An Empirical Test of a Diffusion Model: Predicting Clouded Apollo Movements in a Novel Environment

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Abstract: Functional connectivity is a fundamental concept in conservation biology because it sets the level of migration and gene flow among local populations. However, functional connectivity is difficult to measure, largely because it is hard to acquire and analyze movement data from heterogeneous landscapes. Here we apply a Bayesian state-space framework to parameterize a diffusion-based movement model using capture-recapture data on the endangered clouded Apollo butterfly. We test whether the model is able to disentangle the inherent movement behavior of the species from landscape structure and sampling artifacts, which is a necessity if the model is to be used to examine how movements depend on landscape structure. We show that this is the case by demonstrating that the model, parameterized with data from a reference landscape, correctly predicts movements in a structurally different landscape. In particular, the model helps to explain why a movement corridor that was constructed as a management measure failed to increase movement among local populations. We illustrate how the parameterized model can be used to derive biologically relevant measures of functional connectivity, thus linking movement data with models of spatial population dynamics.

Keywords: animal movement, capture-recapture, random walk, diffusion, corridor, connectivity.

All species disperse, and the dispersal strategy adopted by a given species has fundamental consequences for its ecological, genetic, and evolutionary dynamics (Turchin 1998; Clobert et al. 2001; Hanski and Gaggiotti 2004; Sugden and Pennisi 2006). Dispersal combined with other population dynamic processes can generate complex dynamics and spatial patterns, even without any environmental heterogeneity (Solé and Bascompte 2006) or in the context of simple descriptions of landscape structure, such as the metapopulation concept (Hanski 1998). In heterogeneous environments, the redistribution of individuals also depends on the structure of the underlying landscape, leading to a wide variety of possible outcomes (Goodwin and Fahrig 2002).

Landscape ecological research focuses on the interplay between environmental heterogeneity and ecological processes, especially animal movement (e.g., Taylor et al. 1993; Tischendorf and Fahrig 2000; With 2004; Tischendorf et al. 2005). The rate of movement is associated with the concept of connectivity (Taylor et al. 1993), the exact meaning of which has been heavily debated, partly because connectivity has been defined differently in different fields (Moilanen and Hanski 2001; Tischendorf and Fahrig 2000). In metapopulation biology, the focus is on patch connectivity, which is a property of a particular patch within the landscape (Moilanen and Nieminen 2002). Measures of landscape connectivity can sometimes be obtained by averaging the corresponding measures of patch connectivity over the entire landscape. Connectivity measures can also be classified by structural and functional measures (Goodwin 2003). Structural measures are based solely on the physical landscape structure, whereas functional measures are derived...
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specifically from the viewpoint of the movement behavior of a focal species. The link between structural and functional measures is not straightforward (Goodwin and Fahrig 2002), and simple structural measures of connectivity (or habitat proximity) often correlate poorly with animal movement or other aspects of spatial population dynamics (Moilanen and Nieminen 2002; Bender et al. 2003; Winfree et al. 2005). Unfortunately, measuring functional connectivity is more difficult than measuring structural connectivity, as it requires detailed knowledge of the movement behavior of the species. Measures of functional connectivity are also necessarily species specific (Tischendorf et al. 2003), making it difficult to draw general conclusions.

The importance of distinguishing between structural and functional connectivity is especially evident in research focusing on the role of landscape elements, such as corridors, stepping stones, or barriers. While such landscape elements play a key role in conservation planning (Dramstad and Gillilan 1996), there is very limited evidence to show that, for example, corridors really improve functional connectivity (Chetkiewicz et al. 2006). As a consequence, the empirical support for such landscape elements truly affecting movements is still very limited. Most of the hard evidence comes from experimental settings (Haddad et al. 2003; Levey et al. 2005) rather than from natural populations (Beier and Noss 1998), partly because of lack of effective methods for analyzing observational data from natural populations living in heterogeneous landscapes.

In spite of recent advances in electronic tagging and telemetry techniques, many of the movement data from natural populations are still obtained in the form of spatially referenced capture-recapture data. The statistical properties of such data are affected by (i) the movement behavior of the species, (ii) variation in landscape structure and other environmental conditions, and (iii) the design of the field study, including the frequency and the spatial extent of sampling. One simple method that has been used to analyze such data is to examine the distribution of observed movement distances. However, this confounds all three factors and can hence result in various artifacts (Schneider 2003). As the factors ii and iii are typically known to the researcher, it is, in principle, possible to extract the information about the unknown factor, that is, the movement behavior of the species, from the data. This can be viewed as an inverse problem, where the aim is to solve the underlying movement process that has resulted in the observed capture-recapture data. Because different types of movement behaviors may lead to statistically similar capture-recapture data, the problem is ill-posed in the sense that no unique solution exists. A natural approach is to fit the data to a simple yet biologically plausible movement model and to examine the model fit to assess whether any features of the data cannot be explained by the model. If necessary, the model may then be developed iteratively into a more realistic one.

Such an approach has commonly been taken in the context of state-space modeling, which separates a process model from an observation model. State-space modeling has been applied especially in the case of telemetry data (Anderson-Sprecher and Ledolter 1991; Jonsen et al. 2003, 2005, 2006; Morales et al. 2004; Royer et al. 2005; Franke et al. 2006), which are typically characterized by a large number of observations of relatively few individuals. In the case of capture-recapture data aimed at assessing movements, state-space models (or the related hidden Markov models) have been used mainly in the context of multisite models (Lebreton and Pradel 2002; White et al. 2006), which aim at estimating movement probabilities separately between all sets of sites. In a continuous space setting, movements can be modeled with the help of a dispersal kernel (Fujiwara et al. 2006). The kernel approach, however, assumes that dispersal success depends solely on distance, which can be an oversimplification if the landscape is heterogeneous (Ricketts 2001). A simple alternative for analyzing movements in heterogeneous landscapes is to use random walk models (Tischendorf et al. 2005) or their diffusion approximations (Ovaskainen and Cornell 2003). These modeling frameworks are typically based on classifying the landscape into a number of habitat types and by assuming habitat-specific parameters (e.g., movement rates, habitat selection, and mortality). While diffusion and random walk are just different representations of the same biological model (Turchin 1998), diffusion is mathematically more tractable, leading to major computational advantages, for example, in parameter estimation (Ovaskainen et al. 2007).

The motivation behind this article comes from asking whether diffusion models can be used to examine how movements depend on landscape structure. While it is straightforward to do so using hypothetical parameter values, our main emphasis is in asking whether diffusion is realistic enough to describe animal movements in complex, heterogeneous landscapes. To do so, we consider a case study of an endangered butterfly species, the clouded apollo (Parnassius mnemosyne). We first parameterize the diffusion model using data from a reference landscape and examine the model fit to check whether the data are consistent with the structural assumptions of the model. We then perform a more stringent test of model validation by predicting clouded apollo movements in a structurally different landscape and comparing the model prediction with independent capture-recapture data. In particular, we study whether the model correctly predicts the effect of a movement corridor that was constructed as a management measure to increase movements between two subpopu-
lations. Finally, we illustrate how the diffusion model can be used to derive biologically relevant measures of functional connectivity.

**Material and Methods**

**The Data and the Process Model**

The clouded apollo belongs to a large group of grassland specialist species that are declining due to land-use changes in agriculture (van Swaay and Warren 2006). We consider capture-recapture data on this species of butterfly collected in the two landscapes shown in figure 1. The landscapes are classified into three habitat types that potentially differ from each other in terms of the movement behavior of the species. We label these with the subscripts H (breeding habitat consisting of meadows with the host plant Corydalis solida), C (other meadows and semiopen forests, hypothesized to act as dispersal corridors), and U (unsuitable matrix consisting of closed forests, cultivated fields, and water). An intensive capture-recapture study (Luoto et al. 2001) of the clouded apollo was conducted in the landscape of figure 1A (landscape A) in 1999. The data (shown in fig. C1 in the online edition of the *American Naturalist*) include observations on 1,121 males (with 858 recaptures) and 339 females (with 60 recaptures). We use these data for parameter estimation.

Our aim was to test whether the model is able to predict movements in structurally different landscapes. To do so, we utilize two independent capture-recapture data sets (shown in fig. C1), acquired in the landscape of figure 1B (landscape B). As a management measure, a movement corridor was constructed in this landscape to improve the connectivity between two clouded apollo subpopulations. Capture-recapture data were collected both before (2002) and after (2003) the construction of the movement corridor. The data for 2002 include observations on 249 males (with 213 recaptures) and 142 females (with 53 recaptures), whereas the data for 2003 have observations on 186 males (with 120 recaptures) and 78 females (with 24 recaptures).

We apply the state-space modeling approach of Ovaskainen et al. (2007), which combines a diffusion model (as the process model) with an observation model describing the capture effort. The diffusion model assumes that the individuals are able to assess the local quality of their environment but that they have neither long-term memory nor large-scale information of the landscape structure. More precisely, the diffusion model can be derived by assuming that the individuals follow a random walk (either uncorrelated or correlated), with parameters that may depend on the habitat type at their current location (Patlak 1953; Turchin 1998). Assuming that an individual is initially at a location \( y \), the probability density \( v(x, t; y) \) for the individual’s location \( x = (x_1, x_2) \) at time \( t \) evolves as (Turchin 1998; Ovaskainen 2004)

\[
\frac{\partial v}{\partial t} = D\Delta v - \mu v. \tag{1}
\]

Here the Laplacian \( \Delta \) (second-order spatial derivative)

![Figure 1: Landscapes in which the capture-recapture data were collected. Data from the study area shown in A are used for parameter estimation, whereas data from study area shown in B are used for model validation. The distance between the two study areas is 25 km, both being located in southwest Finland. Study area B is inhabited by two clouded apollo subpopulations (N = northern, S = southern). Corridor C1 was cut through the forest in autumn 2002 as an attempt to improve connectivity between the subpopulations. C2 represents a natural corridor. Red = meadows with the host plant Corydalis solida; yellow = other meadows and semiopen forests; white = cultivated fields; green = closed forests; and blue = water. Note that A and B are shown on different scales.](image-url)
is taken with respect to the variable $x$. Both the diffusion coefficient $D$, which describes the rate of movement, and the mortality rate $\mu$ are assumed to depend on the habitat type at the location $x$. The model accounts for habitat selection at edges between different habitat types, that is, the fact that close to an edge, an individual may bias its movement toward the preferred habitat type. In the diffusion approximation, such behavior translates into a discontinuity in the probability density $v$ (Ovaskainen and Cornell 2003). We parameterize habitat selection by assuming a habitat-specific preference $k$, which is proportional to the value of the probability density $v$ within a given habitat type. Assuming a population of independently moving individuals, the population densities at the two sides of an edge would be proportional to the habitat-specific preferences $k$. Because only the relative values matter, we normalize the preference for the breeding habitat as $k_C = 1$. We note that the probability density $v$ gives the probability of use of a given resource unit, and it can hence be interpreted as a resource selection function (Manly et al. 2002).

Parameter Estimation and Assessment of Model Fit

To connect the movement model to capture-recapture data, we define $p$ as the probability of capturing an individual from a $50 \times 50$-m grid cell, conditional on the individual being there during the search. We use the Bayesian method of Ovaskainen et al. (2007) to estimate the posterior distribution of the model parameters, with prior distributions based on independent studies. The likelihood of the data depends on the time-dependent solution to the diffusion equation (eq. [1]), which we computed numerically with the finite-element method. The problem is computationally demanding, and we used adaptive Monte Carlo Markov chain (MCMC) methods with multivariate proposal distributions to obtain good mixing in the Metropolis-Hastings algorithm (app. A in the online edition of the American Naturalist).

We used lognormal priors for the parameters $k$, $D$, and $\mu$ and a logit-normal prior for the parameter $p$. The medians (and 95% ranges) of the priors were set to $k_C = 0.1 \times (10^{-10} - 10)$; $D_C = 0.01(10^{-10} - 1)$; $D_D$, and $D_U = 10^5 \times (10^{-10} - 10)(m^2 \text{ day}^{-1})$; $\mu_D$, $\mu_C$, and $\mu_U = 0.1(0.01 - 1)(\text{day}^{-1})$; and $p = 0.5(0.1 - 0.9)$. The median values for $k_C$ and $k_U$ are based on transect counts giving abundance estimates within the three habitat types. The median values of the death rates are based on a mean lifetime of 10 days, and the median values for the diffusion coefficients correspond to the assumption (Turchin 1998) that an individual would move on average approximately 1.6 km within its lifetime (in line with Valimäki and Itämes 2003).

We studied differences in the model parameters among the habitat types and between the sexes by calculating the posterior probability for a number of test quantities. For example, to assess whether capture probability is greater for males ($p^M$) than for females ($p^F$), we calculated the probability $P(p^M > p^F)$. To do so, we drew a random sample from the males’ posterior distribution (a random iteration round in the MCMC) and another sample from the females’ posterior distribution. We repeated this 10,000 times and computed $P(p^M > p^F)$ as the fraction of samples for which the inequality $p^M > p^F$ held true.

We assessed the model fit by contrasting the real data (from landscapes A and B) against posterior predictive data separately for males and females. To generate the posterior predictive data, we drew 1,000 samples from the posterior distribution and generated a data set for each sample by following exactly the procedures of the empirical studies. Thus, we assumed that the individuals were first observed at the same times and locations as in the real data, we generated a movement track for each individual, and then we generated capture-recapture data from the movement tracks, assuming the same spatiotemporal capture effort as in the field study. We examined whether the posterior predictive data deviated from the real data in terms of the distribution of observed movement distances and the distribution of days from first to last capture. We also used posterior predictive data to see whether the model predicted correctly the amount of movement between the two subpopulations in landscape B before and after they were connected by a corridor.

The Effect of a Movement Corridor

To assess more generally the effect of a movement corridor, we also considered a simplified landscape consisting of just two habitat patches of radius $r$ and at distance $s$ from each other. We denote by $q_c$ the probability that an individual initially present in one patch will ever visit the other patch, assuming that the rest of the landscape consists entirely of the unsuitable matrix type U. We let $q_c$ denote the same movement probability but with the assumption that the two patches are connected by a corridor consisting of habitat type C. In the case of $q_c$, it is assumed that the corridor is surrounded by totally unsuitable matrix, so that the edges of the corridor work as reflecting boundary conditions. With some simplifying assumptions, both $q$ and $q_c$ can be calculated analytically (app. B in the online edition of the American Naturalist). We utilized the analytical formulas to examine how the effect of the corridor depends on its length and on the sizes of the two habitat patches. We measured the effect of the corridor by the ratio $q_c/q$, so that values greater than unity indicate that the corridor facilitates movement.
meability of a given habitat type. There is much better resolution in the data to estimate permeability $Z$ than its individual components $k$ and $D$ (table 1). Interestingly, the permeability of the corridor habitat is similar for females and males, though the individual components $k$ and $D$ are different, as described above.

### Model Validation

We first contrast posterior predictive data against the same data that we used to estimate the model parameters. While the model fits generally well with both the nonspatial (fig. 2A) and spatial (fig. 2B) facets of the data, it underestimates the number of very short (<100 m) and very long (>900 m) movement distances (fig. 2B). The model assumes that the individuals move independently of each other. Figure 2C, however, shows that movements of females were somewhat shorter if the density of other females was high in the surrounding area. In contrast, female movements were not affected by the density of males (fig. 2D).

We then proceed to the more stringent test of model validation by contrasting model predictions against the two independent data sets collected in landscape B. The model prediction is in good agreement with both capture-recapture data sets (fig. 3A; fig. C6 in the online edition of the American Naturalist). Contrary to expectations, the movement corridor that was opened through the forest did not improve functional connectivity between the two locations (fig. 3B). While many individuals did move to the corridor, the number of movements between the two populations decreased rather than increased, though the

<table>
<thead>
<tr>
<th>Variable</th>
<th>Females</th>
<th>Males</th>
</tr>
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<tbody>
<tr>
<td>$k_H$</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>$k_C$</td>
<td>.086 (.013–.29)</td>
<td>.23 (.17–.30)</td>
</tr>
<tr>
<td>$k_U$</td>
<td>.062 (.006–.31)</td>
<td>.0057 (.003–.0096)</td>
</tr>
<tr>
<td>$D_H$</td>
<td>$1.5 \times 10^4$ ($3,600-3.5 \times 10^4$)</td>
<td>5,800 ($3,700-9,500$)</td>
</tr>
<tr>
<td>$D_C$</td>
<td>$6.0 \times 10^4$ ($1.0 \times 10^4-3.9 \times 10^5$)</td>
<td>8,000 ($3,800-1.4 \times 10^5$)</td>
</tr>
<tr>
<td>$D_U$</td>
<td>$2.100 \times 10^4$ ($200-9.5 \times 10^4$)</td>
<td>$1.9 \times 10^4$ ($1.2 \times 10^3-3.4 \times 10^5$)</td>
</tr>
<tr>
<td>$\mu_H$</td>
<td>.14 (.05–.23)</td>
<td>.16 (.12–.19)</td>
</tr>
<tr>
<td>$\mu_C$</td>
<td>.08 (.01–.53)</td>
<td>.067 (.009–.23)</td>
</tr>
<tr>
<td>$\mu_U$</td>
<td>.17 (.01–.89)</td>
<td>.082 (.009–.56)</td>
</tr>
<tr>
<td>$p$</td>
<td>.080 (.054–.12)</td>
<td>.39 (.36–.43)</td>
</tr>
<tr>
<td>$Z_H$</td>
<td>122 (60–190)</td>
<td>76 (61–97)</td>
</tr>
<tr>
<td>$Z_C$</td>
<td>21 (5–57)</td>
<td>20 (14–28)</td>
</tr>
<tr>
<td>$Z_U$</td>
<td>2.9 (.62–8.6)</td>
<td>2.5 (1.7–3.5)</td>
</tr>
</tbody>
</table>

Note: The values in the table give the median and the 95% credibility intervals. The parameters $k$ (dimensionless), $D$ (m$^2$ day$^{-1}$), $\mu$ (day$^{-1}$), and $p$ (dimensionless) refer to habitat selection, diffusion, mortality, and capture probability, respectively. The preference for the breeding habitat was normalized as $k_i = 1$. The permeability ($Z$) of a given habitat type is defined as $Z = k(D)^{1/2}$. Subscripts $H$, $C$, and $U$ stand for breeding habitat, dispersal corridor, and unsuitable matrix, respectively (see "Material and Methods").
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Figure 2: Model fit against the data used for parameterization. A shows the distribution of number of days between first and last capture, and B shows the distribution of observed movement distances. A and B refer to males; see figure C2 in the online edition of the American Naturalist for corresponding figures for females. C shows, for females, the length of the next observed displacement as a function of the density of other females (no. individuals observed within 5 days and within 50 m of the focal observation); the line depicts a least squares fit ($P = .02$). D compares the slopes of fitted lines, such as the one in C, to corresponding slopes obtained from predictive posterior distributions. In D, $sex_1$ refers to the focal sex, and $sex_2$ refers to the sex according to which the density is measured. Open dots depict the data, while black dots with error bars depict the means and 95% credibility intervals of the posterior predictive distribution.

difference is not significant. Quite strikingly, the model also correctly predicts the counterintuitive effect of the movement corridor (fig. 3B; fig. C5 in the online edition of the American Naturalist). The analysis based on the simplified landscape helps to explain why the corridor did not provide functional connectivity: slow movement rate within the corridor habitat makes a corridor effective only if it is not too long or connects very small patches that would otherwise be hard to find (fig. 3C).

Measures of Functional Connectivity

The parameterized and validated movement model makes it possible to analyze various aspects of functional connectivity from the clouded apollo’s point of view. A clear-cut measure of functional connectivity is given by the probability that an individual will move from one place to another. We hence consider the hitting probability $q(y)$, defined as the probability that an individual initially at a location $y$ will hit a given region before it dies (Ovaskainen and Cornell 2003). Figure 4A shows the probability that a male butterfly in initial location $y$ would ever visit the meadow in the center of the figure. In a homogeneous landscape, only the distance to the initial location would matter, and thus any deviation from a circular pattern is solely due to landscape structure. For example, $q(y)$ attains a high value in the cultivated field northeast of the focal patch. If an individual were released in this region, it would be likely to move fast within the field, after which it would be captured by either of the riverside meadows, both of which direct movements toward the central patch.

As a complementary measure, we consider the occupancy time density $u(x; y) = \int_0^T v(x, t; y) dt$, measuring the time that an individual initially at location $y$ is expected to spend at any location $x$ during its lifetime (Ovaskainen and Cornell 2003). The time an individual is expected to spend in any finite region $X$ is then given by $T_c(y) = \int_X u(x; y) dx$. As expected, the occupancy time density decreases with increasing distance from the initial location (fig. 4B). The periods of time spent in the three habitat classes differ by an order of magnitude due to strong habitat selection at habitat boundaries.

While hitting probability is a relevant measure for predicting colonization to new areas, occupancy time gives
Figure 3: Model validation against independent data. A shows the fit of the model to independent capture-recapture data collected in summer 2002 in landscape B. The colored dots depict the data, and the black dots with error bars indicate the posterior predictive distribution. B shows the fraction of males that moved before (red dots; summer 2002) and after (blue dots; summer 2003) the corridor was cut between subpopulations N and S (A), between either of the subpopulations and corridor C1 (B), and between either of the subpopulations and corridor C2 (C). See figure C6 in the online edition of the American Naturalist for further aspects of the model fit assessed for both the 2002 and 2003 data sets. C shows the effect of a habitat corridor on the likelihood of movement between two patches of radius $r$ at distance $s$ from each other. The contour lines depict the value of $\theta = \log_{10}(q_C/q_U)$, where $q_C$ and $q_U$ represent the probability of interpatch movement with and without a corridor (see “Material and Methods”). Red (blue) indicates that movement is more likely with (without) a corridor. The ellipse shows the part of the parameter space that is relevant for assessment of corridor C1. Parameters in C are set to median estimates for males.

the distribution of time use and is thus relevant for predicting, for example, local dynamics in areas already occupied. The hitting probability is defined for a particular target region and the occupancy time for a particular initial location. Hence, both of them are measures of patch connectivity. Analogous measures of landscape connectivity (Tischendorf and Fahrig 2000) are provided by dispersal success (the per capita number of immigration events into all habitat patches) and search time (the average time an individual spends dispersing between a pair of habitat patches).

Discussion
Predictive understanding of the biological consequences of habitat fragmentation can be based only on rigorous assessment of the responses of individuals and populations to landscape structure. Much of the current theory about population dynamics in fragmented landscapes is based on the metapopulation concept, which assumes that suitable habitats occur in discrete patches surrounded by unsuitable matrix (Hanski 1998; Hanski and Ovaskainen 2000; Hanski et al. 2000; Hanski and Gaggiotti 2004). However, for most species, variation in landscape structure is of a more continuous nature, and there may not exist any well-defined habitat patches (Dennis et al. 2003). This makes it difficult to model movements, as the redistribution of actively moving animals is influenced in a complex way by the details of the landscape structure.

Both in theoretical (Bolker 2004; Solé and Bascompte 2006) and in empirical (Hill et al. 1996; Mennechez et al.
Figure 4: Measures of functional connectivity. A shows the probability $q$ that a male that hatches at a given location will ever visit the central patch (outlined in bold), and B shows the occupancy time $u$ (days m$^{-2}$) that a male butterfly initially in the central patch is expected to spend in any part of the landscape. Both panels show the median estimates for males; see figures C3 and C4 in the online edition of the American Naturalist for spatially varying confidence of these results and for corresponding results for females. Scales are log$_{10}$ transformed; numerical solution obtained by the finite-element method.

2003) literature, dispersal is often quantified with the help of dispersal kernels, which generally describe how dispersal success decreases with increasing distance. In the case of seed or spore dispersal, it is natural to define such a kernel as the probability distribution of the distance traveled by a propagule (Bolker and Pacala 1999). Kernels have, however, been applied also to other types of dispersal where the link to movement behavior is not as straightforward. In the case of many insect species, such as the clouded apollo, dispersal does not take place as a single event before or after reproduction, but the two processes take place simultaneously. In such a case, even knowledge about the distribution of lifetime movement distances is not sufficient for modeling spatial population dynamics, since a more relevant measure could be given by, for example, the distribution of the time that the individuals are expected to spend in various parts of the landscape.

Several recent studies have shown that matrix habitats may differ in their permeability, significantly influencing the effective isolation of habitat fragments (Roland et al. 2000; Ricketts 2001; Bender and Fahrig 2005). A given matrix type may have low permeability either because of a low likelihood of entering the area (our parameter $k$) or because of a slow movement rate within the area (our parameter $D$). We combined these variables here as $Z = k(D)^{1/2}$ to measure the overall permeability of a given habitat type. However, the most relevant measure of matrix permeability also depends on the distance between the habitat fragments separated by the matrix. If the distance is short, emigration rate is the major determinant, but the movement rate within the matrix becomes more important at greater distances. Hence, the permeability of a given habitat type depends on the landscape context and is best measured through the actual probability of moving from one fragment to another (the hitting probability $q$).

Matrix heterogeneity has often been accounted for by measuring the relative amounts of the various habitat types along a straight line (Ricketts 2001) or the least-cost path (Bunn et al. 2000) connecting two locations. In contrast, our measures of functional connectivity account for all possible movement tracks between the two locations. This observation emphasizes the computational advantage of the diffusion model over the alternative, that is, performing replicate simulation of a corresponding random walk model. This is apparent in figure 4A, which shows the probability of hitting the central patch as a function of initial location. To construct this figure with the help of simulations, one should in principle perform an infinite number of simulations, starting from all initial locations. A good approximation would be obtained, for example, by using a grid of 50 × 50 initial locations and performing 10,000 replicate simulations for each. This would require 25 million simulation replicates, each of which would construct the movement track of an individual until it dies or hits the central patch. In contrast, to produce figure 4A with the help of the finite-element method, one needs only to solve a single large but sparse matrix equation, which takes only a fraction of a second.

As the model accounts for the structure of the landscape, it provides a spatial reference model against which more specific hypotheses can be tested. Possible deviations in model fit indicate that the data are not in line with the structural assumptions of the model. In this study, we found that the model underestimated the amount of very
short and very long movement distances. This is probably due to differences in dispersal behavior between individuals (Hanski et al. 2004) or to the individuals switching between being sedentary or dispersive due to age or reproductive state (Van Dyck and Baguette 2005). Another possibility lies in the fact that we simply combined cultivated fields, closed forests, and waters to represent unsuitable habitat. While the butterflies are likely to fly over any of these in a fast and direct manner, they may also follow the edges between these habitat types, a process missing from the present model.

Another discrepancy was casod by nonindependence of movements among female butterflies (fig. 2C). Correlation between habitat quality and the density of females may be a part of the explanation. However, differences between the sexes (fig. 2D) suggest that there are also direct interactions, such as high density of males triggering female movements due to disturbance (Baguette et al. 1998). Extra activity due to intraspecific interactions is likely to be costly for both sexes, which may explain the trend toward higher mortality in the breeding habitat.

We have shown that the diffusion model with parameters estimated from one landscape is able to predict movements in a structurally different landscape, suggesting that our approach is able to extract information about species’ intrinsic movement behavior from capture-recapture data. Our measures of functional connectivity can thus be used to quantify how the movements of individuals depend on landscape structure. In this article, we have restricted our analysis solely to the movement process. Our modeling framework thus describes how the individuals redistribute themselves within one flight season. We end by noting that there are several approaches by which a movement model, such as the one considered here, can be extended to a model of spatial population dynamics. Reaction-diffusion models have been used extensively to study spatial population processes, the reaction term modeling events such as reproduction or density-dependent mortality (Cantrell and Cosner 2003). In the case of the clouded apollo, dispersal takes place as a discrete event during the short flight season, whereas density dependence, for example, is mostly determined at the larval stage. In such a case, the diffusion model can be used simply as a building block for general spatial models of population dynamics, genetics, and evolution (e.g., Hanski et al. 2004).

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