HABITAT-SPECIFIC MOVEMENT PARAMETERS ESTIMATED USING MARK–RECAPTURE DATA AND A DIFFUSION MODEL

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Abstract. I describe a diffusion model aimed at the quantitative analysis of movement in heterogeneous landscapes. The model is based on classifying a landscape into a number of habitat types, which are assumed to differ from each other in terms of the movement behavior of the focal species. In addition to habitat-specific diffusion and mortality coefficients, the model accounts for edge-mediated behavior, meaning biased behavior close to boundaries between the habitat types. I illustrate the model with three examples. In the first example, I examine how the strength of edge-mediated behavior and the size of a habitat patch affect the probability that an individual will immigrate to a patch, the probability that an individual will emigrate from a patch, and the time that an individual is expected to spend in a patch. In the second example, I study how a dispersal corridor affects the probability that an individual will move through a landscape. In the third example, I estimate the movement parameters for a species of butterfly from mark–recapture data. In the butterfly example, I classify the landscape into habitat patches, other open areas, and forests. Edge-mediated behavior is found to have a highly significant effect on the general dispersal pattern of the butterfly: the model predicts that the density of butterflies inside habitat patches is >100 times the density of butterflies in adjacent areas.

Key words: butterflies; correlated random walk; diffusion model; dispersal corridor; edge-mediated behavior; habitat patch size; heterogeneous landscape; mark–recapture; Melitaea diamina; *movement parameters.*

INTRODUCTION

The response of individuals to habitat heterogeneity is one of the most challenging problems in the study of movement behavior. An increasing number of empirical (Odendaal et al. 1989, Conradt et al. 2000, Jonsen and Taylor 2000, Berggren et al. 2001, Ricketts 2001, Ries and Debinski 2001, Schultz and Crone 2001, Bergman and Landin 2002), experimental (Andreassen et al. 1996, Pither and Taylor 1998, Haddad 1999*a b*, 2000, Bélisle et al. 2001), and modeling studies (Tischendorf 1997, Cantrell and Cosner 1999, Tyre et al. 1999, With and King 1999, Ovaskainen and Cornell 2003) demonstrate that spatial heterogeneity is a major factor determining how individuals disperse within a landscape. Because dispersal is a key element in spatially extended population dynamics (Hanski 1999, Bullock et al. 2002), it is evident that the structure of a heterogeneous landscape eventually may have a profound influence on the persistence of a species on a regional scale. As a consequence, ecologists have called for the development of robust indices that would characterize a landscape in terms of a species' dispersal ability (Tischendorf and Fahrig 2000*a, b*, Vos et al. 2001), accounting for the fact that individuals respond to the structure of the landscape differently on different

spatial and temporal scales (Jonsen and Taylor 2000, Johnson et al. 2002).

Much of the theory behind movement analysis is based on correlated random walks and their diffusion approximations (Turchin 1998, Okubo and Levin 2001). Mechanistic random-walk models have often been used by empiricists because their parameters, including the distributions of move lengths, move durations, and turning angles, are readily measured by observing individuals in the field (Odendaal et al. 1989, Kindvall 1999, Jonsen and Taylor 2000, Byers 2001, Schultz and Crone 2001). In contrast, mathematically more tractable diffusion models have been preferred by theoretical ecologists (Othmer et al. 1988, Cantrell and Cosner 1999, Okubo and Levin 2001) and ecologists working with mark–recapture data (Turchin and Thoeny 1993, Schneider 1999, Skalski and Gilliam 2000). A seminal contribution to the theory of movement behavior was made by Patlak (1953), who derived the diffusion approximation for correlated and biased random walks, providing a robust theoretical framework for the analysis of biologically realistic movement patterns. Because diffusion has random walk as its mechanistic background, it is considered most appropriate for species for which the movement behavior is relatively simple. However, on a large enough scale, diffusion also may be an appropriate model for more complex behavior, such as coyote home range patterns (Moorcroft et al. 1999).

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The use of diffusion models in ecology was facilitated by Turchin and Thoeny (1993), who derived an analytical formula for interpreting data from mark–recapture studies. They assumed that space was homogeneous and estimated the model parameters by fitting the cumulative number of recaptures as a function of distance from the release point. Turchin and Thoeny (1993) made an attempt to account for spatial heterogeneity by correlating local environmental variables with the deviations from the expected recapture predicted by the spatially homogeneous model. This approach was further developed by Schneider (1999), who used the variation in catches of unmarked animals to remove the effect of local spatial variation from the data. However, such methods account only for the local characteristics of the landscape around the recapture site and are not able to assess the contribution of the landscape structure to large-scale dispersal patterns. This had been noted by Turchin and Thoeny (1993), who called for further mathematical research for quantifying movement in heterogeneous landscapes.

In diffusion models, spatial heterogeneity appears naturally as smoothly varying parameter values (Patlak 1953, Turchin 1998). However, in order to facilitate the analysis of real data sets, it often would be preferable to divide a landscape into a finite number of habitat types that differ from each other in terms of the individual's movement behavior. In such a case, it is natural to assume that the model parameters (such as diffusivity and mortality) are constant within each habitat type, but that they may undergo an abrupt change at a boundary between two habitat types. Such a description of the landscape has been used to quantify dispersal in metapopulations (Hanski et al. 2000, Ricketts 2001), where the distinction between the habitat patches and the remaining "matrix" habitat often may be clearly determined.

In addition to habitat-specific diffusivity and mortality, an individual's response to boundaries between habitat types may be a major determinant of the overall movement pattern (Stamps et al. 1987, Haddad 1999*a*, Conradt et al. 2000, Josen and Taylor 2000, Morales 2002). For example, Ries and Debinski (2001) tracked the behavior of two butterfly species at four edge types (ranging from low contrast to high contrast) to determine the extent to which habitat boundaries act as a barrier to emigration. A habitat specialist (*Speyeria idalia*) responded strongly to all edge types, both by turning to avoid crossing them and by returning to the patch if it had crossed the edge. In contrast, a habitat generalist (*Danaus plexippus*) responded strongly only to high-contrast (tree line) edges. It responded by not crossing edges, but rarely returned once it had crossed. Schultz and Crone (2001) quantified the movement behavior of Fender's blue butterfly (*Icaricia icarioides fenderi*), which modified it behavior within 10–22 m from the habitat boundary. These kinds of responses

to habitat boundaries have been termed edge-mediated behavior by Fagan et al. (1999).

Diffusion approximations incorporating edge-mediated behavior previously have been previously analyzed by Cantrell and Cosner (1999) and Fagan et al. (1999), who used a boundary condition that was taken from the literature for skew Brownian motion (Walsh 1978, Harrison and Shepp 1981). As pointed out by Cantrell and Cosner (1998), skew Brownian motion predicts that the probability density may have a point mass at the boundary point, meaning that individuals accumulate at the boundary. Although such transient accumulations have been observed in experimental studies (Kaiser 1983), they are not expected to be a major determinant in the redistribution of dispersing individuals. In order to study the effects of edge-mediated behavior on dispersal, Ovaskainen and Cornell (2003) assumed that individuals bias their movement toward the preferred habitat type when they are at a boundary point or at a boundary zone. In contrast to the boundary condition used by Cantrell and Cosner (1999) and Fagan et al. (1999), Ovaskainen and Cornell (2003) showed that biased movement close to a boundary leads to a continuous flux, but a discontinuous probability density for the individual's location across a boundary.

The first attempt to incorporate spatial heterogeneity into a diffusion model was that of Dobzhansky et al. (1979), who divided a 800 × 600-m study area into a grid of 20 × 15 cells. Each cell was classified as one of six habitat types, for which the diffusion coefficients were estimated separately. Unfortunately, the low resolution of the grid and the inefficiency of available computing facilities did not allow for reliable parameter estimation, and the model of Dobzhansky et al. (1979) did not gain much attention among field ecologists. As computing power has increased dramatically, the technical problems faced by Dobzhansky et al. (1979) have largely disappeared, and their model deserves a reintroduction.

The aim of this paper is to develop a model for the quantitative analysis of movement in heterogeneous landscapes. Following Dobzhansky et al. (1979), I classify the landscape into a number of distinct habitat types, within each of which the individual is assumed to follow a correlated random walk with habitat-specific parameter values. In addition, the model considered here accounts for boundary behavior at edges between habitat types, allowing the individual to bias its movement toward the preferred habitat type. In order to facilitate model analysis, I will rely on the diffusion approximation both for within-habitat movement (as derived by Patlak 1953) and for boundary behavior (as derived by Ovaskainen and Cornell 2003).

I will describe the biological model and its diffusion approximation, and how the parameters may be estimated from mark–recapture data. I will then illustrate the model with three examples. Two examples are sim-

ple theoretical exercises, the first examining immigration probabilities, emigration probabilities, and occupancy times, and the second illustrating the effect of a dispersal corridor. In the third example, I use mark–recapture data to estimate the movement parameters of the false heath fritillary butterfly (*Melitaea diamina*). Because the biological model leads to a partial differential equation for which standard numerical solvers do not apply, I describe in the Appendix a finite element scheme by which the diffusion problem may be solved numerically.

THE MODEL

The model described in this section is aimed at quantifying the movement behavior of an individual in a heterogeneous landscape. I assume that the landscape is classified into a number of habitat types, which differ from each other in terms of the individual's movement behavior. In order to set the model into a mathematical framework, I denote the landscape (*d*-dimensional space) by $\Omega \subset \mathbf{R}^d$, and let it consist of n different habitat types Ω_i with $i = 1, \ldots, n$, so that $\Omega = \cup_i \Omega_i$ and $\Omega_i \cap \Omega_j = \emptyset$ for $i \neq j$. I will denote by $\Gamma_i = \partial \Omega_i$ the boundary of Ω_i, and by $\Gamma_{ij} = \Gamma_i \cap \Gamma_j$ the boundary between habitat types Ω_i and Ω_j. The landscape, in most applications, will be two dimensional ($d = 2$).

The fate of an individual is described by three components: movement within a habitat type, behavior at edges between habitat types, and mortality. I start by describing the biological assumptions behind these components.

Movement within a habitat type.—Movement within a habitat type is assumed to follow a random walk or a correlated random walk. Both pure and correlated random walks assume that the path of an individual consists of a series of moves, which may be viewed as straight lines. For each move, the duration and the length of the move are derived from given distributions independently of the previous moves. The pure random walk assumes that the angle between two consecutive moves is completely random, i.e., its distribution is uniform in $[-\pi, \pi]$. The correlated random walk relaxes this assumption by assuming also that the turning angle is derived from a given distribution. Typically, the distribution is symmetric around 0, and values close to 0 are more probable than other values.

A random walk may be straightforwardly implemented into a simulation model, but it is hard to analyze mathematically. For this reason, I assume that the path of an individual consists of a large number of small moves, in which case both pure and correlated random walks may be approximated by diffusion (Patlak 1953). When deriving the diffusion approximation, the distributions specifying the random-walk model aggregate into a single variable D, which is called the diffusion coefficient. In order to account for temporally varying environmental conditions, I let the diffusion coefficient vary with time t, and denote the diffusion coefficient for habitat type i by $D_i(t)$.

Boundary behavior.—In order to account for edge-mediated behavior, I assume that an individual might bias its direction toward either of the habitat types when it is close to a boundary between two habitat types. Ovaskainen and Cornell (2003) showed that in the diffusion approximation, such a bias leads to a discontinuity in the probability density for the individual's location. The strength of the bias is quantified by habitat-specific multipliers k_i by assuming that the relative value of the probability density jumps from k_i to k_j as the boundary between the habitat types Ω_i and Ω_j is crossed. I will assume, for simplicity, that the multipliers k_i do not vary with time.

The values of the multipliers k_i and k_j depend on the parameters of the mechanistic random-walk model, most importantly on the probability that the individual will move toward the preferred habitat type when close to the boundary. To illustrate, let us consider the simplest possible case, in which an individual performs a random walk in a regular one-dimensional grid. Assume that the probability of moving either to the left or to the right is always 1/2 except at a single point, in which the probability of moving to the left (to habitat type 1) is p_1 and the probability of moving to the right (to habitat type 2) is $p_2 = 1 - p_1$. In this case, the boundary multipliers are simply given by $k_1 = p_1$ and $k_2 = p_2$. In a more realistic situation, in which the characteristics of the random walk (such as the move length distribution) may be different for the two habitat types, or the bias may occur at a boundary zone rather than at a single point, the relationship between the boundary multipliers k_i and the probabilities p_i remains qualitatively the same, although the details are more complicated (Ovaskainen and Cornell 2003).

Mortality.—I assume that an individual located in habitat type i has a mortality rate $\mu_i(t)$, corresponding to the assumption that the probability that the individual will die during a short time period dt is given by $\mu_i(t)\,dt$.

As described, the biological model is based on a (correlated) random walk, which is approximated by a diffusion process. The principal variable of the model is $v(\mathbf{x}, t; \mathbf{y})$, the probability density for the individual's location at time t, given that the individual was at location $\mathbf{y} \in \Omega$ at time $t = 0$. In the following, I will simplify the notation by dropping the variable $\mathbf{y}$ whenever it is not explicitly needed. By the previous assumptions, v evolves as

$$v_t(\mathbf{x}, t) = D_i(t)\Delta v(\mathbf{x}, t) - \mu_i(t)v(\mathbf{x}, t) \quad \text{in } \Omega_i \quad (1)$$

where v_t is a shorthand for $\partial v/\partial t$, and Δ denotes the Laplacian operator acting on the spatial variable $\mathbf{x}$. Boundary behavior is accounted for by the condition

$$(1/k_i)v(\mathbf{x}_i, t) - (1/k_j)v(\mathbf{x}_j, t) \to 0 \quad (2)$$

which is assumed to hold whenever $\mathbf{x}_i, \mathbf{x}_j \rightarrow \mathbf{x}_0 \in \Gamma_{ij}$ with $\mathbf{x}_i \in \Omega_i$, $\mathbf{x}_j \in \Omega_j$. Eq. 2 is complemented by requiring that the interior boundaries do not act as sources or sinks, i.e., the flux $D_i(t)v_n(\mathbf{x}_i, t)$ is continuous across the boundary Γ_{ij} (Ovaskainen and Cornell 2003). Here v_n denotes the spatial derivative of v at the direction normal to the boundary Γ_{ij}. In order to make the model well defined, a boundary condition is also needed at the exterior boundary $\partial\Omega$ of the entire landscape Ω. For the sake of simplicity, I will assume a reflecting Neumann condition $v_n(\mathbf{x}, t; y) = 0$ on $\partial\Omega$, although an absorbing Dirichlet condition, for example, could be assumed equally well.

In principle, the application of this model is straightforward. Assume that an individual was in a location $\mathbf{y} \in \Omega$ at time $t = 0$. Then the probability that the individual is in any region $X \subset \Omega$ at time t is given by

$$P_X(t) = \int_X v(\mathbf{x}, t) \, d\mathbf{x} \tag{3}$$

and the probability that the individual has died is given by $1 - P_\Omega(t)$. The main difficulty in applying the model to real heterogeneous landscapes is that the solution to the time-dependent partial differential equation has to be solved numerically, and this may be computationally tedious. Furthermore, due to the nonstandard interior boundary conditions specified by Eq. 2, solvers that would apply to the problem do not seem to be readily available. For this reason, I derive in the Appendix a finite element scheme aimed at finding a numerical solution to the problem. The derivation of the finite element scheme is necessarily technical, and an application-oriented reader may safely jump directly to parameter estimation.

Parameter Estimation

In this section, I describe how the model may be parameterized using mark–recapture data. The parameters to be estimated include the parameters of the diffusion model (habitat-specific diffusion coefficients, habitat-specific boundary multipliers, and habitat-specific mortality rates) and a parameter (or set of parameters) for capture probability. The diffusion model lays the basis for a flexible family of models from which one may choose the one that is biologically and statistically best supported. For example, any of the model parameters may be assumed to be either habitat specific or not, and the parameters may be assumed either to vary with time or to be constants.

I assume that the marked individuals may have been released into multiple sites and on multiple occasions, and that the recaptures have been collected by examining a number of sites in such a manner that the search times are short compared to the times between the searches. In order to estimate parameters from spatial mark–recapture data, one needs to be able to calculate the likelihood of the observed data for any given set of parameter values. The likelihood function may then be utilized, e.g., in maximum likelihood or in Bayesian parameter estimation. The basic ingredient of the likelihood function is the probability that an individual is found or not found in a particular site at a particular time. Before going to the general form of the likelihood function, I will construct some tools that will be needed to calculate the likelihood of observing (or not observing) an individual with a given capture history.

Let us assume that an individual has been released at $t = 0$ in a location $\mathbf{y}$, and then attempt to derive a formula for the probability that the individual is in site X at time t. In principle, all that is needed to do is to supplement the model with the initial condition $v(\mathbf{x}, 0) = \delta(\mathbf{x} - \mathbf{y})$, where δ is the Dirac delta distribution, and to calculate $P_X(t)$ using Eq. 3. However, what complicates the situation is that various sites may have been searched meanwhile without finding the individual. Furthermore, searching is never complete, and thus there is a chance that the individual was present in a site that was searched without observing the individual. It is clear that even uncertain information about an individual's absence in a particular location should decrease the probability that the individual is in that particular location, and increase the probability that the individual is somewhere else or that the individual has died. In order to put this reasoning into a mathematical setting, I assume that a site $X \subset \Omega$ has been searched at time t without observing the individual, and denote by $t-$ and by $t+$ the time just before and just after the search. Let $v(\mathbf{x}, t-)$ be the individual's probability density before the patch was searched, and let $v(\mathbf{x}, t+)$ be the individual's probability density after the search. Let $u = \int_X v(\mathbf{x}, t-) \, d\mathbf{x}$ be the probability (before the search) that the individual was in site X at time t, and let p be the capture probability, i.e., the probability that the individual would have been observed in site X if it were there. Let A_X denote the claim "the individual was in site X at time t," and let B_X denote the claim "the individual was not observed while site X was searched at time t." The probability that the individual was not observed is $P[B_X] = (1 - u) + u (1 - p) = 1 - pu$, and the probability that the individual was in site X but was not observed there is $P[A_X \text{ and } B_X] = u(1 - p)$. Thus the conditional probability that the individual was present, conditioned on that it was not observed, is

$$P[A_X | B_X] = \frac{P[A_X \text{ and } B_X]}{P[B_X]} = \frac{u(1 - p)}{1 - pu}. \tag{4}$$

Similarly, let $Y \subset \Omega$ be another site such that $X \cap Y = 0$, and let $w = \int_Y v(\mathbf{x}, t-) \, d\mathbf{x}$ be the probability (before the observation in site X) that the individual was present in site Y at time t. The probability that the individual was present in Y and not observed in X is $P[A_Y \text{ and } B_X] = w$. Thus the conditional probability that the individual was present in Y, conditioned on that it was not observed in X, is as follows:

$$P[A_Y | B_X] = \frac{P[A_Y \text{ and } B_X]}{P[B_X]} = \frac{w}{1 - pu}. \qquad (5)$$

Because the site Y may be infinitesimally small, Eq. 5 applies not only for probabilities, but also for the probability density outside the site X. Note that in this reasoning, A_Y could as well denote the claim ''the individual was dead at time t.'' Thus, Eq. 5 shows how the probability that the individual has died increases, given that the individual was not observed in a site X.

Equipped with Eqs. 4 and 5 and the finite element scheme described in the Appendix, we are ready to estimate the likelihood of the observed data for a given combination of model parameters. The general procedure goes as follows. Assume that an individual was marked and released in a location $\mathbf{y}$ at time $t = 0$. Assume that subsequently the sites $X_{s_1}, \ldots, X_{s_m}$ were searched at times $t_1, \ldots, t_m$, out of which the first observation of the individual occurred at time t_m. In order to calculate the probability of this series, the initial condition is set to correspond to the location $\mathbf{y}$, after which the diffusion model is run with the finite-element scheme until time t_1. At time t_1, the probability that the individual is in site X_{s_1} is calculated as

$$u_1 = \int_{X_{s_1}} v(\mathbf{x}, t_1) \, d\mathbf{x}$$

after which the density $v(\mathbf{x}, t_1)$ is updated based on Eqs. 4 and 5. Thus, inside the site X_{s_1}, the probability density (or the coefficients of the shape functions in the finite element scheme) is multiplied by $(1 - p)/(1 - pu_1) \le 1$, whereas outside site X_{s_1}, the probability density is multiplied by $1/(1 - pu_1) \ge 1$. Using the updated probability density as the initial condition, the model is next run to time t_2, and the procedure is continued until time t_m. The likelihood of the individual's capture history up to time t_m may now be written as $pu_m \prod_{i=1}^{m-1} (1 - pu_i)$. At time t_m, the location of the observed individual is certain; thus, the model is reinitialized with the individual's present location, and the likelihood until the next recapture (or until the end of the experiment) is calculated as previously described. I assume that the individuals move independently of each other, in which case the same procedure may be run separately for all the individuals, and the likelihood of the data is given as the product of the likelihoods for the individuals.

In practice, the exact point $\mathbf{y}$ in which the individual has been released often is not relevant, as the individual may have been released, e.g., in a particular habitat patch. In such a case, the initial condition given by the delta distribution is changed to an initial condition corresponding to area release (Turchin 1998), which is described by a constant density within the release area and a zero density outside the area. Furthermore, the usage of the finite-element method restricts somewhat the choice of feasible initial conditions. For example, if linear shape functions are used, the probability density may be assumed to be constant within the release area and to decrease linearly to zero within the elements adjacent to the release area.

EXAMPLES

I will illustrate the model with three examples. I first examine how the strength of edge-mediated behavior and the size of a habitat patch affect the probabilities that an individual will immigrate to a patch or emigrate from a patch, or the time that the individual is expected to spend in a patch. In the second example, I study how a dispersal corridor affects the probability that an individual will move through a landscape. In the third example, I estimate the movement parameters for a species of butterfly from mark–recapture data.

Immigration and emigration probabilities and occupancy times

I start with a very simple example, in which I consider a single circular habitat patch surrounded by matrix habitat. Ovaskainen and Cornell (2003) assumed the diffusion model considered in this paper, and used the method of adjoint operators to derive analytical solutions for hitting probabilities and occupancy times for biologically motivated problems, some of which have been studied previously by simulations (see e.g., Kindvall and Petersson 2000). I will use the results of Ovaskainen and Cornell (2003) to see how emigration and immigration probabilities and the time spent in a patch depend on the properties of the species and on the size of the habitat patch, which I measure by its radius r. I denote diffusivity by D_H and D_M and mortality by μ_H and μ_M, where the subscripts refer to the habitat patch and to the remaining matrix habitat. Because only the relative values of the boundary multipliers matter, I scale k_H to $k_H = 1$, so that the strength of the bias is measured by the value of $k = k_M$. I denote by I_ν and K_ν modified Bessel functions of the first and the second kind, respectively (Abramowitz and Stegun 1972).

I will consider three biologically important quantities, for which analytical formulae are available. First, I denote by $P_I(r, s)$ the probability that an individual that is initially at distance s from the boundary of the habitat patch will hit the patch before it dies. As shown by Ovaskainen and Cornell (2003),

$$P_I(r, s) = \frac{K_0[\alpha_M(r + s)]}{K_0(\alpha_M r)} \qquad (6)$$

where $\alpha_M = \sqrt{\mu_M/D_M}$. I will interprete P_I as the immigration probability.

Second, I let $P_E(r, s)$ denote the probability that an individual that is initially at the edge of the patch will reach a distance s from the habitat patch before it dies. As shown by Ovaskainen and Cornell (2003),

$$P_E(r, s) = \left\{ \alpha_M r \left[\beta_1 + \frac{\delta_H I_1(\alpha_H r)\beta_2}{\delta_M I_0(\alpha_H r)} \right] \right\}^{-1} \qquad (7)$$

where

$$\beta_1 = I_1(\alpha_M r)K_0[\alpha_M(r + s)]$$

$$+ I_0[\alpha_M(r + s)]K_1(\alpha_M r) \qquad (8)$$

$$\beta_2 = I_0[\alpha_M(r + s)]K_0(\alpha_M r)$$

$$- I_0(\alpha_M r)K_0[\alpha_M(r + s)] \qquad (9)$$

and $\alpha_H = \sqrt{\mu_H/D_H}$, $\delta_H = k_H\alpha_H D_H$ and $\delta_M = k_M\alpha_M D_M$. I will interpret P_E as the emigration probability.

Third, $T(r, s)$ gives the time that an individual that is initially at the edge of the patch is expected to spend in the patch (possibly in multiple occasions) before it reaches the distance s from the patch or dies. As shown by Ovaskainen and Cornell (2003),

$$T(r, s) = \left\{\mu_H\left[1 + \frac{\delta_M I_0(\alpha_H r)\beta_1}{\delta_H I_1(\alpha_H r)\beta_2}\right]\right\}^{-1}. \qquad (10)$$

Because we would like to measure the time that an individual spends in the patch during its entire lifetime, we would not like to restrict the analysis until the time when the individual reaches a given distance s. To do this, I consider the limit $s \rightarrow \infty$ of Eq. 10, which I denote by $T(r) = \lim_{s \rightarrow \infty} T(r, s)$. A straightforward calculation shows that at the limit, Eq. 10 simplifies to

$$T(r) = \left\{\mu_H\left[1 + \frac{\delta_M I_0(\alpha_H r)K_1(\alpha_M r)}{\delta_H I_1(\alpha_H r)K_0(\alpha_M r)}\right]\right\}^{-1}. \qquad (11)$$

The assumption that the individual is initially at the edge of the patch rather than, e.g., in the center of the patch was made by Ovaskainen and Cornell (2003) for technical reasons. This assumption is not expected to make a large difference because the individual is assumed to bias its movement immediately toward the patch.

Fig. 1 illustrates how emigration and immigration probabilities and occupancy times depend on the interplay between patch area and the properties of a species, using parameter values that closely resemble values estimated for a species of butterfly (see *False heath fritillary butterfly metapopulation*). As expected, the immigration probability increases (Fig. 1A), the emigration probability decreases (Fig. 1B), and the occupancy time increases (Fig. 1C) as patch area increases. Furthermore, keeping other parameter values fixed, the emigration probability decreases (Fig. 1B) and the occupancy time increases (Fig. 1C) as the strength of edge-mediated behavior increases.

A low emigration probability (or a long occupancy time) may be due to two reasons. First, the mobility (measured here in terms of diffusivity) of the individual may be low, in which case the individual is seldom expected to hit the boundary of the patch. Second, the bias at the edge may be strong, in which case the individual is unlikely to cross the boundary. In this view, it is expected that a suitable change in diffusivity, to a certain extent, is able to compensate for a change in edge-mediated behavior. This is illustrated in Fig. 1D–E, in which I have adjusted diffusivity so that the em-igration probability (or the occupancy time) is always the same for a patch with a 50-m radius. If a low emigration probability is due to a strong bias at the edge rather than to low diffusivity, the emigration probability is more sensitive to patch area than in the opposite case (Fig. 1D). Interestingly, the dependence of the occupancy time on patch area is almost independent of whether the individual stays within the patch mainly because of the bias at the edge or because of low diffusivity (Fig. 1E). Fig. 1F shows the value of diffusivity that compensates (either to give a fixed emigration probability P_E or a fixed occupancy time T for a patch of 50-m radius) for a given value of edge-mediated behavior. In both cases, the diffusivity D is inversely related to the coefficient k, $D \approx c/k$, but the proportionality constant c depends on whether the emigration probability or the occupancy time is kept fixed.

Dispersal corridor

Ecological dispersal corridors have gained a lot of recent theoretical and applied interest, the major question being their ability to enhance a species' dispersal between patches of suitable habitat (Andreassen et al. 1996, Haddad 1999*a, b*, Bunn et al. 2000). I will study the effect of a dispersal corridor with a simple theoretical example, which is mostly aimed at illustrating the present modeling framework.

The landscape shown in Fig. 2A is assumed to consist of three different types: the habitat patches H_1 and H_2, the dispersal corridor C, and the remaining "matrix" habitat M. I assume that the individual has identical mortality and diffusion parameters in all three habitat types, but that the individual prefers the habitat patches over the corridor and the matrix habitat. In order to illustrate if and how the dispersal corridor enhances the individual's movement between the two habitat patches, I start by considering a reference model, in which the corridor does not exist, i.e., the habitat types C and M are identical. I assume that the strength of the individual's bias, by which I mean its tendency to avoid the dispersal habitat and thus to stay within the patches, attains a low ($k_C = k_M = 0.1$), an intermediate ($k_C = k_M = 0.01$), or a high value ($k_C = k_M = 0.001$).

The thin lines in Fig. 2B confirm the intuitive result that a species with a strong tendency to bias its movement toward the patch is more likely to be found in the patch H_1 in which it was released than is a species with a lower tendency to stay within a patch. What may be less obvious is that the probability that the individual is found in the other patch H_2 is generally maximized for an intermediate value of the bias (Fig. 2C, line b). To see why this should be the case, I note that if the bias is very high (line c), the individual will stay for a long time in its release patch H_1, and it may even die before it emigrates. On the other hand, if the bias is very low (line a), the individual will emigrate from the release patch H_1 almost immediately, and is thus has
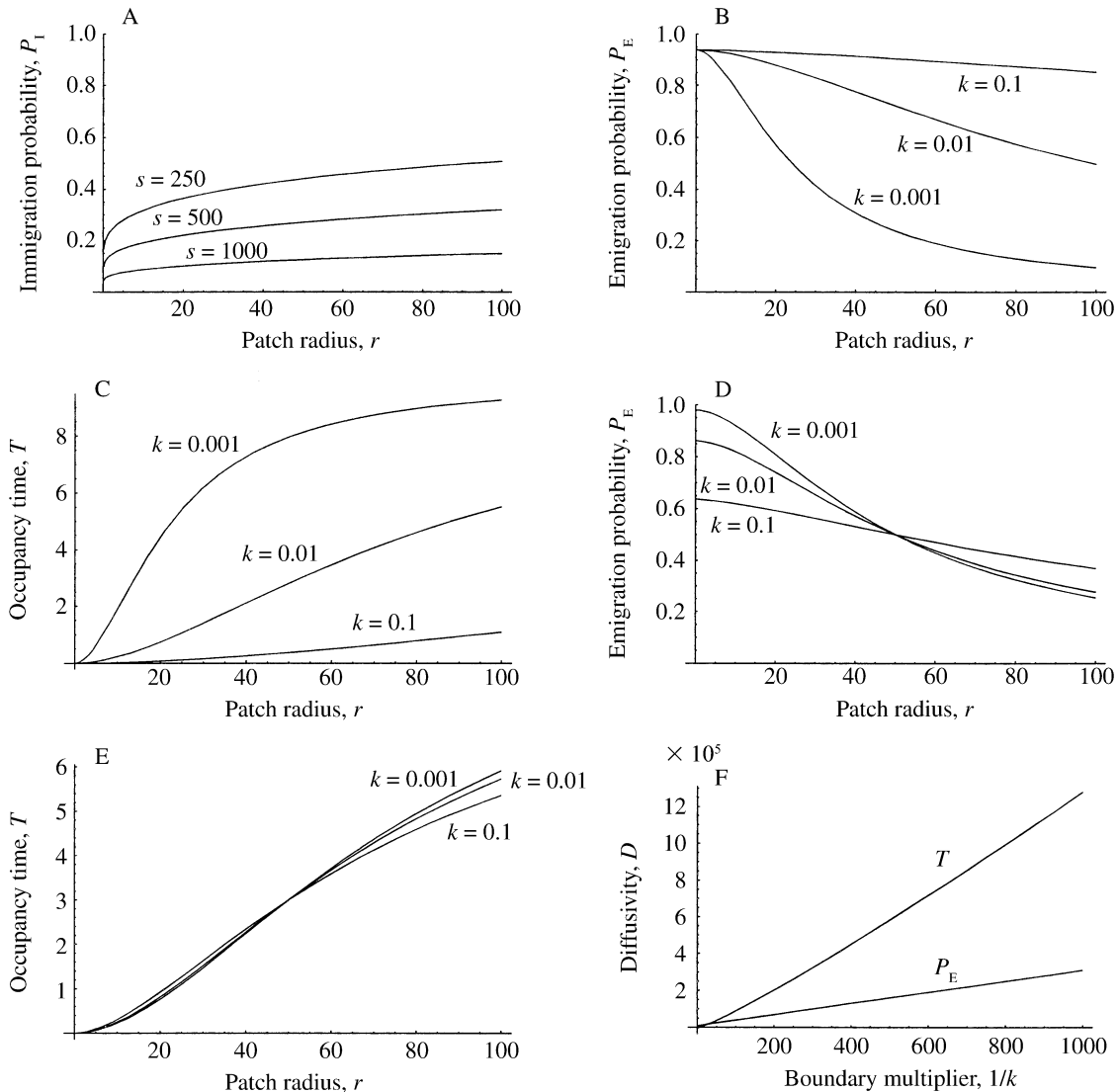
FIG. 1.   Dependence of the immigration probability $P_I(r, s)$ (panel A; based on Eq. 6), the emigration probability $P_E(r, s)$ (panel B; based on Eq. 7), and the occupancy time $T(r)$ (panel C; based on Eq. 11) on patch area. In all panels, diffusivity D and mortality μ are assumed to be the same both for the patch and for the matrix habitat. In panels D and E, I have adjusted the diffusivity D in such a manner that, for varying values of the boundary multiplier k, the emigration probability P_E or occupancy time T, respectively, remains constant for a patch of radius $r = 50$. Panel F shows the diffusivity that compensates (in the sense of panels D and E) for a given value of the boundary multiplier k (note that the y-axis scale numbers for D are 200 000,. . . , 1 200 000). Unless otherwise specified, the parameter values $D = 100\,000$, $\mu = 1/10$, and $s = 500$ have been used.

a high probability of finding the other patch H_2. However, once it has found patch H_2, it has a low tendency to stay there, and thus the probability that the individual will be found in H_2 at any particular time remains low. By this reasoning, the time needed to obtain the maximal probability of being in patch H_2 is shorter for an individual with a low bias than for an individual with a high bias, which explains why some of the lines cross in Fig. 2C. This example illustrates the important difference between hitting probabilities (the probability that an individual will ever visit a particular location)

and occupancy probabilities (the probability that an individual will occupy a particular location at a particular time).

I next add the dispersal corridor by assuming that the species avoids more strongly the matrix habitat ($k_M = 0.001$) than the habitat represented by the corridor ($k_C = 0.1$). As expected, the existence of the dispersal corridor greatly enhances the probability that the individual will move from patch H_1 to patch H_2 (Fig. 2C, thick line). The corridor also decreases the time by which the individual is expected to find the other patch,
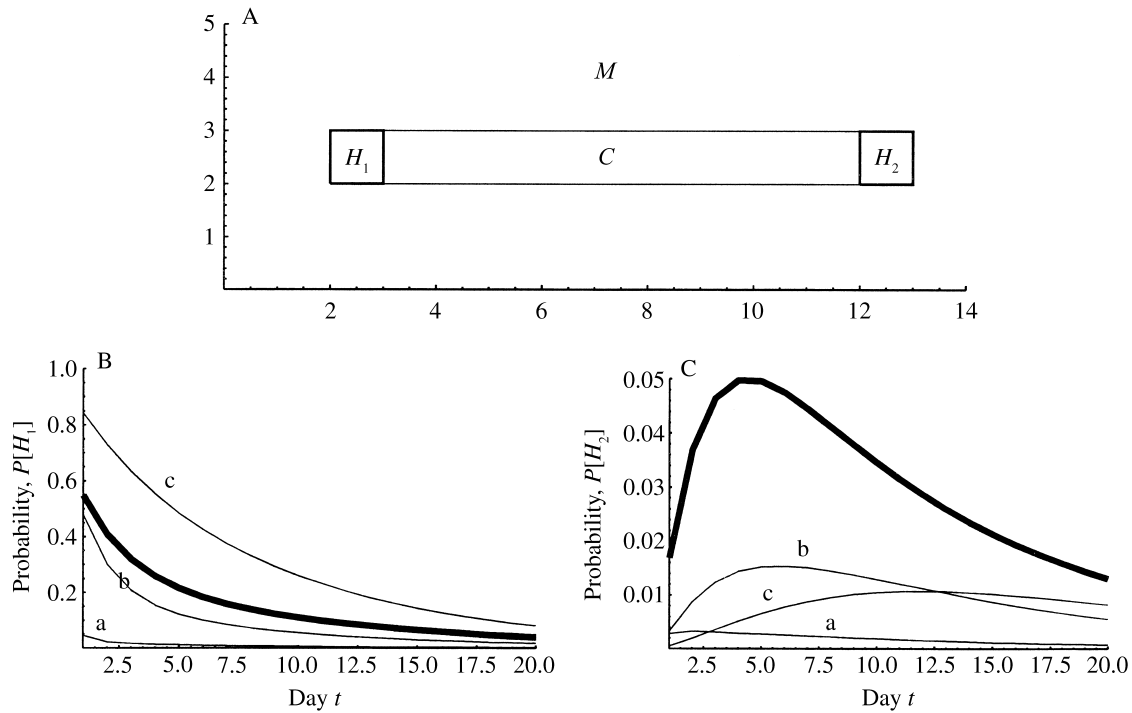
FIG. 2. Panel A shows a landscape consisting of two habitat patches (H_1 and H_2), a corridor (C), and the remaining "matrix" habitat (M). Panels B and C show results of movement behavior in this landscape based on the finite element approximation of the diffusion model. The lines depict the occupancy probability that an individual released in patch H_1 at day $t = 0$ is in patch H_1 (panel B) or in patch H_2 (panel C) at day $t = 1, 2, \dots$. The thin lines refer to a case where the corridor does not differ from the matrix habitat, the preferences being: (a) $k_C = k_M = 0.1$; (b) $k_C = k_M = 0.01$; or (c) $k_C = k_M = 0.001$. The thick line refers to a case where the corridor is present, the preferences being $k_M = 0.001$ and $k_C = 0.1$. Parameter values are: $k_H = 1$, $D_H = D_C = D_M = 20$, $\mu_H = \mu_C = \mu_M = 0.1$.

the main reason being that the corridor essentially changes the two-dimensional diffusion into a more effective one-dimensional diffusion along the corridor.

False heath fritillary butterfly metapopulation

I will next apply the diffusion model to a real example, in which I estimate the movement parameters of the false heath fritillary butterfly (*Melitaea diamina*; see Plate 1) based on mark–recapture data. The data were collected by Wahlberg (1997) between 16 June and 14 July 1995 from a false heath fritillary butterfly metapopulation in a landscape consisting of a set of habitat patches surrounded by dispersal habitat. The data set consists of 557 individually marked male butterflies, with a total of 1301 recaptures made solely in the habitat patches. The data set has been analyzed previously by Hanski et al. (2000), although they used a model that differs fundamentally from the present model. I will compare my results with those of Hanski et al. (2000) in the *Discussion*.

Fig. 3 shows the landscape classified into three habitat types: the habitat patches (denoted by subscript H), other open areas (O), and forests (F). Male butterflies are known to stay most of the time within the habitat patches where females are seeking host plants on which to oviposit. The butterflies are expected to prefer open

areas for dispersal from a habitat patch to another habitat patch, although they are also able to fly inside sparse forests.

The data set has two complications that need to be accounted for. First, patch number 1 (see Fig. 3) was studied more intensively than the others. It was visited daily, whereas the other populations were visited, on average, every second day. This does not cause a problem, because the model is able to account for arbitrary and nonregular visit intervals. However, what causes a slight complication is that patch 1 was studied also more carefully than the other patches; researchers spent approximately four times as much time per unit area there (N. Wahlberg, *personal communication*). A straightforward way to account for this complication would be to assume that the patch was searched each time actually four times, and that each search was independent of the others. By this assumption, one should set the capture probability (the conditional probability that an individual is found in a patch while the patch is searched, given that the individual really is in the patch) to p for all the other patches and to $\hat{p} = 1 - (1 - p)^4$ for patch 1. However, several closely following visits to the same part of a patch are not independent of each other; for example, a butterfly resting close to the ground is likely to be ignored at all times. As a

PLATE 1. False heath fritillary (*Melitaea diamina*) female. Photo credit: T. Haahtela.

result, I decided to estimate the capture probability $\hat{p}$ separately for patch 1.

The second complication is due to varying weather conditions. The study period included some rainy and cloudy periods, during which the butterflies are known not to move. In order to account for this, I assumed that the diffusion parameter $D_i(t)$ depends on the particular day t. N. Wahlberg (*personal communication*) estimated the proportion $q(t)$ of each day t during which the butterflies were able to fly, using the scale $q(t) = 0, 1/3, 2/3, 1$. Letting D_i denote the diffusion coefficient

corresponding to a day that is fully suitable for flight, I assume that the realized diffusion coefficient for day t is given by $q(t) D_i$. The way in which weather conditions affect mortality is more complex, and I have made the simplifying assumption that the mortality rates μ_i are independent of time.

I discretized the landscape shown in Fig. 3 by generating a mesh of 2890 triangles, and utilized the finite-element scheme described in the Appendix with linear shape functions for finding the numerical solution to the time-dependent diffusion problem. The usage of
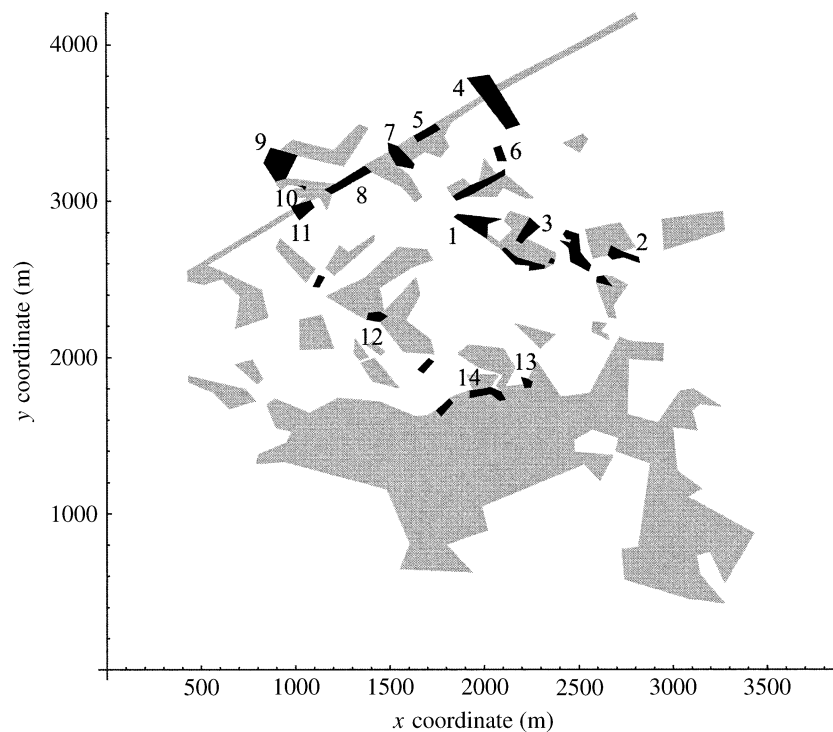

FIG. 3. The landscape in which the mark–recapture study of the false heath fritillary butterfly was conducted. Black depicts habitat patches; gray, other open areas; and white, forests. The numbered patches were used as release and recapture sites.

TABLE 1. Estimated parameter values (with their 95% confidence intervals), obtained by the maximum likelihood method using the finite element approximation of the diffusion model (see *False heath fritillary butterfly metapopulation*).

Parameter†	Unit	Model A	Model B
μ_H	d^{-1}	0.10 (0.09–0.13)	0.10 (0.07–0.11)
μ_O	d^{-1}	0.10 (0.09–0.13)	0.00 (0.00–1.06)
μ_F	d^{-1}	0.10 (0.09–0.13)	0.17 (0.05–0.56)
D_H	$10^3 \ m^2/d$	94 (73–160)	213 (55–672)
D_O	$10^3 \ m^2/d$	94 (73–160)	94 (57–211)
D_F	$10^3 \ m^2/d$	94 (73–160)	100 (72–154)
k_H		1.0	1.0
k_O	10^{-3}	8.7 (5.2–9.3)	7.6 (4.0–11.0)
k_F	10^{-3}	8.7 (5.2–9.3)	8.7 (6.8–8.7)
p	%	34 (27–40)	34 (28–40)
$\hat{p}$	%	57 (52–63)	58 (51–62)

† The parameters are mortality (μ), diffusivity (D), the boundary multiplier (k), and capture probability ($\hat{p}$ for patch 1, p for all others patches). The subscripts denote habitat patches (H), open areas (O), and forests (F).

effective C++ sparse matrix libraries reduced the computational effort needed to evaluate the fate of a single butterfly to 1–5 seconds in a 1000-MHz PC. In spite of this, the method was computationally tedious for two reasons. First, all of the butterflies with different capture histories had to be evaluated individually, because the history of an individual affects the way the probability density is updated. Some of the butterflies shared the same history (e.g., butterflies released to a particular patch and never seen afterward), so the number of different histories was 355 out of the total 557 individuals. Second, the likelihood of several hundreds of parameter combinations had to be calculated to ensure that the estimation procedure had converged to the global maximum likelihood.

I start with the simplest possible model (Model A), which ignores the distinction between forests and open areas. I thus assume that the diffusion and mortality coefficients are the same everywhere ($D_H = D_O = D_F$, $\mu_H = \mu_O = \mu_F$), and that the boundary multipliers are identical for open areas and forests ($k_O = k_F$). Because only the relative values of the boundary multipliers matter, I set $k_H = 1$ without losing generality. Thus, Model A has five free parameters that remain to be estimated: the global diffusion coefficient, the global mortality rate, the boundary multiplier for the matrix habitat, the capture probability for patch 1, and the capture probability for the other patches. The maximum likelihood estimates for these five parameters are shown in Table 1. The 95% confidence intervals are based on bootstrapping, i.e., estimating the maximum likelihood parameters for 557 randomly chosen individuals, some of which may be duplicates. Due to the computational intensity of the method, only 100 bootstrap estimates were calculated, and thus the confidence intervals remain somewhat suggestive.

The mortality parameter has a straightforward biological interpretation, suggesting that the average lifetime of an individual would be $1/\mu \approx 10$ d. The longest confirmed lifetime observed during the study was 22

d, whereas the average time between the first and the last observations was 4.3 d. The diffusion coefficient D is easier to assess intuitively once it is transformed to the distance r that an individual moves in a homogeneous environment during its lifetime, measured along a straight line from the release point to the point of death. The expected value and the variance of r are given by (Turchin 1998)

$$E[r] = \frac{\pi}{2}\sqrt{\frac{D}{\mu}} \qquad \text{var}[r] = \frac{D}{\mu}\left(4 - \frac{\pi^2}{4}\right) \qquad (12)$$

giving $E[r] \approx 1.5$ km with a standard deviation of 1.2 km for the maximum likelihood parameter estimates. The boundary multipliers also have a straightforward interpretation, suggesting that the density of butterflies within habitat patches would be some $1/k \approx 115$ times higher than the density of butterflies in the adjacent areas. The separately estimated capture probability $\hat{p} \approx 0.57$ for patch 1 is considerably higher than the capture probability $p \approx 0.34$ for the remaining patches, and the difference between these two estimates is statistically highly significant. The 95% confidence intervals shown in Table 1 indicate that the parameter values estimated for the diffusion coefficient D and the boundary multiplier k include a large amount of uncertainty. This is to be expected, as these two parameters are correlated with each other, high diffusivity being able to compensate for a strong bias at the boundary. Additional and preferably complementary data would be needed to improve the separation between these two parameters. For example, a fraction of the individuals could be released within the matrix habitat, in which case the time it takes before the individuals appear in the habitat patches would give direct information about diffusivity. Fig. 4 illustrates Model A by showing a snapshot of the time evolution of the probability density for an individual's location.

So far I have assumed that forests and open areas have identical parameter values. I will next drop this
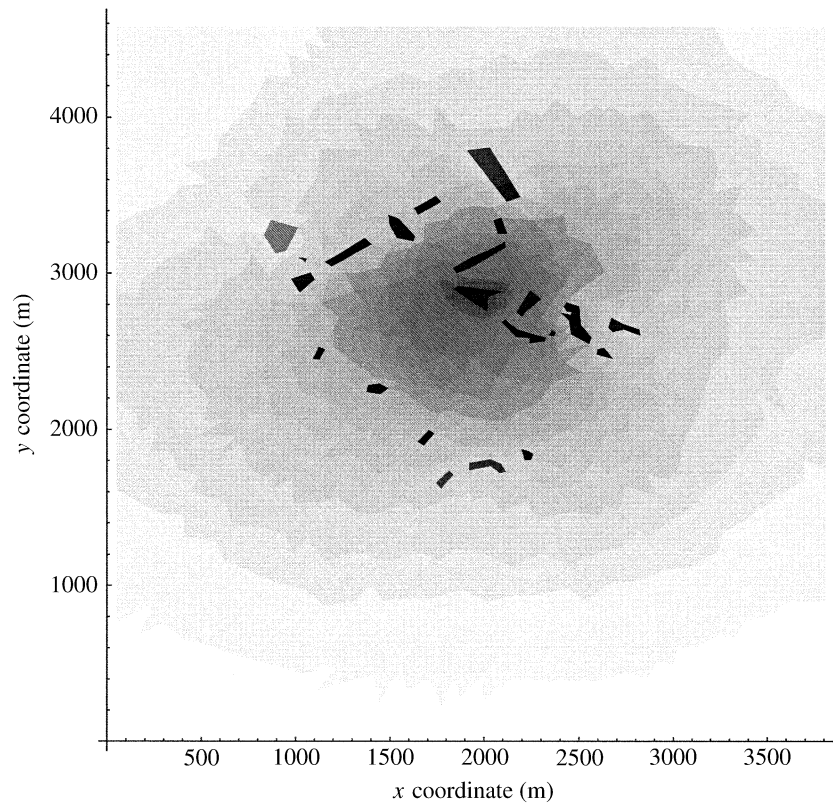
FIG. 4. The probability density of an individual's location three days after it has been released in patch 1 in the landscape shown in Fig. 3. The value of the probability density at a particular location is shown with a gray scale, black depicting the highest and white the lowest value. The probability density has been calculated using the finite element method with parameter values set to the maximum likelihood values of Model A (Table 1).

assumption, and consider the full model (Model B) with 10 free parameters (three diffusion coefficients, three mortality rates, two boundary multipliers, and two capture probabilities). Because some of the parameters are partly able to compensate each other, it is hard to estimate all of the parameters reliably from the present data set, as illustrated by the wide confidence limits in Table 1. Furthermore, the distribution of forests and open areas in the butterfly landscape (Fig. 3) appears to be so fine scaled that it does not make a major difference to the movement rates between most pairs of patches, and the model largely failed to separate the parameters between forests and open areas. The only difference between Model A and Model B that is almost statistically significant is that in 93 out of the 100 bootstrapped parameter combinations, mortality was higher within the forests than within the habitat patches, corresponding with the view that increased dispersal mortality is a major cost for species living in fragmented landscapes (Fahrig 2002). However, as the estimated diffusion and mortality coefficients are not significantly different in the different habitat types in the full model, I conclude that the best supported model for this data set is the simple model A.

The model with estimated parameter values provides a tool that may be used to obtain further biological inferences. As an example, I used the model to study the time that individuals are expected to spend in different parts of the network. To do this, I assumed that an individual was born in a particular habitat patch and I ran the diffusion model for a period of 30 days. In each time step, I integrated the probability density over space to obtain the probabilities that the individual is in any of the habitat patches or that it is in the matrix habitat. Fig. 5 shows how the probabilities that the individual is in its natal patch, is in the other habitat patches, or is dispersing evolve in time. Note that the sum of these three probabilities gives the probability that the individual is still alive. Integrating curves such as the ones shown in Fig. 5 over time gives the amount of time that an individual is expected to spend in different parts of the network. Comparison of such mean times shown in Table 2 with the map shown in Fig. 3 leads to intuitive conclusions. For example, because patch 1 is larger than patch 2, a butterfly that is born in patch 1 is expected to spend more time in its natal patch than a butterfly born in patch 2. As patch 12 is a very isolated patch, a butterfly born there spends the
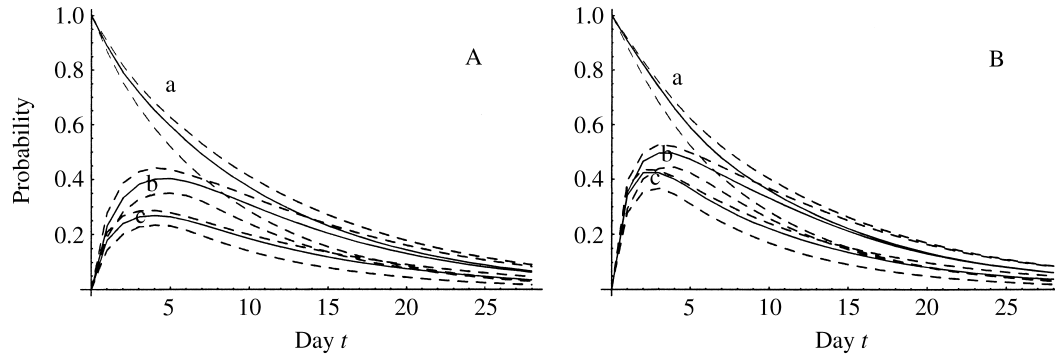
FIG. 5. The time evolution of the probabilities that a butterfly is in its natal patch (line a), in other habitat patches (line b), or dispersing (line c). The individual is assumed to be born in patch 1 (panel A) or in patch 12 (panel B) in the landscape shown in Fig. 3. The continuous lines correspond to the maximum likelihood parameter values of Model A (Table 1), and the dashed lines show the 95% confidence intervals. Results are based on the time-dependent finite element approximation, which has been integrated at each time step separately over the natal patch, over the other habitat patches, and over the remaining landscape.

most time dispersing, because it is not easy to find other patches. Patch 5 is relatively small but very well connected, so a butterfly born there is likely to spend much time in the other habitat patches. Note that the confidence limits are narrower for the integrated quantities shown in Table 2 than they are for the original parameter values (Table 1). This is to be expected, as the parameters may partly compensate each other so that the parameter combinations are always able to reproduce the observed movement behavior in a reasonable manner. The difference between Model A and Model B for the quantities shown in Table 2 is small and not statistically significant.

Fig. 6 shows how the time that the individuals are expected to spend in different parts of the network depends on the size and on the connectivity of their natal patch. As expected, the time that an individual spends in its natal patch increases with the size of the patch (Fig. 6A). The line in Fig. 6A represents the theoretical result for $T(r, s)$, which assumes a single circular habitat patch (with area equal to that of the actual patch) surrounded by matrix habitat. The distance s has been set to $s = s_{\min} \approx 287$ m, corresponding to the average distance to the nearest patch. The predictions of the model deviate only little from the theoretical line, suggesting that the area of the natal patch is the major determinant of the time spent in the patch, the shape of the patch and the configuration of the remaining network having only a minor effect. Fig. 6B examines the time that an idividual is expected to spend in the habitat patches excluding the natal patch. In order to reach the other habitat patches, the individual first must emigrate from its natal patch i. The probability that it will succesfully emigrate may be approximated by $P_E(r_i, s)$, where r_i is the radius of the circle with area equal to that of the natal patch. Once the individual has emigrated, it must immigrate to another habitat patch j, and this happens with probability $P_I(r_j, d_{ij})$, where r_j is the radius of the target patch and d_{ij} is the

distance between patches i and j. Once the individual has immigrated, it is expected to spend time $T(r_j, s)$ in the patch j before it dies or emigrates to a distance s from the patch. By this reasoning, the time that an individual born in patch i is expected to spend in the other patches may be approximated by $\Lambda = P_E(r_i, s) \, S_i(s)$, where S_i is the connectivity of patch i, defined by

$$S_i(s) = \sum_{j \neq i} P_I(r_i, d_{ij})T(r_j, s). \tag{13}$$

The distance s in the formulae for $P_E(r, s)$ and $T(r, s)$ should represent typical migration distances in the network, and I thus set $s = s_{\min}$. As illustrated by Fig. 6B, the measure Λ correlates very well with the actual predictions based on the full model. It tends to give an overestimate because it ignores the fact that the patches are in sense competing for the migrant.

Table 2 and Fig. 6 also show the estimates obtained for the same data by Hanski et al. (2000), which will be discussed.

DISCUSSION

Quantifying dispersal is a key issue, especially in metapopulation dynamics, where the regional persistence of a species is based on compensation of local extinctions by recolonizations of empty habitat patches (Hanski 1999). Most multistate dispersal models have either been purely statistical models without an explicit assumption about the shape of the dispersal kernel (Hestbeck et al. 1991, Lebreton and Pradel 2002), or assumed that dispersal success decreases with increasing distance between the habitat patches. An attempt to account for the heterogeneity of the dispersal habitat in the metapopulation context was made by Ricketts (2001), who classified the matrix habitat into two classes and recorded the vegetation types along linear transects connecting each pair of sampling sites. Based on these connectivity measures and mark–recapture data,

TABLE 2. Areas of the habitat patches as measured from the Fig. 3 map (A) and as given by Hanski et al. (2000) (A_{VM}), and the number of days that a butterfly is expected to spend in its natal patch, in the other patches, and during dispersal.

Natal patch	A	A_{VM}	Days spent	Model A	Model B	VM
1	1.58	1.70	in natal patch	3.2 (2.7–3.7)	3.1 (2.7–3.7)	3.9
			in other patches	2.7 (2.1–3.2)	2.7 (2.1–3.1)	2.9
			dispersing	3.9 (2.9–4.4)	3.7 (2.7–4.4)	
2	0.81	0.70	in natal patch	2.4 (2.0–2.8)	2.3 (1.9–2.8)	3.3
			in other patches	1.6 (1.2–2.0)	1.5 (1.1–1.9)	1.0
			dispersing	5.7 (4.4–6.2)	5.0 (3.3–6.5)	
3	0.88	0.60	in natal patch	2.2 (1.8–2.5)	2.2 (1.8–2.6)	3.3
			in other patches	2.7 (2.1–3.1)	2.6 (2.1–3.2)	2.8
			dispersing	4.7 (3.6–5.2)	4.4 (3.3–5.3)	
4	3.58	2.28	in natal patch	5.3 (4.6–6.1)	5.1 (4.4–6.2)	3.9
			in other patches	1.5 (1.3–1.8)	1.4 (1.2–1.9)	2.1
			dispersing	2.2 (1.6–2.6)	1.9 (1.1–2.7)	
5	0.67	0.50	in natal patch	2.0 (1.7–2.4)	2.0 (1.7–2.4)	3.6
			in other patches	5.0 (3.9–5.6)	4.7 (3.8–5.6)	3.7
			dispersing	2.6 (1.8–2.8)	2.3 (1.4–3.0)	
6	0.43	0.24	in natal patch	1.3 (1.0–1.5)	1.2 (1.0–1.6)	3.0
			in other patches	4.9 (3.8–5.5)	4.8 (3.8–5.5)	3.5
			dispersing	4.0 (3.0–4.2)	3.7 (2.6–4.3)	
7	1.21	1.20	in natal patch	2.9 (2.4–3.3)	2.8 (2.4–3.3)	3.6
			in other patches	4.3 (3.4–4.9)	4.1 (3.4–5.0)	3.5
			dispersing	2.4 (1.7–2.7)	2.2 (1.4–2.9)	
8	1.27	0.64	in natal patch	3.0 (2.5–3.5)	2.9 (2.4–3.4)	3.7
			in other patches	4.4 (3.5–5.2)	4.1 (3.4–5.2)	3.6
			dispersing	2.5 (1.7–2.8)	2.2 (1.3–3.0)	
9	2.37	2.24	in natal patch	4.8 (4.1–5.5)	4.7 (4.0–5.5)	4.6
			in other patches	2.4 (1.8–2.9)	2.3 (1.7–2.8)	2.1
			dispersing	2.5 (1.7–2.7)	2.1 (1.0–3.0)	
10	0.06	0.01	in natal patch	0.4 (0.4–0.5)	0.4 (0.4–0.5)	2.4
			in other patches	7.1 (5.8–8.3)	6.9 (5.4–8.0)	5.2
			dispersing	2.8 (1.9–3.2)	2.4 (1.2–3.3)	
11	0.83	0.60	in natal patch	2.6 (2.1–3.0)	2.5 (2.0–3.0)	4.3
			in other patches	4.6 (3.4–5.3)	4.1 (3.3–5.2)	2.8
			dispersing	3.2 (2.2–3.4)	2.6 (1.4–3.6)	
12	0.52	0.50	in natal patch	2.2 (1.9–2.7)	2.2 (1.7–2.7)	2.8
			in other patches	2.3 (1.7–2.9)	2.1 (1.3–2.7)	0.4
			dispersing	5.2 (3.9–5.6)	4.5 (2.4–6.0)	
13	0.27	0.12	in natal patch	1.3 (1.1–1.6)	1.4 (0.9–1.7)	3.0
			in other patches	2.8 (2.3–3.3)	2.8 (1.6–3.3)	1.0
			dispersing	5.8 (4.4–6.2)	5.2 (2.2–6.9)	
14	0.90	0.08	in natal patch	2.9 (2.4–3.4)	3.0 (1.9–3.5)	2.7
			in other patches	1.6 (1.3–1.9)	1.6 (0.9–1.9)	2.0
			dispersing	5.6 (4.1–6.0)	5.1 (2.1–6.8)	

Notes: The results for Models A and B are based on integrating time-dependent solutions (such as those in Fig. 5) over time, whereas results for the virtual migration (VM) model were taken from Hanski et al. (2000) and are based on the mean of 10 simulation runs. The VM model does not allow the estimation of the time spent during dispersal.

Ricketts (2001) used maximum likelihood methods to estimate the relative resistances of the two habitat classes. Another approach was taken by Bunn et al. (2000), who used a graph-theoretical approach and least-cost path modeling to assess the functional distances between habitat patches.

Hanski et al. (2000) used a phenomenological "virtual migration" (VM) model to estimate the movement parameters of the false heath fritillary butterfly from the same data set that I have analyzed in the examples. Hanski et al. (2000) assumed that the matrix habitat is homogeneous, that dispersal success decays exponen-

tially with distance, and that emigration and immigration rates scale as a power of patch area. Comparison with the parameters estimated by Hanski et al. (2000) is not straightforward, as the two models are based on different assumptions. Furthermore, the habitat patches without an identity number in Fig. 3 were located only after the study of Hanski et al. (2000), and some of the old patches were later found to have covered a wider area (Table 2). However, some comparisons can be made, for example between the simplest model considered by Hanski et al. (2000) (six parameters excluding the capture probabilities) and the present Mod-
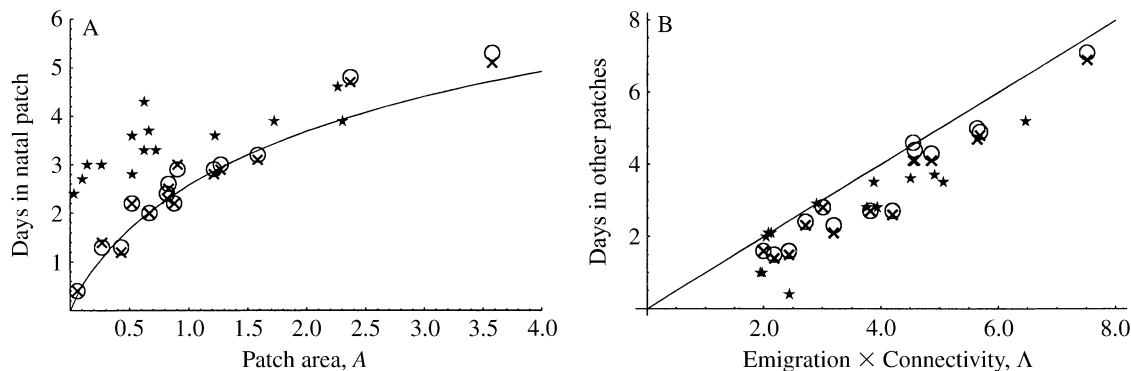
FIG. 6.   Number of days that the butterflies are expected to spend in their natal patch and in the other patches. The circles and crosses correspond to the values given in Table 2 for Models A and B, respectively, whereas the stars correspond to the virtual migration (VM) model of Hanski et al. (2000). The time spent in the natal patch (panel A) is plotted with respect to the area of the natal patch. The curve represents the function $T(r, s_{min})$ (based on Eq. 10 and parameter values corresponding to Model A), where r is the radius of the circle with area equal to that of the actual patch, and the parameter s_{min} is the average distance to the nearest patch in the network ($s_{min} = 287$ m). The time spend in the other patches (panel B) is plotted with respect to the measure Λ, which is defined as the product of the emigration probability P_E and the connectivity S with parameter values corresponding to those of Model A (Eq. 13). The line represents identity.

el A (four parameters excluding the capture probabilities). Hanski et al. (2000) estimated that the within-patch survival probability would be 0.89 per day, which is very close to the mortality rate of 0.1 estimated in my study. They estimated that the mean dispersal distance would be ~200 m (1/α in their Table 1), in contrast to the mean dispersal distance of 1.5 km estimated in this study. The large difference between these two figures is easily explained, as the two estimates relate to different time scales. While the estimate of Hanski et al. (2000) refers to a single dispersal event (from a patch to another patch), I estimated the distance that an individual is expected to move during its entire lifetime if it is released to a homogeneous area. Hanski et al. (2000) estimated that the capture probability (in patches other than patch 1) would be 0.26, whereas I have estimated that the capture probability is 0.34. This difference is most likely explained by the fact that the VM model used by Hanski et al. (2000) does not account for the time that the butterflies spend dispersing between the habitat patches; thus they assumed that the butterflies are always in one of the patches. The most interesting comparison can be made between the times that the butterflies spend in various parts of the network (Table 2, Fig. 6). The VM model does not account for the time that an individual spends dispersing, so it generally overestimates the time that the individuals spend in their natal patches. An especially large difference between the present model and the VM model appears for the smallest habitat patches (Fig. 6A). This results from different structural assumptions, especially the power-law scaling assumed in the VM model. The largest deviations appear for patches that are most extreme in their size or isolation, such as the very isolated patch 12. This is not surprising, as the parameter estimates are largely based on data from "typical" patches, and

thus the predictions for "atypical" patches are extrapolations that depend on the structural assumptions behind the models.

In this paper, I have taken the model of Dobzhansky et al. (1979) as a starting point and have developed it in two ways. First, I have used effective finite-element methods to solve the partial differential equation in an irregular triangular mesh that can be adapted well to real landscapes. Second, the present model is able to account for biased behavior at edges between habitat types. Not surprisingly, such behavior turned out to be a major determinant in the butterfly example, the estimated density of butterflies inside the habitat patches being more than 100 times higher than their density in adjacent areas. Compared with earlier methods for estimating movement parameters from spatial mark–recapture data, the present method has several advantages. First, the model has a mechanistic background; consequently, all the model variables have a clear biological interpretation. Second, the model is able to account for habitat heterogeneity, using information about the spatial configuration of the landscape. Third, the present model uses information about the absence of an individual to update the probability density for the individual's location in a natural way. Fourth, even in the case in which the matrix habitat is assumed to be homogeneous, the present model is not restricted to interpatch distances, but accounts for the actual locations of the habitat patches. This may make a difference because the habitat patches are, in a sense, competing for the migrating individuals. This is captured by the present model, in which the addition of a new patch between two existing patches decreases dispersal between the two patches (Ovaskainen and Cornell 2003). Finally, the present model is not restricted to metapopulations inhabiting highly fragmented landscapes,

but it applies to arbitrary landscapes. The main disadvantage of the present model is that its parameterization is computationally tedious. However, as demonstrated by the butterfly example, the model may be applied to real landscapes, including substantial detail about the landscape configuration. Computing speed is likely to continue to increase; hence, the computational disadvantage should decrease in the future. I hope that the present modeling approach will provide a robust framework for quantifying movement behavior in heterogeneous landscapes.

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APPENDIX

Numerical solutions by the finite element method are available in ESA's Electronic Data Archive: *Ecological Archives* E085-003-A1.