



Promoting the Science of Ecology

Bayesian Methods for Analyzing Movements in Heterogeneous Landscapes from Mark-Recapture Data

Author(s): Otso Ovaskainen, Hanna Rekola, Evgeniy Meyke, Elja Arjas

Reviewed work(s):

Source: *Ecology*, Vol. 89, No. 2 (Feb., 2008), pp. 542-554

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/27651566>

Accessed: 08/03/2012 09:38

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

BAYESIAN METHODS FOR ANALYZING MOVEMENTS IN HETEROGENEOUS LANDSCAPES FROM MARK–RECAPTURE DATA

OTSO OVASKAINEN,^{1,3} HANNA REKOLA,² EVGENIY MEYKE,¹ AND ELJA ARJAS²

¹*Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65 (Viikinkaari 1), FI-00014 University of Helsinki, Finland*

²*Department of Mathematics and Statistics, University of Helsinki, P.O. Box 68 (Gustaf Hällströmin katu 2b), FI-00014 University of Helsinki, Finland*

Abstract. Spatially referenced mark–recapture data are becoming increasingly available, but the analysis of such data has remained difficult for a variety of reasons. One of the fundamental problems is that it is difficult to disentangle inherent movement behavior from sampling artifacts. For example, in a typical study design, short distances are sampled more frequently than long distances. Here we present a modeling-based alternative that combines a diffusion-based process model with an observation model to infer the inherent movement behavior of the species from the data. The movement model is based on classifying the landscape into a number of habitat types, and assuming habitat-specific diffusion and mortality parameters, and habitat selection at edges between the habitat types. As the problem is computationally highly intensive, we provide software that implements adaptive Bayesian methods for effective sampling of the posterior distribution. We illustrate the modeling framework by analyzing individual mark–recapture data on the Glanville fritillary butterfly (*Melitaea cinxia*), and by comparing our results with earlier ones derived from the same data using a purely statistical approach. We use simulated data to perform an analysis of statistical power, examining how accuracy in parameter estimates depends on the amount of data and on the study design. Obtaining precise estimates for movement rates and habitat preferences turns out to be especially challenging, as these parameters can be highly correlated in the posterior density. We show that the parameter estimates can be considerably improved by alternative study designs, such as releasing some of the individuals into the unsuitable matrix, or spending part of the recapture effort in the matrix.

Key words: Bayesian estimation; diffusion; dispersal; edge-mediated behavior; Glanville fritillary butterfly; heterogeneous landscape; individual mark–recapture; *Melitaea cinxia*; random walk.

INTRODUCTION

Mark–recapture methods are central in many areas of ecological research, ranging from the estimation of population size to the estimation of individual-level parameters such as survival, fecundity, and movements. There is a versatile and well-developed body of statistical theory for the analysis of nonspatial mark–recapture data (Lebreton et al. 1992, Schwarz and Seber 1999). These methods have been implemented in user friendly software such as the program MARK (White and Burnham 1999), which is widely used as a standard tool for the estimation of demographic parameters from mark–recapture data.

Due to the increasing interest in spatial phenomena, considerable effort has been spent in acquiring data on movements of individuals (see, e.g., Turchin 1998, Clobert et al. 2001, Hanski and Gaggiotti 2004). Questions addressed by such data range from pest control and epidemiology to ecology and evolutionary biology of threatened species. For example, Bancroft and

Smith (2005) used mark–recapture to quantify the dispersal behavior of an invasive beetle species to provide a basis for eradication strategies. Maciel-De-Freitas (2006) conducted mark–recapture experiments to assess movements of yellow fever mosquitoes in forests vs. human-modified environments. Schtickzelle et al. (2006) conducted mark–recapture studies on the butterfly *Procllossiana eunomia* in contrasting landscapes to examine evolutionary responses to habitat loss and fragmentation. One possibility to analyze these kinds of spatially referenced mark–recapture data is to use multisite models, which generalize the standard nonspatial mark–recapture models by assuming that the individuals move between a finite set of sites (Lebreton and Pradel 2002). Such models have been used extensively for birds (Kendall and Nichols 2004, Breton et al. 2006), but also, e.g., for butterflies (Casula 2006) and fish (Chen and Xiao 2006).

Multisite models involve the estimation of movement probabilities between all pairs of sites, and are hence best suited for situations with a limited number of well defined sites. However, this requirement is rarely met, especially in studies of insect dispersal, where the number of suitable habitat patches can be very large

Manuscript received 14 March 2007; revised 16 May 2007; accepted 18 June 2007. Corresponding Editor: S. T. Buckland.

³ E-mail: otso.ovaskainen@helsinki.fi

(e.g., Hanski 1999), or variation in landscape structure may be of more or less continuous nature (e.g., Varkonyi et al. 2003). While data not suitable for multisite models have been analyzed using a variety of approaches, methods that would allow the estimation of movement parameters in an effective and unbiased manner appear to be still lacking. One commonly used alternative is to apply a purely statistical approach. For example, Mennechez et al. (2003) used constrained linear models to compare dispersal distances of a species of butterfly in two structurally dissimilar landscapes. A drawback in that approach is that it lacks the resolution to examine the causal factors behind the observed patterns. Indeed, observed movement distances may be different due to dissimilar sampling in the two landscapes, due to dissimilar structure of the two landscapes, or due to inherently dissimilar behavior of the butterflies inhabiting the two landscapes. The biological interpretation would be fundamentally different in these three cases, as they correspond to a sampling artifact, an ecological effect, and an evolutionary response to landscape structure, respectively. Furthermore, the size of the area included for the mark-recapture study can have a large effect especially on parameters relating to long-distance dispersal. Schneider (2003) compared five mark-recapture studies conducted on the same species of butterfly, and found quite strikingly that the estimated mean movement distance depended linearly on the size of the study area. A variety of methods have been proposed for correcting for these types of artifact. For example, Albanese et al. (2003) noted that in a typical study design short distances are sampled more frequently than long distances, and suggested that the resulting bias in movement estimates could be reduced by carefully constructed study designs. Yamamura et al. (2003) noted that, in studies where individuals need to be trapped for recapture, high trapping intensity in short distances can lower the amount of long-distance dispersal. The authors suggested that such a bias can be corrected for by arranging the traps in a regular lattice structure, and by making assumptions about random movement and constant settlement rate.

Due to the rapid development of computational methods such as Markov chain Monte Carlo (MCMC), likelihood-based estimation methods have become increasingly popular in a wide range of ecological research (Hobbs and Hilborn 2006). An approach that combines a process model with an observation model seems especially natural in the case of spatial mark-recapture data, as it allows one to account for an arbitrary study design, and should make it possible to derive unbiased dispersal estimates without additional correction factors. However, process-based modeling approaches are still scarce in spatial mark-recapture literature. An exception is given by Fujiwara et al. (2006), who built a maximum likelihood estimation scheme based on a stochastic model describing the movements and survival of individuals. In their model,

movement was modeled through a dispersal kernel with a scale parameter to be estimated. Fujiwara et al. (2006) applied the model to data on brown trout living in streams, and thus assumed a one-dimensional dispersal kernel, but the same approach would extend to two-dimensional domains as well. Another related approach is the virtual migration (VM) model, which uses a dispersal kernel to model movements between a set of habitat patches surrounded by so called matrix, i.e., unsuitable habitat (Hanski et al. 2000).

As dispersal kernels are typically radially symmetric and have no dependence on landscape structure, they are best suited for homogeneous environments or for species with passive propagule dispersal (Turchin 1998). However, it has been frequently observed that, especially in the case of actively moving animals, variation in landscape quality can have a large influence on movement patterns (e.g., Ricketts 2001, Levey et al. 2005). Schooley and Wiens (2004) studied the movements of cactus bug using a combination of mark-recapture methods and direct analysis of movement paths, and concluded that in a variable environment it is not possible to treat dispersal distances of a species as fixed traits independent of landscape structure.

As an attempt to model insect dispersal in heterogeneous landscapes, Ovaskainen (2004) developed a diffusion-based movement model that accounts for spatially varying movement and mortality rates, and for habitat selection at edges between habitat types. In this paper, our aim is to extend the maximum likelihood method of Ovaskainen (2004) to a full Bayesian approach, including the usage of posterior predictive distributions to assess the model fit. As the computational problem is very complex, we have developed flexible software (see Supplement) that can be used for parameter estimation, analysis of the resulting movement models, and generation of simulated data. We first briefly summarize the model, and describe an adaptive MCMC method that allows for computationally effective Bayesian parameter estimation. We then test the performance of the estimation scheme against simulated data, including a power analysis illustrating how accuracy in parameter estimates depends on the amount of data and the study design. Finally, we apply the estimation scheme to a real mark-recapture data set collected on the Glanville fritillary butterfly (*Melitaea cinxia*; Kuussaari et al. 1996). In this example, we illustrate how results derived by the present method compare with results derived earlier using a purely statistical approach.

MATERIAL AND METHODS

The model

We consider mark-recapture data collected from a landscape that is classified into a number of habitat types, which are a priori assumed to differ from each other in terms of the species behavior. The landscape is presented technically as a set of polygons, which form a

landscape layer that is used to define the process model. The observation model is defined by describing the spatiotemporal effort used to search for recaptures. We assume that a discrete set of sites is used for recapture, so that the search effort can be described through a matrix indexing which sites were searched at a given instance.

We assume that the movements of the individuals can be modeled by diffusion with habitat-specific movement and mortality rates, supplemented by habitat selection at edges between the habitat types (Ovaskainen and Cornell 2003, Ovaskainen 2004). Given that an individual is initially at time t_0 in a location $\mathbf{y} \in \mathbb{R}^2$, we denote the conditional probability density of the individual's location \mathbf{x} at time t by $v(\mathbf{x}, t; \mathbf{y}, t_0)$. The probability density v evolves as

$$\partial_t v(\mathbf{x}, t) = a(\mathbf{x})\Delta v(\mathbf{x}, t) - c(\mathbf{x})v(\mathbf{x}, t) \quad (1)$$

where ∂_t is the partial derivative with respect to time, Δ is the Laplacian given by second spatial derivatives, and the coefficients $a(\mathbf{x})$ (diffusion) and $c(\mathbf{x})$ (mortality) may depend on the habitat type at location \mathbf{x} . We assume for simplicity isotropic diffusion, and no deterministic drift (no term with first spatial derivative), but our methods are not restricted to these simplifications. Habitat selection is modeled by a discontinuity in the probability density across the edges between the habitat types, so that $v(\mathbf{x}, t; \mathbf{y}, t_0) = k(\mathbf{x})\hat{v}(\mathbf{x}, t; \mathbf{y}, t_0)$, where k describes the preference for a given habitat type, and \hat{v} is continuous across the edges. We utilize the method of Ovaskainen (2004) to calculate the likelihood of mark-recapture data for a given parameter set. Briefly, if a marked individual has been released to a location \mathbf{y} at time t_0 , the initial condition is given by a delta distribution concentrated at \mathbf{y} . The probability that the individual is at time $t > t_0$ in a region X is

$$P_X(t) = \int_X v(\mathbf{x}, t; \mathbf{y}, t_0) d\mathbf{x}. \quad (2)$$

Performing the integration over all space gives the probability that the individual is somewhere, i.e., that it has not died before time t . An approximation for P_X can be calculated using the finite-element method, which translates the partial differential equation into a large but sparse matrix equation (Ovaskainen 2004). Also searching for but not finding an individual modifies the probability density. Assuming that a site X is searched for without finding the individual, the probability density decreases in site X and increases outside the site X . The updating rules are based on a simple probability calculation, and they depend on the capture probability p , i.e., the probability of observing an individual while a site is searched, given that the individual actually was at the site (Ovaskainen 2004).

The main aim of this paper is to extend the maximum-likelihood estimation scheme of (Ovaskainen 2004) to a more flexible Bayesian framework. To do so, we assign a log-normal prior for all parameters that are restricted to

be positive (k , a , c), and a logit-normal prior for the capture probability $p \in (0, 1)$. We utilize a Markov chain Monte Carlo (MCMC) method, in which the posterior distribution is sampled using a simulation approach. To illustrate the size of the computational problem, assume that there are data for 10 time steps (e.g., days) and for 1000 individuals. If there are 10 parameters to be estimated, and if the MCMC is run for 10 000 iterations, the underlying matrix equation needs to be solved 10^9 times. To improve computational efficiency, we have replaced the iterative solver of Ovaskainen (2004) by a direct solver that utilizes the sparse Cholesky decomposition, and implemented adaptive methods as described below.

Adaptive MCMC

We apply Bayesian parameter estimation through the Metropolitan-Hastings MCMC algorithm, in which the parameters are updated either one by one, or in blocks (Gelman et al. 2004). We use log-normal (for k , a , c) or logit-normal (for p) proposal distributions, or corresponding multinormal distributions if parameters are updated in blocks. In order to obtain a sufficient mixing in the MCMC, a good choice of the proposal distribution is a necessity. We have implemented two methods that adjust the proposal in an adaptive manner.

The first method (to be called ACCEPT, from acceptance ratio) is based on adjusting the variance of the proposal distribution so that the acceptance ratio attains a prescribed value α^* . In the case of multinormal target and proposal distributions, the optimal acceptance ratio is about $\alpha^* = 0.44$ if a single parameter is updated, and it decreases to about $\alpha^* = 0.23$ if many parameters are updated in a block (Gelman et al. 2004). As the proposal distribution is modified after each iteration round, it is advantageous to base the adjustment on a recent acceptance ratio rather than the overall acceptance ratio since the first iteration round. We define the recent acceptance ratio after iteration round n as $\alpha_n = z_n/w_n$, where $z_n = \sum_{i=1}^n o_i r^{n-i}$ and $w_n = \sum_{i=1}^n r^{n-i}$, $r \leq 1$ is a damping ratio, and o_i is an indicator variable with $o_i = 1$ if the proposal was accepted at iteration round i and $o_i = 0$ otherwise. If the acceptance ratio is too high, the variance of the proposal distribution should be increased, whereas for an acceptance ratio that is too low, the variance should be decreased. This is done by multiplying the variance of the proposal distribution after each iteration round n by $q^{z_n - \alpha^*}$, where the parameter $q > 1$ describes how greedy the algorithm is. A large value of q leads to quick adaptation, but can also lead to oscillatory behavior, whereas a small value of q corresponds to a slower but more stable strategy. We used as defaults the parameter values $r = 0.9$ and $q = 2$. Note that z_n and w_n satisfy the recursions $z_n = rz_{n-1} + o_n$, $w_n = rw_{n-1} + 1$, and they may hence be updated with very limited computational cost.

While the ACCEPT method can be used to adjust the acceptance ratio close to an optimal one, it has the

drawback that it does not account for the covariance structure of the posterior distribution. To improve the mixing, highly correlated parameters should be updated in a block using a joint proposal that mimics the correlation structure of the posterior density. Haario et al. (2001) developed an adaptive method (called AM), in which the covariance matrix of the multinormal proposal distribution is set (after iteration round n) to

$$C_n = s_d \text{Cov}(X_1, \dots, X_n) + \varepsilon s_d \mathbf{I}_d \quad (3)$$

where d is the number of parameters in the block, X_i refers to the values of the d parameters at iteration round i , \mathbf{I}_d is the identity matrix, and $\varepsilon > 0$ is a small constant that ensures that the covariance matrix remains nonsingular. The parameter s_d is a scaling factor for which an optimal value (assuming multinormal distributions) is approximately $s_d = 2.4^2/d$ (Gelman et al. 2004).

While the AM method is superior to the ACCEPT method in the sense that it is able to account for the covariance structure of the posterior density, it is likely to initially mix poorly if the first proposal distribution is not very carefully selected. Haario et al. (2006) overcame this problem by developing a mixed method called DRAM, which combines delayed rejection (DR) with the adaptive method (AM). While the usage of the AM method ensures finding an asymptotically efficient proposal, the DR method can considerably shorten the burn-in period. We utilize a very similar idea by combining the ACCEPT algorithm with the AM algorithm as follows. First, we run the MCMC using the single-component ACCEPT algorithm for a short period such as 1000 iterations. While this period is likely to be too short for exploring the full posterior density, it provides information about the covariance structure, and this information can be utilized to construct a better proposal distribution. Based on this initial sample, we group the variables that are highly correlated with each other (e.g., correlation coefficient at least 0.85), and calculate the covariance matrices for each group based on Eq. 3. We then fix the proposal distribution for each block to the multinormal distribution defined by the covariance matrix, and run the MCMC again to obtain a sample from the posterior density. As this procedure resulted typically in a very good mixing in the final stage, a relatively short MCMC (e.g., 10 000 iterations) seemed usually sufficient.

In general, adaptive adjustment of the proposal distribution may make the MCMC fail to converge to the correct target distribution (Gelman et al. 2004). Haario et al. (2001) showed that, under certain conditions, the AM method converges to the correct target distribution even if the adaptation is continued throughout the computation. The strategy we have chosen is conservative in the sense that we adapt the proposal only during a burn in period, and fix it for the final sampling of the posterior density.

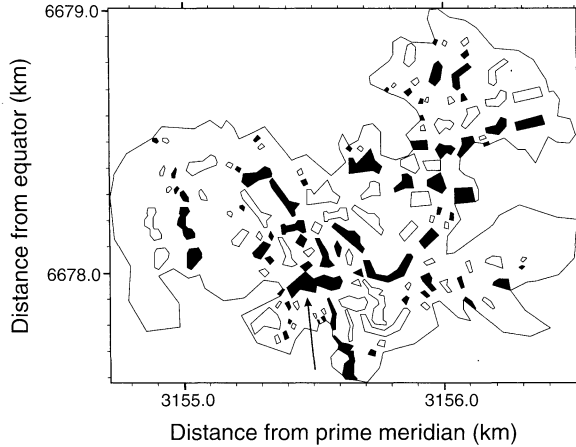


FIG. 1. Map of Husö island (part of the Åland Islands in southwest Finland). The landscape consists of 65 patches (black) and the unsuitable matrix (white). The duplicates of the habitat patches (black outlines with no fill) consist of matrix, and they are used as hypothetical mark–recapture sites when generating simulated data (see *Materials and methods: Simulated data*, designs D2 and D3). The patch indicated by the arrow had an exceptionally high density of nectar plants and is treated separately in the analysis of real data.

Simulated data

We used simulated data to conduct an analysis of statistical power, i.e., to examine how much and what kind of data are needed to achieve a given accuracy in the estimates of the model parameters. We generated data assuming the landscape shown in Fig. 1, from which the real data for the Glanville fritillary were collected. We generated the simulated data using the parameter values $k_h^* = 1$, $k_m^* = 0.01$, $a_h^* = a_m^* = 10^5 \text{ m}^2/\text{d}$, $c_h^* = c_m^* = 0.1 \text{ d}^{-1}$, and $p^* = 0.5$, where the subscripts refer to the habitat patches (h) and the matrix (m), and the star (*) indicates that these are the underlying “true” parameter values. We thus assumed that the density of individuals is a hundred times larger in the habitat patches than in the matrix, and that mortality rates and diffusion coefficients do not differ between the patches and the matrix. The mortality rate $c = 0.1 \text{ d}^{-1}$ corresponds to the mean lifetime of 10 days, and the diffusion coefficient would lead to an expected lifetime displacement of $r = (\pi/2)\sqrt{a/c} = 1571 \text{ m}$ in a homogeneous environment (Turchin 1998). These parameter values can be considered to be representative for many butterflies such as the Glanville fritillary. As the landscape is an isolated island, it is natural to assume reflecting boundary conditions.

We assumed that a number of marked individuals were released to the study area during the first day of a 20-day study period, and considered three possibilities for the study design. The basic design (D1) corresponds to the most common type of spatial mark–recapture study, in which marked individuals are initially released into the habitat patches, and searching for recaptures takes place solely in the habitat patches. We let the

release location rotate systematically over the 65 habitat patches, and assumed that all habitat patches were searched once per day, starting on day 2. In design D2, part of the searching was conducted in the matrix. To keep the searching effort identical to that of design D1, we duplicated the shape of each patch and placed the copy inside the matrix (Fig. 1). We assumed that on day 1 the patches 1, 3, 5, ... were searched, whereas for patches 2, 4, 6, ... the duplicate was searched. For day 2 we switched the patches for which the duplicate was searched, and continued the rotation so that each day half of the search effort took place in the matrix and half in the habitat patches. In design D3, all searching was conducted in the habitat patches, but we assumed that half of the individuals were released into the matrix. To do so, we assumed again that the release location rotated systematically over the 65 patches, but that in every second case the individual was released into the duplicate located in the matrix (Fig. 1) instead of the actual habitat patch. For each of the three study designs, we generated 10 replicates of four data sets, which consisted of 1, 10, 100, and 1000 individuals.

We considered two types of models when estimating the parameters back from simulated data. First, in model M1, we assumed a priori that $a_h = a_m$ and $c_h = c_m$, whereas in model M2 we relaxed this assumption by estimating the diffusion and mortality parameters separately for the matrix and for the patches. To examine the sensitivity of the posteriors to the prior distributions, we did not assume a prior centered around the true value, but assumed a prior for which the medians (0.025, 0.975 quantiles) were $k_m = 0.1$ (0.01, 1), $a_h = a_m = 10^4$ (10^3 , 10^5), $c_h = c_m = 0.2$ (0.1, 0.4), and $p = 0.3$ (0.1, 0.62). We calculated the posterior distributions using a combination of the ACCEPT and AM methods (1000 iterations for the adjustment of the proposal and 10 000 iterations to sample the posterior), and compared the results against the known true values.

The Glanville fritillary case study

Kuussaari et al. (1996) conducted an experimental introduction of the Glanville fritillary butterfly into the isolated island of Husö (Fig. 1) in the Åland archipelago in southwest Finland in 1992 (see Plate 1). The island was classified into 64 habitat patches based on the presence of the host plant *Plantago lanceolata* L. (subscript h), and the surrounding matrix (subscript m). The butterflies were collected as caterpillars from different parts of the main Åland Island, reared in outdoor cages, and moved into a house after pupation to synchronize the emergence. A total of 822 (427 males and 455 females) newly eclosed butterflies were marked individually and released into 16 habitat patches. Each of the 64 habitat patches was visited daily starting from day 2. On the sixth day, the researchers noticed that the butterflies were attracted to a patch with plenty of nectar plants but no host plants (shown by arrow in Fig. 1; subscript h*), and from that day on this patch was also

included in the survey. The mark–recapture study was continued for 14 days, and the data consist of 341 recaptures for males and 247 recaptures for females.

We estimated habitat preferences separately for the habitat patches (k_h), for the patch with nectar plants (k_{h^*}), and for the matrix (k_m). As only the relative values of the habitat preferences matter, we normalized the habitat preference for the habitat patches as $k_h = 1$. Diffusion (a_h and a_m) and mortality (c_h and c_m) were estimated separately for the patches (assuming no difference between habitat patches and the patch with nectar plants) and for the matrix. As the capture effort was kept constant per unit area (1 min/100 m²), we assumed that the capture probability p was equal for all patches. We assumed the relatively uninformative priors for which the medians (and 0.025 and 0.975 quantiles) were $k_m = 0.01$ (10^{-4} , 1), $k_{h^*} = 1$ (0.01, 100), $a_h = a_m = 10^5$ (10^3 , 10^7), $c_h = c_m = 0.1$ (0.01, 1), and $p = 0.5$ (0.1, 0.9). To examine possible differences between males and females, we modeled the data for the two sexes separately. As the butterflies avoid flying on top of water, we assumed reflecting boundary conditions around the island.

Software

We implemented the estimation schemes in two pieces of software, called Mapper and Disperse, both available in the Supplement. Mapper is a GIS-based interface for the triangulation of the layers representing the landscape and the set of mark–recapture sites. Triangulation is a prerequisite for finite element based methods implemented in Disperse. In addition to the adaptive MCMC methods (both AM and ACCEPT) for parameter estimation, Disperse can be used to generate simulated data and posterior predictive data. Disperse can also be used to calculate a variety of biologically relevant variables ranging from hitting probabilities to occupancy times (see Ovaskainen and Cornell 2003). Mapper can be used to visualize mark–recapture data and spatial variables such as the time evolution of the probability density v .

RESULTS

We first assess the performance of the estimation schemes based on simulated data, and then move on to the Glanville fritillary case study.

Performance of the estimation schemes

We estimated the posterior distributions for all simulated data sets using the combination of ACCEPT and AM methods described in *Materials and methods*. This resulted in very good mixing of the MCMC after the burn-in period (Fig. 2), in spite of the high (negative) correlation between the parameters k_m and a_m (Fig. 3e). During the burn-in (iteration rounds 1–1000), in which each parameter was updated in turn, the parameters k_m and a_m mixed very poorly. To keep the acceptance ratio

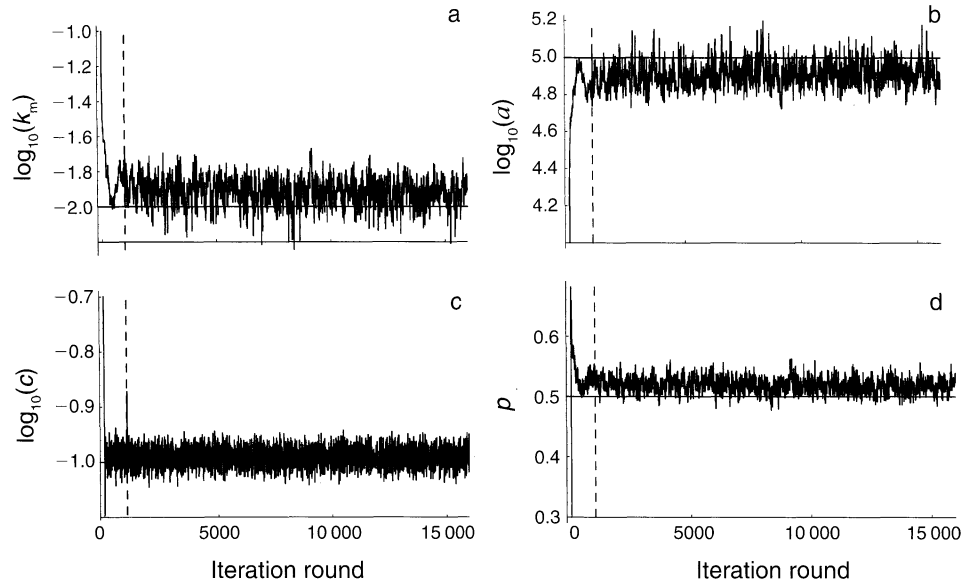


FIG. 2. Mixing of the Markov Chain Monte Carlo (MCMC) method based on adaptation of the proposal distribution using a combination of the ACCEPT and adaptive (AM) methods. The first 1000 iteration rounds were run with ACCEPT, all parameters being updated individually. The remaining 15000 steps (after the dashed vertical line) were based on grouping the parameters k_m (habitat preference for the matrix) and a_m (diffusion rate in the matrix), and fixing the proposal distributions based on the sample generated by iteration rounds 101–1000 using Eq. 3. The four panels illustrate the MCMC for the parameters (a) k_m , (b) a , (c) mortality (c), and (d) capture probability (p). Data were generated using design D1 for 1000 individuals; parameters were back estimated assuming model M1. The initial proposal distribution (before adaptation) was set to the prior distribution. Horizontal lines depict the true parameter values.

sufficiently high, ACCEPT greatly decreased the variance in the proposal distributions for these two parameters. This resulted in very small jumps between the iteration rounds, and hence ACCEPT failed to explore rapidly the full parameter space. However, the sample collected by ACCEPT led to a good approximation of the covariance structure of the joint posterior distribution. After the covariance structure was accounted for by grouping the parameters k_m and a_m (iterations 1001–11000), mixing of the chain was dramatically improved (Fig. 2a, b). In contrast, the other model parameters were not highly correlated in the posterior density, and they mixed well also when updated individually (Fig. 2c, d).

The marginal posterior densities for both models M1 and M2 are compared with the prior densities and with the true values in Fig. 3 for single replicates of data consisting of 1, 10, 100, and 1000 individuals constructed by design D1. As expected, when the data consist of a single individual the posteriors are very similar to the priors, but with an increasing amount of data the posteriors center around the true values with increasing confidence. For model M2, diffusion (a) can be estimated reliably only for the matrix, as the patches are so small that it is not possible to infer within patch movement rates from this kind of data. On the other hand, mortality (c) can be estimated reliably only for the patches, as the individuals spend only a small fraction of their time in the matrix. While the data contain very limited resolution to estimate the parameters a_h and c_m ,

we note that their inclusion in the model did not affect the estimates for the other parameters greatly. As the amount of data increases, the parameters k_m and a_m become highly negatively correlated with each other (Fig. 3e). Thus, while there is not enough resolution in the data for accurate estimation of these two parameters separately, there is much more information about their joint distribution. In other words, it is hard to disentangle whether the individuals go seldom to the matrix and move there fast, or if they go frequently to the matrix and move there slowly. Indeed, both options could result in the same number of observed movements between the habitat patches.

We constructed designs D2 and D3 to examine whether it is possible to better disentangle the parameters k_m and a_m by performing part of the searching in the matrix (D2), or by releasing some of the individuals into the matrix (D3). Design D2 is expected to provide direct information about the parameter k_m , whereas design D3 is expected to provide direct information about the parameter a_m . Searching in the matrix resulted in only a few recaptures, and hence the total number of recaptures was smallest in design D2. The mean number of recaptures per individual within the patches (\pm SE over the 10 replicates with 1000 individuals) was 3.65 (\pm 0.03), 1.84 (\pm 0.02), and 3.58 (\pm 0.03) in designs D1, D2, and D3, respectively. In design D2, 0.016 (\pm 0.001) recaptures per individual were in addition obtained in the matrix. We note that while in design D3 some of the individuals may have been lost in

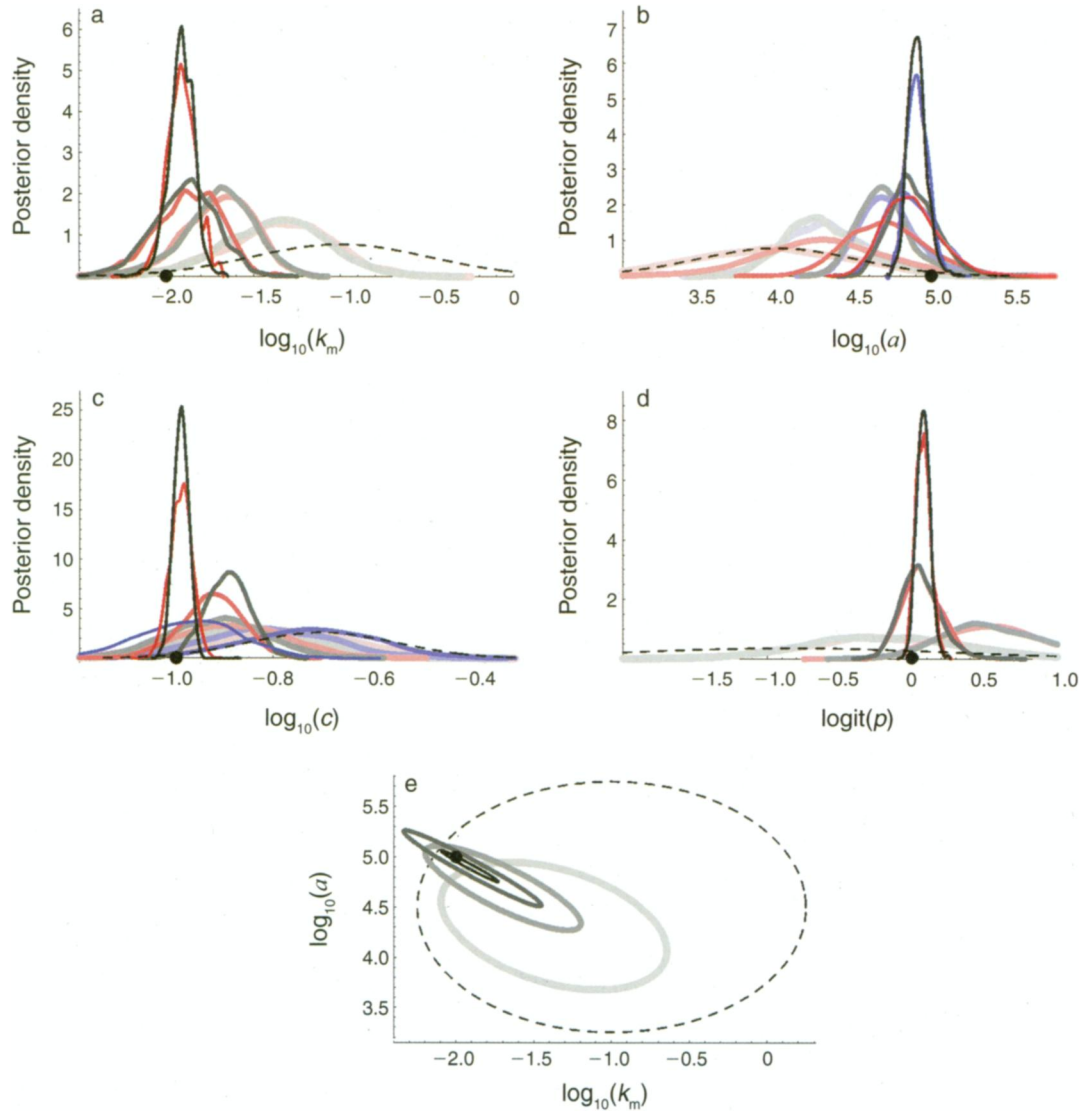


FIG. 3. Marginal posterior densities of model parameters for Design D1. The five panels depict the parameters (a) k_m (relative density in the matrix), (b) a_m and a_h (diffusion rate in the matrix and in the habitat patches), (c) c_m (mortality rate in the matrix) and c_h (mortality rate in the habitat patches), (d) p , and (e) the 95% ellipsoidal quantile of the joint distribution of parameters k_m and a_m . The lines from light and thick to dark and thin correspond to simulated data (a single replicate) with 1, 10, 100, and 1000 individuals, respectively. The gray lines correspond to model M1, and the red (parameters k_m , a_h , c_h , p) and blue (parameters a_m , c_m) lines to model M2. The solid circle on each x-axis depicts the true value used in data generation, and the dashed lines show the prior distributions.

the matrix before they reached any of the habitat patches, in the relatively dense network of patches (Fig. 1) there was no great reduction in the total number of recaptures.

Somewhat surprisingly, the possibility to obtain direct information about the density of individuals in the matrix compensated well for the lower recapture rate, and design D2 performed best in the estimation of the most difficult parameters k_m and a_m (Fig. 4a, b). With respect to these parameters, also the design D3 slightly outperformed the basic design D1 for a sample size of 100 individuals (Fig. 4a, b). With respect to estimation

of mortality and capture probability, the three designs performed in a very similar manner (Fig. 4c, d).

The Glanville fritillary case study

Fig. 5 shows the marginal posterior distributions of the model parameters based on the real mark-recapture data on the Glanville fritillary butterfly. The median value of parameter k_m suggests that the density of individuals was about 1000 times larger in the patches than in the matrix, the results being almost identical for the two sexes. Males clearly preferred the exceptional patch with a high density of nectar plants [$P(k_h > 1) >$

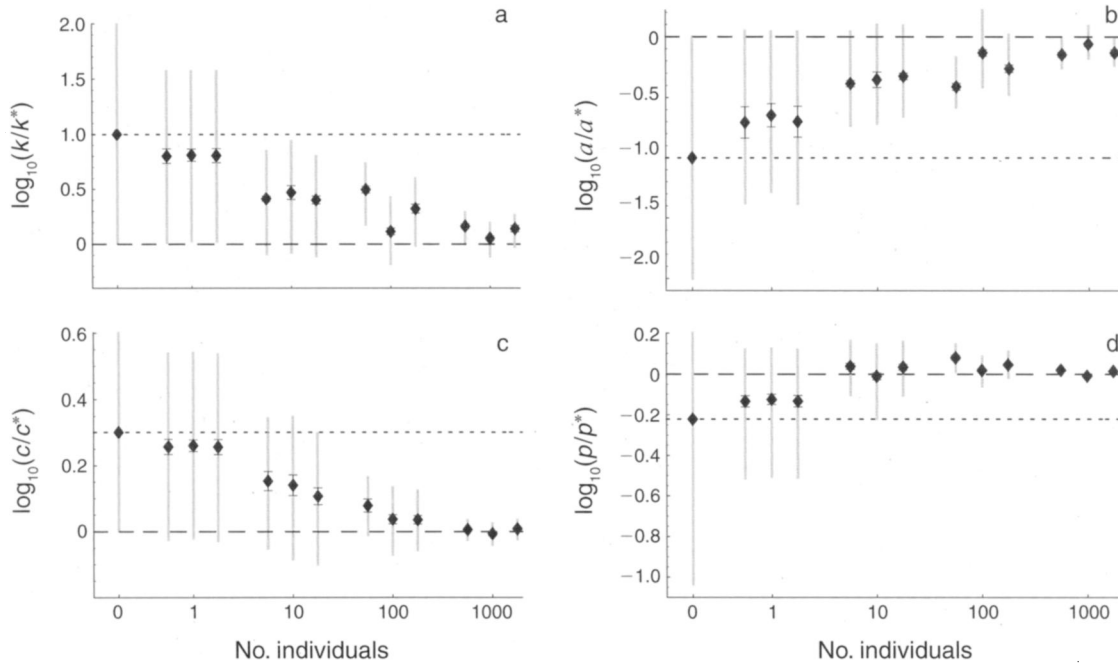


FIG. 4. Comparison between the posterior densities obtained for the three study designs assuming model M1. The accuracy of the posterior density is measured as the ratio of the estimated value and the underlying true value [term followed by an asterisk (*)]. The four panels refer to the parameters (a) k_m , (b) $a_m = a_h$, (c) $c_m = c_h$, and (d) p . The three sets of results refer to designs D1, D2, and D3 (from left to right), each based on 10 replicates. The solid diamonds and error bars show the mean and standard error (over the 10 replicates) of the median estimate. The gray bars show the mean (over the 10 replicates) of the 95% highest posterior density interval. A point at the dashed line corresponds to an unbiased estimate; a point above (or below) implies that the parameter value is overestimated (or underestimated). The dotted line corresponds to the median of the prior.

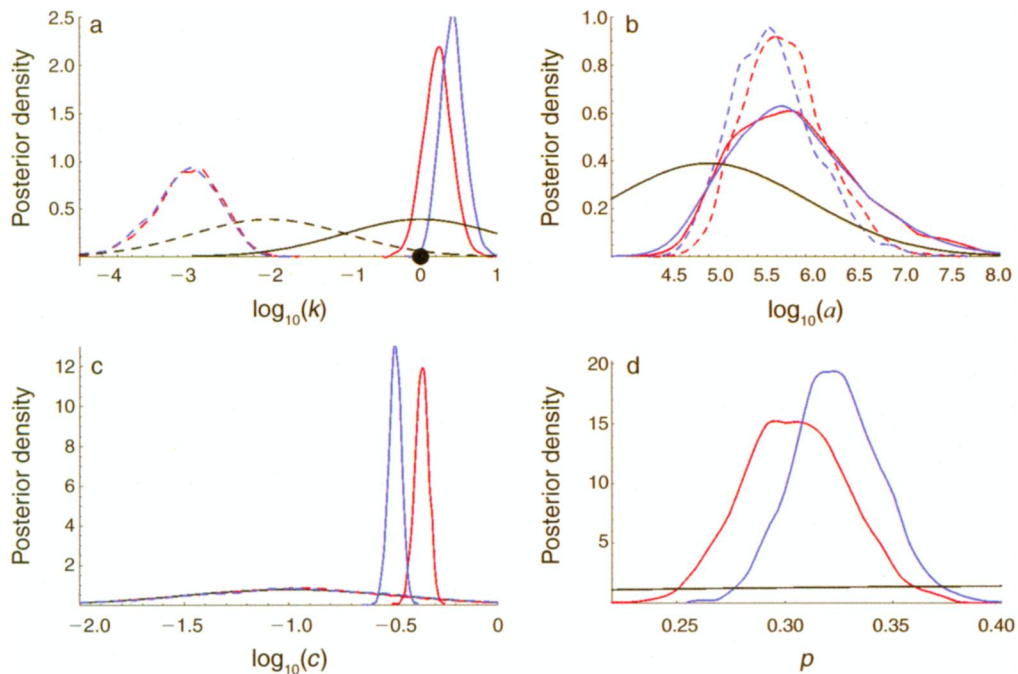


FIG. 5. Marginal posterior densities for model parameters based on data on the Glanville fritillary butterfly (*Melitaea cinxia*). The four panels depict the parameters (a) k_m, k_h, k_r , (b) a_m, a_h , (c) c_m, c_h , and (d) p . Red lines correspond to females, blue lines to males, and black lines to prior distributions. Dashed lines correspond to parameters referring to the matrix (k_m, a_m, c_m), and solid lines correspond to habitat patches, except in panel (a), where the solid lines correspond to the patch with high density of nectar plants, and the solid circle indicates the actual habitat patches (scaled to 1).

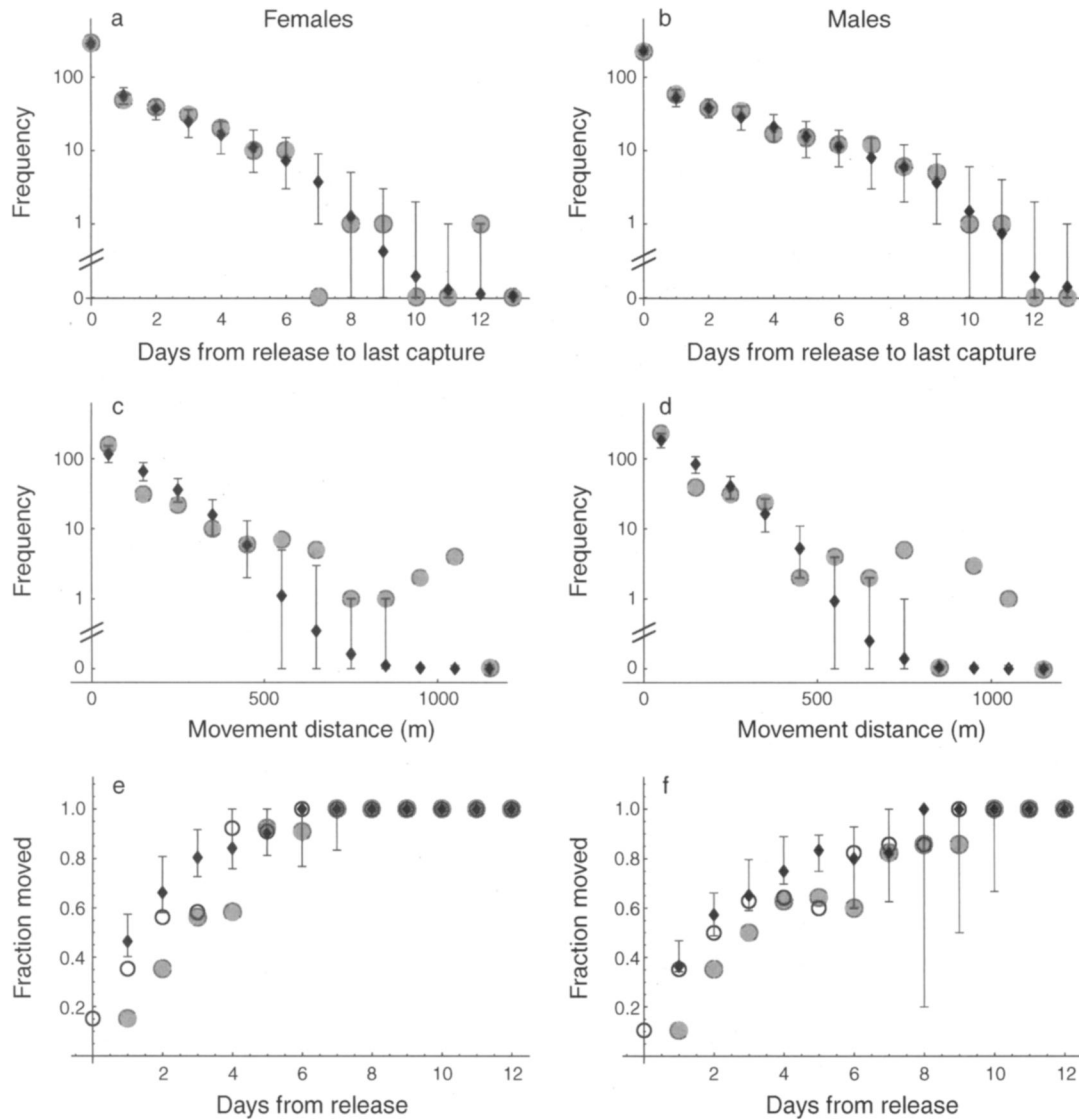


FIG. 6. Model fit for the Glanville fritillary data (females, left; males, right). Gray dots depict the real data; black dots with error bars show the mean and 95% highest posterior density interval of the predictive posterior distributions. Panels (a) and (b) show the distribution of the number of days between first and last capture, panels (c) and (d) show the distribution of observed movement distances, and panels (e) and (f) show the fraction of individuals that have been observed to move between habitat patches. The open circles in panels (e) and (f) represent the real data shifted by one day.

0.99], whereas for females the posterior probability was somewhat smaller [$P(k_h > 1) = 0.88$]. As with simulated data, diffusion could be estimated reliably only for the matrix and mortality only for the habitat patches. There was no difference between the two sexes in terms of their diffusion rate, but mortality was much higher for females (median estimate $c_h^F = 0.44 \text{ d}^{-1}$) than for males (median estimate $c_h^M = 0.32 \text{ d}^{-1}$), the difference being well established in the posterior, $P(c_h^F > c_h^M) > 0.99$. Capture probability was somewhat greater for males (median estimate 0.32) than for females (median estimate 0.30), $P(p^M > p^F) = 0.89$. As was the case with simulated data, the posteriors are much more concentrated than the priors for mortality and capture

probability, whereas habitat preferences and diffusion rates were more difficult to estimate.

The fit of the model is examined in Fig. 6, which compares the data against predictive posterior distributions. We note that as we use the same data for parameter estimation and for model validation, our check of model fit is not about the generality of the estimated parameter values, but about the validity of the structural model assumptions. For example, the upper panels show that the model prediction is consistent with the data for the distribution of days from release to last recapture. This suggests that the assumption of constant mortality rate is in line with these data. The middle panels show a slight bias in the distribution of observed

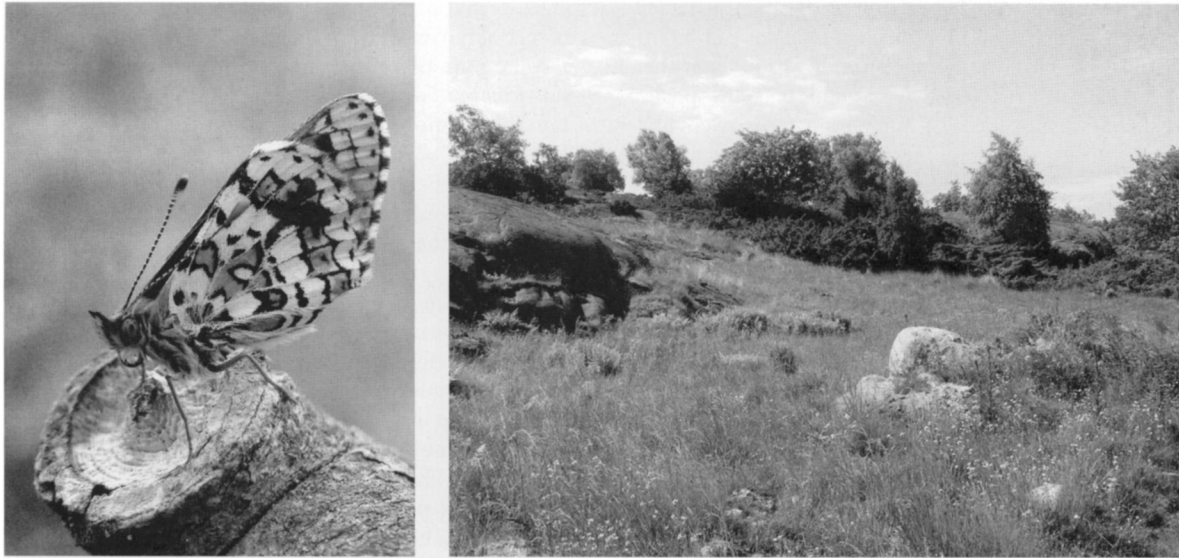


PLATE 1. (Left) A Glanville fritillary butterfly used in a mark–recapture experiment. (Right) A Glanville fritillary butterfly habitat patch on Husö Island, southwest Finland. Photo credits: Pave Väisänen.

movement distances, the model underestimating the frequency of individuals that stayed in the same patch (included in distance class 0–100 m), and the frequency of very long movements. The lower panels illustrate that while the model assumes that the individuals started the dispersal phase right after the release, both females and males tended to stay in the release patch for a while before they started moving. The bias may be partly explained by the fact that the individuals were released in the evening, and thus the time until the first search for recaptures did not include a full day. However, the bias remains even if the data are shifted conservatively by one full day (open circles in Fig. 6e, f).

DISCUSSION

The diffusion model provides a simple but reasonably realistic spatial reference model, which can be used to extract information from mark–recapture data in two ways. First, the posterior distribution provides direct information about the underlying parameters such as movement and mortality rates. Second, the agreement or disagreement between the real data and the posterior predictive distribution can be used to examine how the observed movement behavior deviates from the null hypothesis of random walk. As the modeling approach described here separates the movement process from the observation process, it makes it possible to disentangle the inherent movement behavior of the species from possible sampling artifact, leading to more robust and refined inferences compared to what could be obtained by straightforward statistical approaches. We next illustrate these points by comparing the original results of Kuussaari et al. (1996) on the Glanville fritillary to the results obtained here.

To start with, Kuussaari et al. (1996) noted that a larger fraction of males than females was recaptured. This could be explained by the capture probability being higher for males, the males living longer, or the males spending less time in the unsearched matrix. Based on the differences in the posterior densities for the two sexes, we conclude that the major factor was likely to be the longer lifetime of males (Fig. 5c). Additionally, the males appeared to have a somewhat higher capture probability (Fig. 5d).

Kuussaari et al. (1996) concluded that the two sexes behaved differently with respect to the timing of emigration. They defined the emigration rate as the fraction of individuals (out of all captured individuals) that were found outside their natal patch. Drawing a figure similar to our Fig. 6e, f, they found that emigration rate increased as a function of time since release similarly for the two sexes for the first four days. However, the two sexes differed in that, while almost all females did emigrate from the natal patch within a week from the release, a fraction of the males seemed to remain in their natal patch. Our analyses illustrate additionally that the emigration rate did not remain constant, but increased for both sexes with age. This is revealed by Fig. 6e, f, which show that a model assuming an age-independent movement rate overestimates the amount of between-patch movements during the first five days. Starting the between-patch movements only after five days makes biological sense, as it gives the individuals time to reproduce in their natal patch before taking the risk of entering the matrix to search for the other patches. Bergman and Landin (2002) observed a similar behavior in the butterfly *Lopinga achine*, where females typically moved only after laying two-thirds of their eggs in the natal site.

Kuussaari et al. (1996) reported that males seemed to move somewhat shorter distances (mean 311 m) than females (403 m), though their result was not statistically significant ($P = 0.093$). We found that the posterior distributions for the diffusion parameter a_m were almost identical for the two sexes (Fig. 5b), the one for the females suggesting only slightly greater values. Thus our analyses would suggest that males and females do not differ greatly in their inherent movement behavior. However, a small difference showing shorter movement distances for males than for females is seen also in the posterior predictive distributions. In the case of males, the median distance between two captures (and its 95% highest posterior density interval [HPDI] based on the 1000 samples from the predictive posterior distribution) was 161 m (134, 187), whereas the corresponding figure for females was 187 m (152, 201). In addition to the slightly greater diffusion rate for the females, this is explained by the fact that males had a somewhat greater capture probability. As they were captured more frequently, the distances between consecutive captures were likely to remain smaller.

The mortality rates estimated here suggest an average lifetime of only a few days. This is in contrast to many other studies on the Glanville fritillary, which have reported mean lifetimes up to almost two weeks (e.g., Hanski et al. 2006). The high mortality rate is likely to be explained by the exceptionally hot weather during the mark-recapture study (Kuussaari et al. 1996), which made the butterflies very active, and may have led to dehydration due to poor availability of nectar. We note that the model assumption of age-independent death rate was in agreement with the data, as there is no bias in Fig. 6a, b. This may be partly explained by the fact that most individuals had much shorter lives than would be their maximal life span, and hence possible effects of senescence were not realized in these data.

We found that the model prediction deviated from the real data in terms of the distribution of observed movement distances, as the real data contain a higher frequency of very short and very long movement distances than predicted by the model (Fig. 6c, d). The likely explanation for the leptokurtic shape of the distribution of movement distances is a combination of several factors. First, variation among individuals is likely to play a major role, as Glanville fritillaries show great variation in terms of their flight ability, largely based on differences in their metabolic performance (Hanski et al. 2004, 2006). Second, Van Dyck and Baguette (2005) asked whether between-patch movements result from "routine movements" due to accidental drifting out from the habitat patches, or whether they are "special movements" based on an active decision to leave. In the diffusion based model considered here, emigration rate is based on edge-mediated behavior, which can be viewed to result either from routine movements or from special movements. However, the age-dependence in the emigration rate (Fig. 6e, f)

suggests that between-patch movements may arise partly as special movements, or that between-patch movements may be part of routine movement behavior for older individuals. Even if individuals were identical, age-dependent mobility could result in a leptokurtic distribution of movement distances due to random variation in the individual's lifetime. Third, we assumed here a relatively simple description of the landscape, considering the unsuitable matrix as a single homogeneous habitat type. In reality the matrix is heterogeneous, and may contain linear elements such as road sides which can act as dispersal corridors leading to occasional long-distance movements.

We used simulated data to ask what kind of a study design would be optimal in terms of providing most accurate parameter estimates for a given effort in the field. As was illustrated both for simulated and real data, estimation of the nonspatial parameters (mortality and capture probability) was much easier than estimation of the spatial parameters (movement rates and habitat preferences). The strong negative correlation between the parameters a_m and k_m provided a technical challenge, as we needed to develop adaptive methods to adjust the proposal distribution before a good mixing was obtained in the MCMC. The correlation led also to a difficulty in the interpretation of the posterior densities, as the marginal distributions of the parameters a_m and k_m remained relatively uninformative. This is not very surprising, as the basic mark-recapture design (D1) does not contain any direct information about the relative density of the individuals in the matrix. We tested with simulated data whether it would be possible to better separate between these parameters by either performing part of the searching in the matrix (D2) or by releasing some of the individuals into the matrix (D3). Our initial expectation was that design D3 would be superior, as it gives direct information about movement rate in the matrix without compromising greatly the number of recaptures. Somewhat surprisingly, design D2 turned out to give the most unbiased estimates, although the total number of recaptures was only half of that of designs D1 and D3. That D3 did not perform much better than D1 is likely to be explained by the fact that with the assumed parameter values a majority of the individuals did move between the patches in both designs. If only a small fraction of the individuals would emigrate from their natal patch, design D3 would be expected to lead to a much larger number of observed movements and hence outperform design D1.

The idea of measuring movement rates by releasing individuals into the matrix has been used in a number of mark-recapture studies. For example, Harrison (1989) noted that the Bay checkerspot butterfly tends to leave its habitat so infrequently that it is impractical to measure spontaneous interpatch movements, and released individuals into matrix at varying distances (0–5.6 km) from a target habitat patch. Jonsen et al. (2001) released

individuals of a flea beetle into two matrix types 100–200 m from a target patch to study whether movement rates were different between the matrix types, and Hein et al. (2005) released grasshoppers into the matrix to study whether individuals were able to detect their preferred habitat from a distance. In contrast, direct searching of the matrix has not been often done for the obvious reason that it results only in a very limited number of recaptures, and hence does not seem cost effective. However, as illustrated by the good performance of design D2, also quantifying how rarely individuals are found in the matrix is valuable data. While such data provide direct resolution to estimate the density of individuals in the matrix, they also indirectly facilitate the estimation of other parameters such as the movement rates. Our results hence suggest that using a fraction of the search effort in the matrix may actually be cost-effective. An alternative is to use other types of data (e.g., transect counts) to obtain an estimate (or upper bound) for the density of the individuals in the matrix, which information can be included in the prior distribution.

In this paper, we have extended the maximum likelihood (ML) method of Ovaskainen (2004) to a full Bayesian approach. In the Appendix, we compare the numerical results obtained by these methods in the case of the false heath fritillary butterfly data considered in Ovaskainen (2004). While the two methods can be considered very similar in the sense that they are both based on the same likelihood expression, they have some important differences. First, the Bayesian approach allows one to also incorporate prior information on the model parameters that are to be estimated. Second, the Bayesian credibility intervals and the confidence intervals derived in the case of ML estimation (based on bootstrapping in Ovaskainen [2004]) have completely different meanings in statistical inference. The Bayesian credibility intervals provide a direct probabilistic evaluation of the “true” values of the model parameters given the observed data, whereas the confidence limits obtained by bootstrapping refer to sample variability in repeated sampling under similar circumstances. Third, an advantage of the Bayesian inferential methods used here is that they allow one to directly consider joint distributions of all model parameters of interest, thereby marginalizing, in each case, over the “nuisance parameters” that are left out.

The main assumption behind the diffusion model is that of a Markov process, i.e., that an individual's future behavior does not depend on its past behavior. While this assumption may be violated for species with good learning capabilities, for many species of insects in particular it provides a natural null model against which more sophisticated behaviors can be tested. Other structural model assumptions that we have made include those of exchangeable individuals, constant environmental conditions, and no spatial or temporal variation in capture rate. Accounting for various sources of variation has become an integral part of the analysis of

nonspatial mark–recapture data (Lebreton et al. 1992, Schwarz and Seber 1999). A challenge for the future is to develop hierarchical Bayesian approaches including both random effects and covariates in the context of spatially referenced mark–recapture data.

ACKNOWLEDGMENTS

We thank Ilkka Hanski, Phil Harrison, Ken Newman, and an anonymous referee for helpful comments. The Academy of Finland is thanked for funding (grants 213457 and 211173).

LITERATURE CITED

- Albanese, B., P. L. Angermeier, and C. Gowan. 2003. Designing mark–recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. *Transactions of the American Fisheries Society* 132:925–939.
- Bancroft, J. S., and M. T. Smith. 2005. Dispersal and influences on movement for *Anoplophora glabripennis* calculated from individual mark–recapture. *Entomologia Experimentalis et Applicata* 116:83–92.
- Bergman, K. O., and J. Landin. 2002. Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation* 108:361–369.
- Breton, A. R., A. W. Diamond, and S. W. Kress. 2006. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) metapopulation. *Ecological Monographs* 76:133–149.
- Casula, P. 2006. Evaluating hypotheses about dispersal in a vulnerable butterfly. *Ecological Research* 21:263–270.
- Chen, D. G., and Y. S. Xiao. 2006. A general model for analyzing data from mark–recapture experiments with an application to the Pacific halibut. *Environmental and Ecological Statistics* 13:149–161.
- Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. 2001. *Dispersal*. Oxford University Press, Oxford, UK.
- Fujiwara, M., K. E. Anderson, M. G. Neubert, and H. Caswell. 2006. On the estimation of dispersal kernels from individual mark–recapture data. *Environmental and Ecological Statistics* 13:183–197.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian data analysis*. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Haario, H., M. Laine, A. Mira, and E. Saksman. 2006. DRAM: Efficient adaptive MCMC. *Statistics and Computing* 16:339–354.
- Haario, H., E. Saksman, and J. Tamminen. 2001. An adaptive metropolis algorithm. *Bernoulli* 7:223–242.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, New York, New York, USA.
- Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81:239–251.
- Hanski, I., C. Erälahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7:958–966.
- Hanski, I., and O. Gaggiotti, editors. 2004. *Ecology, genetics, and evolution in metapopulations*. Academic Press, London, UK.
- Hanski, I., M. Saastamoinen, and O. Ovaskainen. 2006. Dispersal-related life-history trade-offs in a butterfly metapopulation. *Journal of Animal Ecology* 75:91–100.
- Harrison, S. 1989. Long-distance dispersal and colonization in the Bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* 70:1236–1243.

- Hein, S., H. J. Poethke, and T. Hovestadt. 2005. Computer-generated null models as an approach to detect perceptual range in mark–re-sight studies: an example with grasshoppers. *Ecological Entomology* 30:225–233.
- Hobbs, N. T., and R. Hilborn. 2006. Alternatives to statistical hypothesis testing in ecology: a guide to self teaching. *Ecological Applications* 16:5–19.
- Jonsen, I. D., R. S. Bouchier, and J. Roland. 2001. The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge patches. *Oecologia* 127:287–294.
- Kendall, W. L., and J. D. Nichols. 2004. On the estimation of dispersal and movement of birds. *Condor* 106:720–731.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* 65:791–801.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton, J. D., and R. Pradel. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics* 29:353–369.
- Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309:146–148.
- Maciel-De-Freitas, R., R. Brocki, J. M. Goncalves, C. T. Codeco, and R. Lourenco-De-Oliveira. 2006. Movement of dengue vectors between the human modified environment and an urban forest in Rio de Janeiro. *Journal of Medical Entomology* 43:1112–1120.
- Mennechez, G., N. Schtickzelle, and M. Baguette. 2003. Metapopulation dynamics of the bog fritillary butterfly: comparison of demographic parameters and dispersal between a continuous and a highly fragmented landscape. *Landscape Ecology* 18:279–291.
- Ovaskainen, O. 2004. Habitat-specific movement parameters estimated using mark–recapture data and a diffusion model. *Ecology* 85:242–257.
- Ovaskainen, O., and S. J. Cornell. 2003. Biased movement at a boundary and conditional occupancy times for diffusion processes. *Journal of Applied Probability* 40:557–580.
- Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- Schneider, C. 2003. The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecological Entomology* 28:252–256.
- Schooley, R. L., and J. A. Wiens. 2004. Movements of cactus bugs: patch transfers, matrix resistance, and edge permeability. *Landscape Ecology* 19:801–810.
- Schtickzelle, N., G. Mennechez, and M. Baguette. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87:1057–1065.
- Schwarz, C. J., and G. A. F. Seber. 1999. Estimating animal abundance: review III. *Statistical Science* 14:427–456.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- Van Dyck, H., and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- Varkonyi, G., M. Kuussaari, and H. Lappalainen. 2003. Use of forest corridors by boreal *Xestia* moths. *Oecologia* 137:466–474.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Yamamura, K., M. Kishita, N. Arakaki, F. Kawamura, and Y. Sadoyama. 2003. Estimation of dispersal distance by mark–recapture experiments using traps: correction of bias caused by the artificial removal by traps. *Population Ecology* 45:149–155.

APPENDIX

A comparison between the maximum likelihood and Bayesian approaches (*Ecological Archives* E089-029-A1).

SUPPLEMENT

Software for estimating movement parameters from spatially referenced mark–recapture data (*Ecological Archives* E089-029-S1).