panels compare the quasi-stationary distributions predicted by the two model types. The SPOM reproduces very closely the full presence-absence dynamics generated by the IBMs in both cases 1 and 2, though in the latter case some patch-specific occupancy probabilities show somewhat greater deviations.

Discussion

Stochastic patch occupancy models have been criticized for being overly simple and thus not very helpful descriptions of real metapopulations (Harrison 1991, 1994). Much of the criticism has been directed toward the use of metapopulation models without any spatial structure, such as the classic Levins model (Levins 1969), which indeed are more appropriate for qualitative analysis rather than for making quantitative predictions. Another concern has been to what extent the classic metapopulation models with emphasis on extinction-colonization dynamics suffice to describe the dynamics of real metapopulations with much variation in the sizes of local populations or much movements of individuals among populations or both. There is no conceptual difficulty in modeling such population structures with individual-based simulations, but individual-based simulations will not easily lead to helpful generalizations.

Here we have analyzed whether one family of simple metapopulation models, the spatially realistic SPOM, is able to replicate the behavior of IBM. Our case study was the Glanville fritillary butterfly, whose metapopulation biology is exceptionally well known (Hanski 1999; many chapters in Ehrlich and Hanski 2004). We first constructed an IBM that incorporated information about the life history and movement behavior of the focal butterfly and then attempted to capture the dynamics produced by the IBM with a SPOM. The IBM predicted much variation in local population sizes, in agreement with what happens in real populations, but in spite of this, the SPOM approximations replicated remarkably well the behavior of the IBMs at the metapopulation level. This is an encouraging result, suggesting that SPOMs are indeed relevant tools in metapopulation studies in spite of their simplicity. Apart from analyzing SPOMs derived directly from the corresponding IBMs, we have also compared the dynamics predicted by the IBMs with those predicted by the spatially realistic Levins model (see, e.g., Ovaskainen 2002), with similarly positive results (appendix). The good performance of the latter model was not necessarily anticipated because it is based on different structural assumptions than the IBMs and the SPOMs derived in this article. This example highlights the general utility of SPOMs as metapopulation-level descriptions of population dynamics.

The fact that the SPOMs derived here have a mechanistic basis has several advantages. First, all of the model parameters relate directly to the life cycle of the species and thus have a clear biological interpretation. Second, in traditional SPOMs, such as the spatially realistic Levins model or the incidence function model (Hanski 1994), the functional form of the colonization rate is based on heuristic assumptions about how patch area affects emigration and immigration (typically power laws) and how interpatch distances affect the success of migration (typically exponential functions). The present modeling framework replaces these assumptions with scaling laws that follow directly from the movement behavior of individuals. The underlying model of individual movements is correlated random walk with bias at habitat patch boundaries. This is not a universally valid model for all organisms but is appropriate for many much-studied taxa such as butterflies. Third, the present SPOMs include a mechanistic description of the rescue effect, which has been previously modeled in a mechanistic manner only in homogeneous patch networks (Gyllenberg and Hanski 1992; Etienne 2000, 2002; Harding and McNamara 2002). In the spatially realistic metapopulation theory, the rescue effect has been either ignored or modeled through heuristic assumptions (e.g., Hanski 1999; Ovaskainen and Hanski 2001). Fourth, because of their mechanistic basis, the present SPOMs are expected to make valid predictions about the dynamics in landscapes affected by habitat loss and fragmentation. This

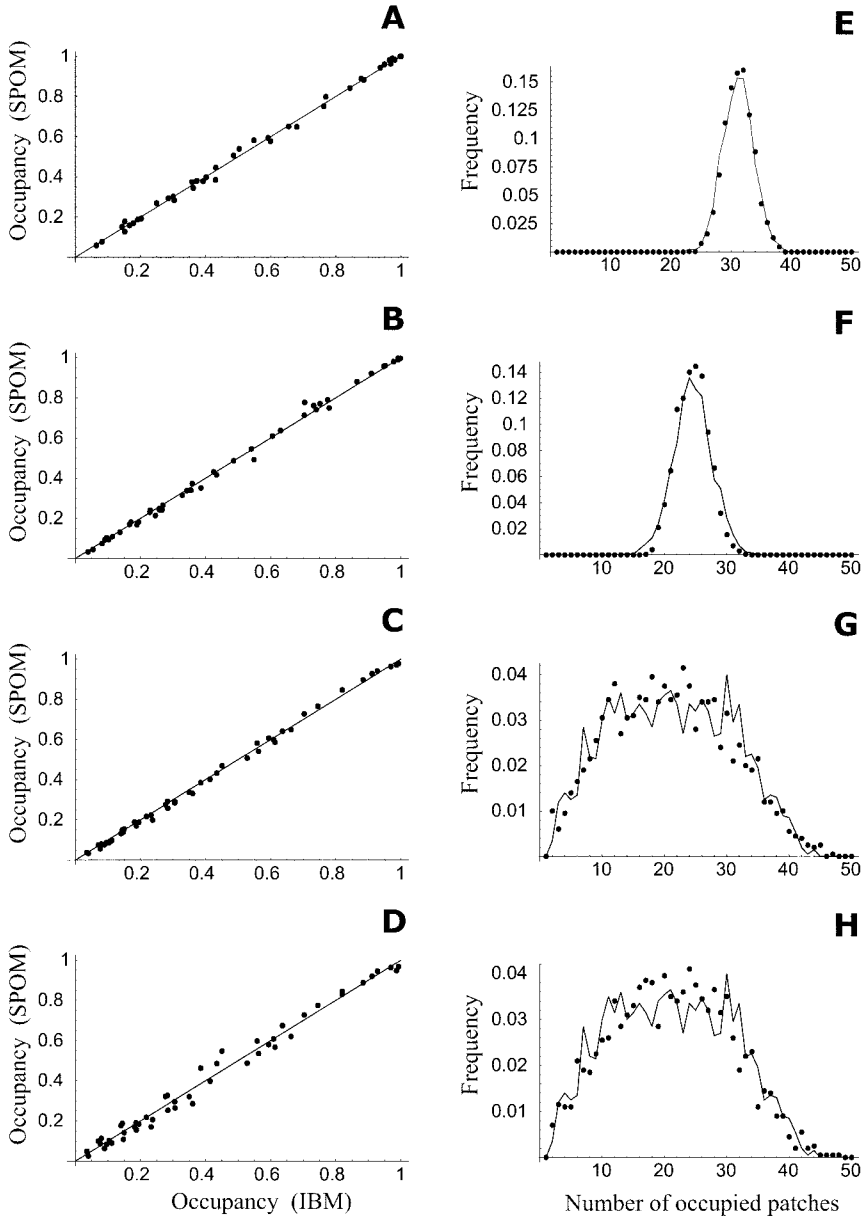


Figure 5: Comparison between the IBMs and the SPOMs. The left-hand panels compare patch-specific occupancy probabilities, with lines depicting identity. The right-hand panels compare the quasi-stationary distributions for the number of occupied patches, which are approximated here using data from 2,000-year-long simulation runs. In the right-hand panels, the lines correspond to the IBMs, and the circles correspond to the SPOMs. *A*, *E*, Case 1, model A. *B*, *F*, Case 1, model B. *C*, *G*, Case 1, model C. *D*, *H*, Case 2, model C. (Models A and B behave in a comparable manner; not shown here.) Parameter values for case 1: $c = 0.96$ (model A); $c = 0.92$, $e_S^{\mathrm{SPOM}} = e_S^{\mathrm{IBM}}$ (model B); $c = 0.96$, $e_S^{\mathrm{SPOM}} = 1.4e_S^{\mathrm{IBM}}$ (model C). Parameter values for case 2: $c = 0.36$, $e_S^{\mathrm{SPOM}} = 1.3e_S^{\mathrm{IBM}}$ (model C).

is not necessarily the case with traditional SPOMs, which do not account for the fact that habitat patches essentially "compete" for the migrants or which model such competition with heuristic assumptions (such as the ones used in Hanski et al. 2000). When the landscape becomes more fragmented, the effect of such competition is reduced, and hence the parameter values obtained for the original landscape do not necessarily apply for the more fragmented landscape.

An appealing feature of the present SPOMs is their simplicity. Most strikingly, model A with demographic stochasticity has just three free parameters. Matrix **M**, which

incorporates information about patch areas and spatial locations, depends nonlinearly only on the scale of migration distances $\alpha = (D/\mu)^{1/2}$ and the boundary multiplier k. The absolute values of the diffusion coefficient D and the mortality rate μ affect **M** only through a multiplicative constant, which may be included in the parameter δ. Similarly, models B (with environmental stochasticity) and C (with regional stochasticity) have four free parameters, the additional parameter e_ζ measuring the strength of environmental stochasticity. In contrast, the spatially realistic Levins model, though also a simple model, has three more parameters. The reduction in the number of parameters is explained by two factors. First, the present model does not involve separate descriptions of how patch area affects emigration, immigration, and extinction (table A1 in the online edition of the *American Naturalist*), which all follow from the modeling of individual movement behavior with bias at habitat boundaries. Second, the present model generates local extinctions and recolonizations from the same processes of individual movements and reproduction; hence, there is no need for specific extinction and colonization parameters.

The present models are based on practically the simplest possible assumptions, so they should hence be considered as baseline models on top of which additional complexity could be built. For example, we have ignored most types of interactions that could occur among individuals, the exception being density dependence in local dynamics, but other types of interactions could be added. Such modifications are likely to result in nonlinearities in the model structure, and they could thus change the qualitative model behavior. Another simplification made here is the assumption that the diffusion coefficients and the mortality rates are identical for the habitat patches and for the matrix. This assumption can be relaxed, which would add one or two more parameters (see appendix). Even more fundamentally, one could change the basic assumptions about the life history of the species, which we tailored for the Glanville fritillary. For example, we assumed that migration and reproduction occur in a continuous fashion throughout the adult life and that the reproductive output depends on the amount of time that individuals spend in the habitat patches. Although these assumptions are justified for many insects, other assumptions are needed for other species inhabiting fragmented landscapes. One issue that remains to be studied further is the length of the transient period in local dynamics following establishment of new populations. One could envision situations in which the transient is much longer than in our examples (see fig. 4). On the other hand, the classic metapopulation approach may be generally less helpful for situations in which the transients are very long because this implies very large habitat patches and hence low population turnover. The combination of long transients and fast turnover (e.g., Ronce et al. 2000) seems unlikely for natural metapopulations.

The SPOMs constructed here have an individual-based background, which leads to the possibility of combining data collected with different methods in parameter estimation, such as presence-absence surveys, mark-recapture studies, and life-history studies. For example, the dispersal parameters D, μ (or their habitat-specific versions), and k may be estimated with mark-recapture studies. While doing so, one may also include more detail about the landscape structure by accounting for, for example, arbitrary patch shapes and variation in matrix quality. Such a spatially explicit diffusion model can be parameterized with mark-recapture data using the finite element method (Ovaskainen 2004), after which the model can be used for the construction of the matrix **M**. Mark-recapture data can also be used to estimate local population sizes, and these estimates can be used to construct a relationship between r_i and the size, quality, and isolation of a patch (e.g., Hanski et al. 1994). Following these steps, only one (model A) or two (models B and C) parameters remain to be estimated from presence-absence occupancy data. Another possibility for combining the different sources of data is to use Bayesian techniques and to use the estimates based on one data type as prior distributions for parameter estimation based on another type of data.

A major concern about SPOMs has been that they apply only to classic metapopulations with a substantial amount of population turnover (Harrison 1994). Because many studies conducted in fragmented landscapes have described the assemblages of local populations as patchy populations rather than as classic metapopulations (e.g., Harrison 1991; Hill et al. 1996; Sutcliffe et al. 1997; Matthysen 1999; Szacki 1999; Roslin and Koivunen 2001), models typified as being appropriate for the latter have been suggested to be of limited general value. A major advantage of the present modeling approach is that one may analyze a range of spatially structured populations varying greatly in the magnitude of migration. Hence, the message is that there is no need for the patchy population versus classic metapopulation dichotomy. Rather than attempting to describe different (meta)population "types," it is helpful to focus on the relevant processes, for example, the magnitude of migration (Hanski 1999). Naturally, the SPOM approximations are not relevant for situations where there is no population turnover at all and hence no variation in the spatial pattern of patch occupancy, but as our study shows, the applicability of SPOMs is not restricted by the amount of migration among local populations. Indeed, the models that we have constructed unify the patchy population and classic metapopulation models.

Acknowledgments

We thank S. Cornell, T. Crist, A. Moilanen, T. Snäll, and an anonymous reviewer for valuable comments. This study was supported by the Academy of Finland (grant 50165) and the Finnish Centre of Excellence Programme 2000–2005 (grant 44887). O.O. is grateful to the Isaac Newton Institute for Mathematical Sciences, Cambridge, for financial support and intellectual stimulus during the program "From Individual to Collective Behaviour in Biological Systems."

Literature Cited

Abramowitz, M., and I. A. Stegun. 1972. A handbook of mathematical functions. Dover, New York.

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology 45:41–75.

Byers, J. A. 2001. Correlated random walk equations of animal dispersal resolved by simulation. Ecology 82: 1680–1690.

Casagrandi, R., and M. Gatto. 1999. A mesoscale approach to extinction risk in fragmented habitats. Nature 400: 560–562.

Conradt, L., E. J. Bodsworth, T. J. Roper, and C. D. Thomas. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. Proceedings of the Royal Society of London B 267:1505–1510.

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variable patch size and position. Theoretical Population Biology 48:333–360.

Ehrlich, P. R., and I. Hanski, eds. 2004. On the wings of checkerspots: a model system for population biology. Oxford University Press, New York.

Etienne, R. S. 2000. Local populations of different sizes, mechanistic rescue effect and patch preference in the Levins metapopulation model. Bulletin of Mathematical Biology 62:943–958.

———. 2002. A scrutiny of the Levins metapopulation model. Comments on Theoretical Biology 7:257–281.

Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8:124–137.

Fownes, S., and J. Roland. 2002. Effects of meadow suitability on female behaviour in the alpine butterfly *Parnassius smintheus.* Ecological Entomology 27:457–466.

Frank, K., and C. Wissel. 2002. A formula for the mean lifetime for metapopulations in heterogeneous landscapes. American Naturalist 159:530–552.

Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs 68:349–370.

Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115:275–282.

Grimmett, G., and D. Stirzaker. 2001. Probability and random processes. 3d ed. Oxford University Press, Oxford.

Gu, W., R. Heikkilä, and I. Hanski. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17:699–710.

Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: a structured model. Theoretical Population Biology 42:35–61.

———. 1997. Habitat deterioration, habitat destruction and metapopulation persistence in a heterogeneous landscape. Theoretical Population Biology 52:198–215.

Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. Ecology 66:335–343.

———. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

———. 1998. Connecting the parameters of local extinction and metapopulation dynamics. Oikos 83:390–396.

———. 1999. Metapopulation ecology. Oxford University Press, Oxford.

———. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372–381.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404:755–758.

———. 2003. Metapopulation theory for heterogeneous fragmented landscapes. Theoretical Population Biology 64:119–127.

Hanski, I., and D.-Y. Zhang. 1993. Migration, metapopulation dynamics and fugitive coexistence. Journal of Theoretical Biology 163:491–504.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia.* Ecology 75:747–762.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578–590.

Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81:239–251.

Harding, K. C., and J. M. McNamara. 2002. A unifying framework for metapopulation dynamics. American Naturalist 160:173–185.

Harrison, S. 1991. Local extinction in a metapopulation

context: an empirical evaluation. Biological Journal of the Linnean Society 42:73–88.

———. 1994. Metapopulations and conservation. Pages 111–128 *in* P. J. Edwards, R. M. May, and N. R. Webb, eds. Large-scale ecology and conservation biology. Blackwell Scientific, Oxford.

Hastings, A. 1991. Structured models of metapopulation dynamics. Pages 57–71 *in* M. Gilpin and I. Hanski, eds. Metapopulation dynamics. Academic Press, London.

Hastings, A., and C. L. Wolin. 1989. Within-patch dynamics in a metapopulation. Ecology 70:1261–1266.

Heino, M., and I. Hanski. 2001. Evolution of migration rate in a spatially realistic metapopulation model. American Naturalist 157:495–511.

Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. Journal of Animal Ecology 65:725–735.

Ims, R. A. 1995. Movement patterns in relation to landscape structures. Pages 85–109 *in* L. Hansson, L. Fahrig, and G. Merriam, eds. Mosaic landscapes and ecological processes. Chapman & Hall, London.

Jager, H. I., J. A. Chandler, K. B. Lepla, and W. Van Winkle. 2001. A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. Environmental Biology of Fishes 60:347–361.

Kawecki, T. J. 2004. Ecological and evolutionary consequences of source-sink population dynamics. Pages 387–446 *in* I. Hanski and O. Gaggiotti, eds. Ecology, genetics and evolution of metapopulations. Academic Press, San Diego, Calif.

Keeling, M. J. 2002. Using individual-based simulations to test the Levins metapopulation paradigm. Journal of Animal Ecology 71:270–279.

King, A. W., and K. A. With. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? Ecological Modelling 147:23–39.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Lande, R., S. Engen, and B.-E. Saether. 1998. Extinction times in finite metapopulation models with stochastic local dynamics. Oikos 82:383–389.

———. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. American Naturalist 154:271–281.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Lorek, H., and M. Sonnenschein. 1999. Modelling and simulation software to support individual-based ecological modelling. Ecological Modelling 115:199–216.

Matthysen, E. 1999. Nuthatches (*Sitta europaea: Aves*) in forest fragments: demography of a patchy population. Oecologia (Berlin) 119:501–509.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology 80:1031–1043.

———. 2000. The equilibrium assumption in estimating the parameters of metapopulation models. Journal of Animal Ecology 69:143–153.

———. 2002. Implications of empirical data quality to metapopulation model parameterization and application. Oikos 96:516–530.

———. 2003. SPOMSIM: software for analyzing stochastic patch occupancy models of metapopulation dynamics. http://www.helsinki.fi/science/metapop/softa.

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. American Naturalist 152:530–542.

Nieminen, M., M. Siljander, and I. Hanski. 2004. Structure and dynamics of *Melitaea cinxia* metapopulations. Pages 63–91 *in* P. R. Ehrlich and I. Hanski, eds. On the wings of checkerspots: a model system for population biology. Oxford University Press, New York.

Odendaal, F. J., P. Turchin, and F. R. Stermitz. 1989. Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). Oecologia (Berlin) 78:283–288.

O'Hara, R. B., E. Arjas, H. Toivonen, and I. Hanski. 2002. Bayesian analysis of metapopulation data. Ecology 83: 2408–2415.

Ovaskainen, O. 2002. The effective size of a metapopulation living in a heterogeneous patch network. American Naturalist 160:612–628.

———. 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. Ecology 85:242–257.

Ovaskainen, O., and S. J. Cornell. 2003. Biased movement at boundary and conditional occupancy times for diffusion processes. Journal of Applied Probability 40:557–580.

Ovaskainen, O., and I. Hanski. 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theoretical Population Biology 60:281–304.

———. 2002. Transient dynamics in metapopulation response to perturbation. Theoretical Population Biology 61:285–295.

———. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? Theoretical Population Biology 64:481–495.

Patlak, C. S. 1953. Random walk with persistence and

external bias. Bulletin of Mathematical Biophysics 15: 311–338.

Pettifor, R. A., R. W. G. Caldow, J. M. Rowcliffe, J. D. Goss-Custard, J. M. Black, K. H. Hodder, A. I. Houston, A. Lang, and J. Webb. 2000. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. Journal of Applied Ecology 37:103–135.

Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. Journal of Animal Ecology 70:840–852.

Ronce, O., F. Perret, and I. Olivieri. 2000. Evolutionary stable dispersal rates do not always increase with local extinction rates. American Naturalist 155:485–496.

Roslin, T., and A. Koivunen. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia (Berlin) 127:69–77.

Saether, B.-E., S. Engen, and R. Lande. 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. Proceedings of the Royal Society of London B 266:113–118.

Schiegg, K., J. R. Walters, and J. A. Priddy. 2002. The consequences of disrupted dispersal in fragmented red-cockaded woodpecker *Picoides borealis* populations. Journal of Animal Ecology 71:710–721.

Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. Ecology 82:1879–1892.

Sjögren-Gulve, P., and I. Hanski. 2000. Metapopulation viability analysis using occupancy models. Ecological Bulletins 48:53–71.

Sutcliffe, O. L., C. D. Thomas, and D. Peggie. 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia (Berlin) 109:229–234.

Szacki, J. 1999. Spatially structured populations: how much do they match the classic metapopulation concept? Landscape Ecology 14:369–379.

ter Braak, C. J. F., and R. S. Etienne. 2003. Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. Ecology 84:231–241.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253–1266.

———. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Mass.

Whitlock, M. C. 2004. Selection and drift in metapopulations. Pages 153–174 *in* I. Hanski and O. Gaggiotti, eds. Ecology, genetics and evolution of metapopulations. Academic Press, San Diego, Calif.

Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. Oecologica (Berlin) 63:23–29.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Associate Editor: Rolf A. Ims

Copyright of American Naturalist is the property of University of Chicago Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.