

Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly

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Abstract. The complexity of mathematical models of ecological dynamics varies greatly, and it is often difficult to judge what would be the optimal level of complexity in a particular case. Here we compare the parameter estimates, model fits, and predictive abilities of **two models of metapopulation dynamics**: a detailed individual-based model (IBM) and a population-based stochastic patch occupancy model (SPOM) derived from the IBM. The two models were fitted to a 17-year time series of data for the Glanville fritillary butterfly (*Melitaea cinxia*) inhabiting a network of 72 small meadows. The data consisted of biannual counts of larval groups (IBM) and the annual presence or absence of local populations (SPOM). The models were fitted using a Bayesian state-space approach with a hierarchical random effect structure to account for observational, demographic, and environmental stochasticities. The detection probability of larval groups (IBM) and the probability of false zeros of local populations (SPOM) in the observation models were simultaneously estimated from the time-series data and independent control data. Prior distributions for dispersal parameters were obtained from a separate analysis of mark–recapture data. Both models fitted the data about equally, but the results were more precise for the IBM than for the SPOM. The two models yielded similar estimates for a random effect parameter describing habitat quality in each patch, which were correlated with independent empirical measures of habitat quality. The modeling results showed that variation in habitat quality influenced patch occupancy more through the effects on movement behavior at patch edges than on carrying capacity, whereas the latter influenced the mean population size in occupied patches. The IBM and the SPOM explained 63% and 45%, respectively, of the observed variation in the fraction of occupied habitat area among 75 independent patch networks not used in parameter estimation. We conclude that, while carefully constructed, detailed models can have better predictive ability than simple models, this advantage comes with the cost of greatly increased data requirements and computational challenges. Our results illustrate how complex models can be helpful in facilitating the construction of effective simpler models.

Key words: Bayesian estimation; cross-validation; diffusion; dispersal; habitat quality; individual-based model (IBM); Markov chain Monte Carlo (MCMC); mark–recapture; *Melitaea cinxia*; random effects; state-space model (SSM); stochastic patch occupancy model (SPOM).

INTRODUCTION

The complexity of mathematical models employed in ecology varies greatly, and it is often difficult to judge in advance which level of complexity would strike the optimal balance between the conceptual clarity of simple models and the apparent realism and potentially greater predictive power of complex models. Greater complexity typically involves additional assumptions that provide flexibility, but complex models are often criticized because the large number of parameters rarely can be rigorously estimated and structural model assumptions are difficult to test (LaDeau 2010, Lavine 2010, Lele

2010, Waller 2010). Simple models do not account for all relevant sources of uncertainty (Clark 2003, Buckland et al. 2004), including uncertainty concerning empirical observations, which compromises the predictive power of the models (Calder et al. 2003, Harwood and Stokes 2003). On the other hand, overly complex models can also perform poorly (Adkison 2009).

In the case of metapopulation dynamics, ecologists have used a range of modeling approaches from general but very simple models, such as the classic Levins model (Levins 1969, 1970), to very specific and complex simulation models, such as RAMAS/metapop (Witte-man and Gilpin 1995), which have been used to predict the dynamics of metapopulations for management and conservation purposes (Akçakaya and Sjögren-Gulve 2000). In the middle ground there is a family of models called stochastic patch occupancy models, SPOMs (ter Braak and Etienne 2003, Moilanen 2004, Ovaskainen and Hanski 2004b), which aim at a compromise between

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generality and realism. SPOMs can be either defined statistically or derived from an underlying individual-based model, IBM (Ovaskainen and Hanski 2004a). Technically, a discrete-time SPOM is a homogeneous first-order Markov chain in which the occupancy states of local populations in the metapopulation at one point in time depend only on the occupancy states of the local populations in the previous time point (Moilanen 2004).

SPOMs can be supplemented with assumptions about the influence of the spatial configuration of the habitat patch network on the processes of local extinction and colonization, which leads to models that have been called “spatially realistic” (Hanski 2001) and can be parameterized with data from real metapopulations (Hanski 1984, Etienne et al. 2004, Moilanen 2004). These models typically assume that the probability of local extinction is a decreasing function of patch area, on the assumptions that large patches tend to have large populations when occupied, and the colonization probability of an unoccupied patch is an increasing function of connectivity to existing local populations (Ovaskainen and Hanski 2004b). With additional assumptions, one may incorporate into SPOMs, albeit in a nonmechanistic manner, the rescue effect (reduced extinction risk due to immigration) and regional stochasticity, and one may include in the parameter estimation the probability of occupied patches being recorded as unoccupied (Moilanen 2004).

The main simplifying feature of SPOMs is that local population dynamics are modeled only in terms of habitat patches being either occupied or unoccupied, a feature that greatly facilitates mathematical analysis and model fitting procedures. A drawback of the SPOM approach is that it is difficult to utilize individual-based data, which are often available, for example, on individual movements among local populations (Petit et al. 2001) and on various environmental factors that influence local dynamics (Hanski and Meyke 2005). However, such information can be utilized for parameterizing SPOMs if the model has been derived from an appropriate IBM by integrating out the extra life-history stages but retaining the underlying assumptions of the IBM. Such a SPOM, which we shall examine in this paper, is more realistic than a SPOM defined based on more phenomenological assumptions (Ovaskainen and Hanski 2004b). More generally, model simplification through integrating out intermediate states over space, time, or age class is one example of the array of mathematical and statistical methods available for linking simple and complex models of the same phenomenon (Fahse et al. 1998, Pascual and Levin 1999, Ngoc et al. 2008, Pagel et al. 2008).

Here, we construct metapopulation models for the Glanville fritillary butterfly (*Melitaea cinxia*), which has a large and well-studied metapopulation in Finland and for which data are available for nearly 20 years (Hanski 1999a, Nieminen et al. 2004). We first construct an IBM that is tailored to the life history of the Glanville

fritillary and that takes into account the various sources of information that are available. We then derive the respective SPOM by appropriate simplification of the IBM. The two models are fitted to the data using computer-intensive Bayesian modeling, which allows the parameterization of nonlinear and high-dimensional models and the use of prior information from previous studies (Clark 2005). We employ the state-space modeling approach, which allows the inclusion of all major sources of uncertainty in the modeling (Buckland et al. 2004), including observational uncertainty that is difficult to account for in traditional models (Clark 2003). A further advantage of the Bayesian approach is that the posterior distribution describes parameter uncertainty simultaneously for the joint distribution of all model parameters, and it thus identifies parameters that cannot be identified alone but can be identified conditional on the values of some other parameters.

We show that the IBM and the SPOM fit the data equally well, which is expected as the SPOM is derived from the IBM and thus shares the same structural assumptions. However, the IBM leads to more precise predictions, which is also expected, because the IBM utilizes more information (abundance data) than the SPOM (presence-absence data only) in parameter estimation. Previous studies on the Glanville fritillary have shown that habitat quality, e.g., the availability of host plants and nectar plants, influences migration (Kuussaari et al. 1996), establishment of new populations (Austin et al. 2011), and habitat patch occupancy (Hanski 1999b). Here we model spatial variation in habitat quality through a random effect. We show that the IBM and the SPOM yield very similar estimates of habitat quality, and that these estimates correlate with independent, direct measures of habitat quality. Importantly, the modeling approach enables us to ask why habitat quality matters. The results show that habitat quality influences patch occupancy mainly through movement behavior, whereas it influences population size in occupied patches mainly through the carrying capacity.

STUDY SPECIES AND DATA

The Glanville fritillary butterfly (*Melitaea cinxia*) has a large metapopulation in the Åland Islands, southwestern Finland, in a network of ~4000 small dry meadows (average size 0.17 ha) with one or both of the two larval host plant species, *Plantago lanceolata* and *Veronica spicata* (Hanski 1999a, Nieminen et al. 2004). The entire network covers an area of 50 × 70 km, and it has been divided into 75 sub-networks, which are occupied by dynamically relatively independent metapopulations (Hanski et al. 1996). Within each sub-network, the distances among the meadows are short enough to allow frequent movements, whereas movements are infrequent between sub-networks (Hanski et al. 1996). We will call these 75 sub-networks of the entire 4000-patch network as “networks” for short, and the butterfly metapopula-

tions living in individual networks are referred to as “metapopulations.”

The Glanville fritillary has one generation per year in Finland. The adults fly in June and females lay eggs in large clutches of 150–200 eggs. Larvae live gregariously. Half-grown larvae overwinter in a compact web (“winter nest”) spun by the larvae at the stem of the host plant; they resume feeding in the following spring and pupate in May. Further details on the life cycle are given by Kuussaari (1998), Hanski (1999a) and several chapters in Ehrlich and Hanski (2004).

Mark–recapture data

Most butterflies move away from the typically small natal population at some point in their adult life, and many individuals, including ovipositing females, end up visiting multiple habitat patches within a network. Mark–recapture studies have been conducted to characterize the rate and pattern of movements (Hanski et al. 1994, Kuussaari et al. 1996). The results have been analyzed using a diffusion approximation of a correlated random walk model (Ovaskainen et al. 2008b), which allows for habitat-specific parameter values and includes the process of habitat selection, i.e., it assumes biased movements at habitat boundaries. Although the diffusion model is a very simplistic description of movement, it has been successfully validated against independent data for another species of butterfly (Ovaskainen et al. 2008a).

Here, we estimate the movement parameters using data collected by Hanski et al. (1994) for 518 female and 1204 male Glanville fritillaries in 1991. A helpful feature of this mark–recapture data set is that the largest habitat patch (2.18 ha) was split into several parts, allowing us to estimate the within-patch diffusion rate in addition to the between-patch diffusion rate. The mark–recapture study was conducted in network #61 with 72 habitat patches (Fig. 1b), although only 50 patches were recognized at the time of the mark–recapture experiment.

Long-term survey data

The Glanville fritillary metapopulation in the Åland Islands has been surveyed twice a year since 1993. During these surveys, all the meadows known at the time of the survey have been visited by field assistants. In the years 1993–1997, a network of ~1600 patches was surveyed. A more accurate mapping of the entire study area in 1998–1999 resulted in the current network of ~4000 patches. Most of the newly discovered patches are small or relatively small. In this study, we use all of the available data, and population sizes in the meadows not surveyed prior to the remapping of the study area in 1998–1999 are treated as missing data.

Relatively accurate surveys of the Glanville fritillary at the very large spatial scale are possible due to the gregarious larval behavior and the conspicuous winter nests that the larvae spin in late summer. The winter nests have been counted on all the meadows during the

autumn survey in early September. Out of the total of ~4000 meadows, 500–800 have been occupied in any one year. All of the occupied meadows have been revisited in late April in the following spring and the surviving larval groups have been counted.

For the purpose of estimating the parameters of the metapopulation model, we used the same focal network (#61) that was used for the mark–recapture study. The movement model was parameterized using a detailed description of the landscape (Fig. 1b), but in the metapopulation model we approximated the habitat patches by circles to enable the use of the analytical formulae for movement probabilities (see Zheng et al. 2009). Because the analytical formulae assume that the radii of habitat patches are substantially less than the interpatch distances (see Zheng et al. 2009), some of the patches were merged to give a total of 49 habitat patches in network #61 (Fig. 1c).

Control data to estimate detection probability

Not every winter nest is detected in the autumn surveys. In four years (1994, 1995, 1997 and 2009), additional data have been collected to estimate the detection probability. In the first three years, intensive surveys of four populations (different populations in each year) were conducted to find out the “true” number of winter nests. Following the intensive search, eight independent pairs of field assistants conducted the regular survey of the same populations with the standard search effort to estimate the number of nests. In 2009, comparable data were collected for 71 habitat patches, although the standard survey was done by only one pair of field assistants, prior to the intensive survey. In the online Supplement we provide information regarding the focal network (including the spatial locations and areas of the patches); the long-term survey data; and the control data to which the state-space models were fitted.

STATE-SPACE MODELS

A state-space model, hereafter SSM (Buckland et al. 2004, Thomas et al. 2005, Harrison et al. 2006), incorporates two parallel and simultaneous processes: the state process, which models the true but unknown state of the population, and the observation process, which links the state process to a time series of observational data. The states are represented by a vector of the true number of individuals in each state, categorized according to the developmental stage, spatial location, and so forth. These states evolve according to a process model in which the states at each time point are a stochastic function of the states in the previous time point. The observations are a stochastic function of the states at each time point as described by an observation model. Demographic, environmental, and observational stochasticities are incorporated through the use of probability distributions.

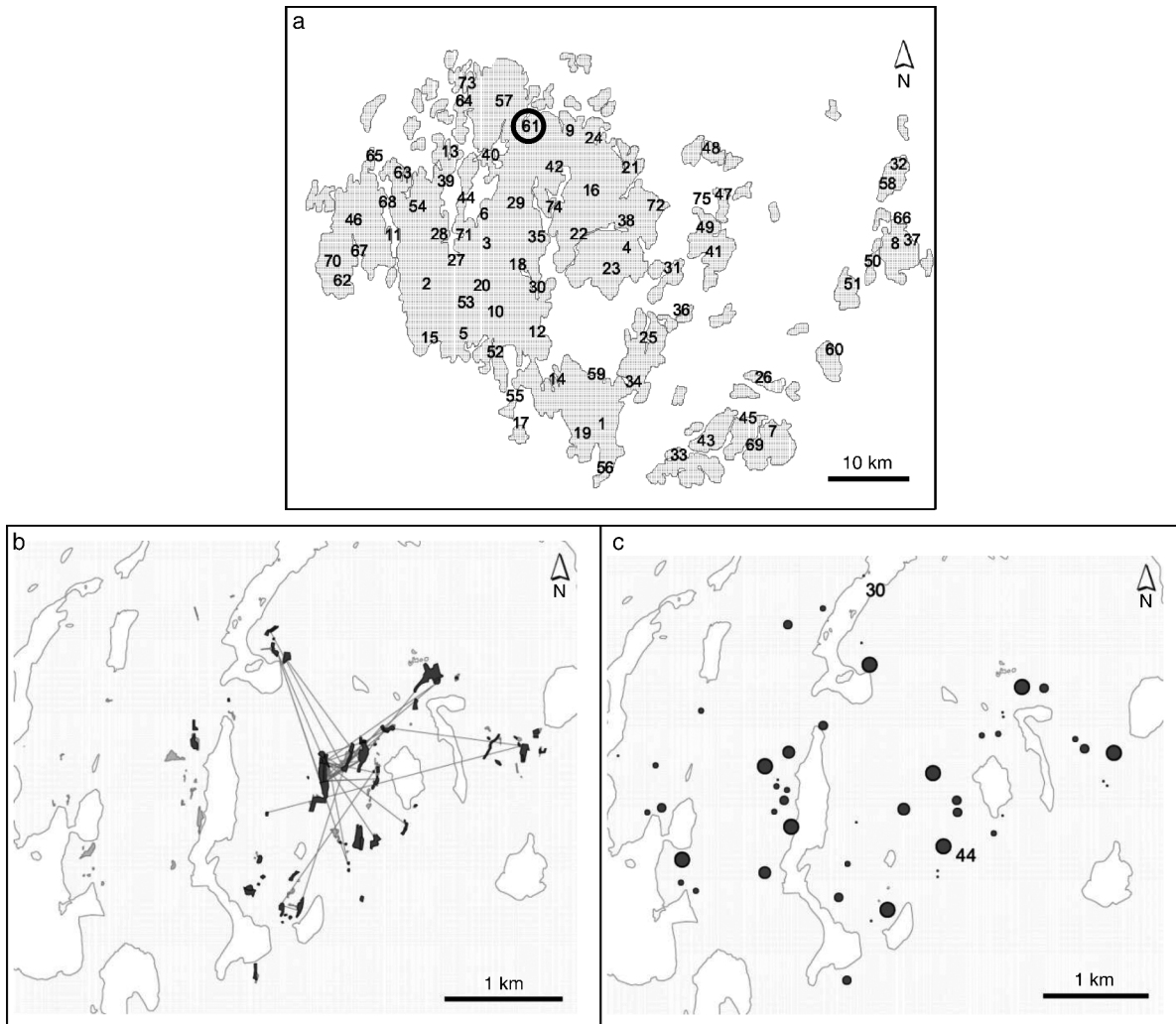


FIG. 1. Map showing (a) locations of the numbered habitat patch networks on Åland Island, southwestern Finland, and (b, c) locations of the habitat patches within the focal network (#61, circled) used for parameterizing the models. Panel (b) shows the detailed landscape structure used for the mark-recapture model: dark-gray shaded areas for habitat patches visited during the mark-recapture study and light-gray shaded areas for patches not visited; and straight lines for the observed movements of Glanville fritillary butterflies (*Melitaea cinxia*) among the habitat patches. Panel (c) shows the circular approximations used for the patches (size proportional to patch area) for the state-space models (SSMs), where some of the patches from panel (b) have been merged for reasons explained in the text. Patches #30 and #44 are identified by numbers; Fig. 6 gives some results for them as examples.

In what follows we give details of the subprocess models, which describe overwinter survival of larval groups, eclosion of adult butterflies, movements and oviposition by adult females, and the spinning of the winter nests by gregarious larvae. We then derive a simplified patch occupancy model (SPOM) from the individual-based model (IBM). Three types of observation models are needed for the three types of data detailed. Concerning model analysis, we describe the model-fitting strategy, posterior predictive tests to assess the model fit, generation of simulated trajectories, and cross-validation tests with data from independent networks. Finally, we examine the relationships between model parameters and selected environmental variables.

The directed acyclic graph (DAG) in Fig. 2 offers a visual aid to understand the model structure. Table 1 lists the main model parameters. Technical details are presented in a series of Appendices, A–F.

Process models

Overwinter survival.—We define $N_{i,t}$ as the number of winter nests present in patch i at the time of the autumn survey in year t . The number of nests surviving over the winter, $S_{i,t}$, is distributed binomially as $S_{i,t} \sim \text{Bin}(N_{i,t}, e_t)$, where e_t is the winter survival probability. Overwinter survival is strongly influenced by the climatic conditions (Nieminen et al. 2004). To capture this weather-induced variability, we use a random effects

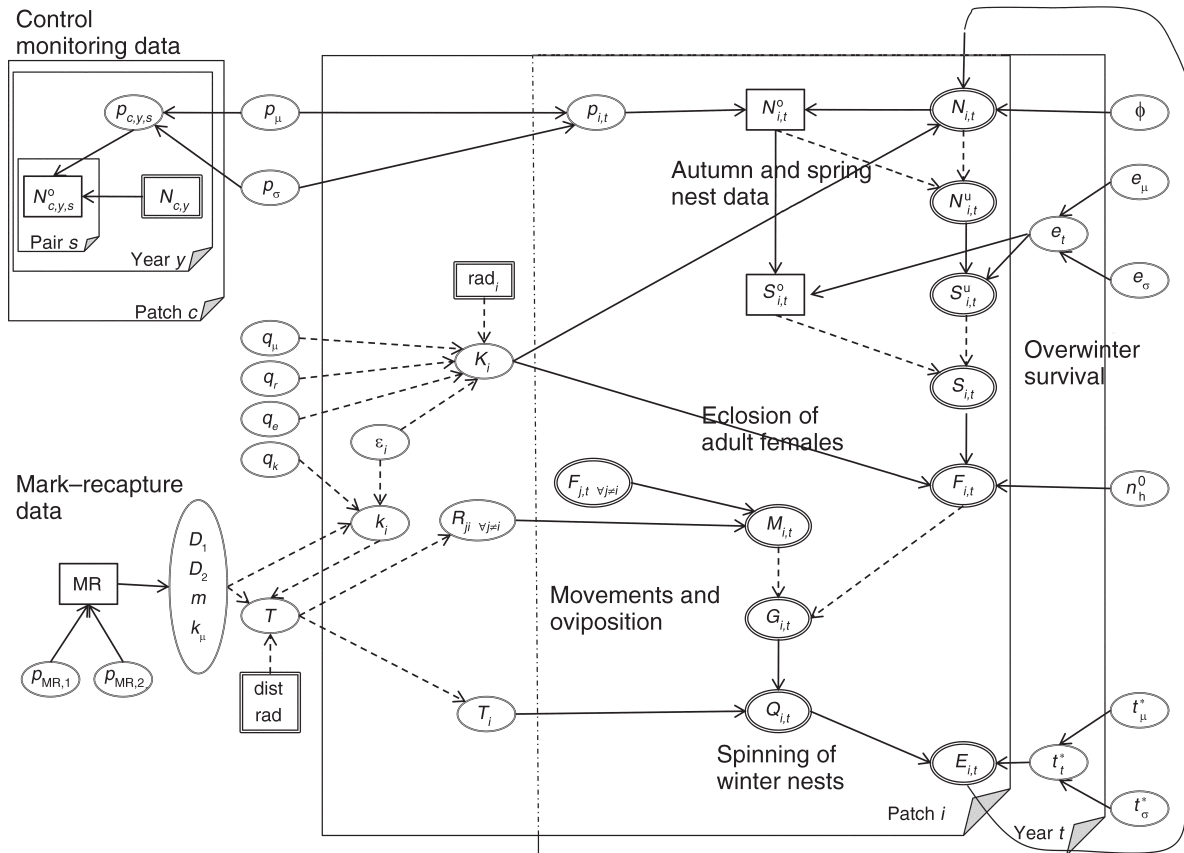


FIG. 2. Directed acyclic graph (DAG) for the state-space individual-based model (IBM). The quantities in the double ellipses are the states, and the quantities in the single ellipses are the parameter values being estimated. In the single boxes are the observations and in the double boxes are the fixed quantities. The full arrows give stochastic relationships (i.e., those that have probability distributions associated with them), and the dashed arrows are for deterministic relationships. The folding sheets give repeat structures. Descriptions of the abbreviations used for the main outer parameters are given in Table 1; other terms are defined in detail in Appendix A: Table A1. The states are subscripted i and t for patch and year, respectively. N is the number of autumn nests, and S is the number of surviving nests (superscripts o and u indicate observed and unobserved); F is the number of successfully hatched females; M is the number of adult females visiting patch i , but originating from a different patch; Q is time spent by all females in the patch; E is the number of egg groups oviposited on the patch; R is the probability that an individual from another patch (indexed j) will visit focal patch i in its lifetime; T_i is the time a visitor to or native of patch i will spend in patch i in its lifetime; K is carrying capacity; MR refers to the mark-recapture experiment with detection probabilities p ; dist and rad are distance between patches and patch radius, respectively. See *Process models* and *Observation models* for further information.

model, in which the logit-transformed survival probability is assumed to be normally distributed, $\text{logit}(e_t) \sim \mathcal{N}(e_{\mu}, e_{\sigma}^2)$. Hence, we assume that there is a common mean around which the yearly survival values are fluctuating.

Eclosion of adults.— $F_{i,t}$ denotes the number of females that eclose as adult butterflies. To account for density dependence due to intraspecific competition, which occurs especially during the final larval instar (Kuussaari et al. 2004), we assume that $F_{i,t}$ is Poisson distributed as $F_{i,t} \sim \text{Pois}(K_i[1 - \exp(-S_{i,t} \times n_h^0/K_i)])$, where n_h^0 gives the mean number of females that would hatch from a larval group in the absence of density dependence. Again using a random effects model, we assume that the carrying capacity for patch i , K_i , follows

$\log(K_i) = q_{\mu} + q_r \log(\text{rad}_i) + q_e \epsilon_i$, where q_{μ} is the mean value, q_r scales the effect of the patch radius rad_i (in meters), and $q_e (>0)$ scales the effect of patch quality ϵ_i , which is a standard normal random variable (mean zero and unit variance). Patch quality ϵ_i is used also in our calculation of habitat selection by dispersing females. By “log” we refer to the natural logarithm throughout the paper.

Movements and oviposition.—Following the diffusion approximation of Ovaskainen and Cornell (2003), we denote by T_i the time that an individual presently in patch i is expected to spend in patch i during its lifetime. T_i depends on the diffusion coefficients D_1 and D_2 in the habitat matrix and in the habitat patches, respectively, the mortality rate m (assumed to be the same in the

TABLE 1. Main parameters of the state-space models for the Glanville fritillary butterfly (*Melitaea cinxia*) metapopulation in the Åland Islands, southwestern Finland.

Symbol	Description
ϕ	Probability that larvae from an egg group survive to spin a winter nest
e_μ	Mean of the random effect model of winter survival
e_σ	Standard deviation of the random effect model of winter survival
n_h	Average number of females developing from a larval group in the absence of density dependence
t_μ^*	Mean of the random effect model for oviposition
t_σ^*	Standard deviation of the random effect model for oviposition
p_μ	Mean of the random effect model for detection probability (IBM only)
p_σ	Standard deviation of the random effect model for detection probability (IBM only)
z	Probability of false negative occupancy state (SPOM only)
ρ	Scaling constant in the estimation of population size (SPOM only)
q_k	Positive scalar of habitat quality in the equation for habitat selection
D_1	Diffusion coefficient in the matrix
D_2	Diffusion coefficient in the habitat patches
m	Mortality rate of adult females
k_μ	Mean value in the equation for habitat selection
q_μ	Mean value in the equation for the carrying capacity
q_r	Scalar of patch radius in the equation for the carrying capacity
q_e	Positive scalar of habitat quality in the equation for the carrying capacity

Note: IBM and SPOM refer to the individual-based model and the stochastic patch occupancy model, respectively.

matrix and in the patches), and on parameter k_i , which determines the strength of edge-mediated behavior, i.e., the tendency of butterflies to stay within a habitat patch. We refer to k_i as the habitat selection parameter and we model it as a random effect $\log(k_i) = k_\mu + q_k \varepsilon_i$, where k_μ is the mean and $q_k (>0)$ scales the effect of patch quality ε_i on habitat selection. $M_{i,t}$ denotes the numbers of adult females originating from patches other than patch i but which visit patch i in year t . We assume that $M_{i,t}$ is Poisson distributed as

$$M_{i,t} \sim \text{Pois} \left(\sum_{j \neq i} F_{j,t} R_{ji} \right)$$

where R_{ji} is the probability that an individual initially in patch j will visit patch i in its lifetime (Appendix A). $G_{i,t} = F_{i,t} + M_{i,t}$ gives the total number of females that visit patch i in year t . $Q_{i,t}$, the pooled time spent by all females in patch i , is assumed to be Gamma distributed as $Q_{i,t} \sim \text{Gamma}(G_{i,t}, T_i)$, where $G_{i,t}$ gives the shape and T_i the scale (hence we assume that the time spent by an individual in a patch is exponentially distributed). The numbers of egg groups oviposited, $E_{i,t}$, is Poisson distributed as $E_{i,t} \sim \text{Pois}(Q_{i,t}/t_i^*)$, where t_i^* is the mean number of butterfly-days required to oviposit one egg group in year t . Given that survival in the adult stage depends on weather conditions (Kuussaari et al. 1996), we again use a random effect model, in which the log-transformed value of t_i^* is assumed to be normally distributed over the years:

$$\log(t_i^*) \sim \mathcal{N}(t_\mu^*, (t_\sigma^*)^2).$$

Spinning of winter nests.—Larvae hatch after two to three weeks, and the groups that survive until late

summer spin a winter nest. At this point in the model, time t is incremented by one step and we return to where we started in the annual life cycle, assuming that $N_{i,t+1}$ is binomially distributed as $N_{i,t+1} \sim \text{Bin}(E_{i,t}, \phi)$, where ϕ is the probability that an egg group laid by a female survives to the winter nest stage.

A simplified patch occupancy model

We denote by $O_{i,t} \in \{0, 1\}$ the true occupancy state of patch i in the autumn of year t . Thus an occupied patch is equivalent to $N_{i,t} > 0$ in the IBM. We denote by the vector $\mathbf{o}_t = \{O_{i,t}\}_{i=1}^n$ the state of the entire metapopulation. A stochastic patch occupancy model (SPOM) describes the transition probability from the state \mathbf{o}_t to the state \mathbf{o}_{t+1} . We derive this probability by working backward in time, first noting that as $N_{i,t+1} \sim \text{Bin}(E_{i,t}, \phi)$ the probability that no egg groups yield a winter nest is $P[O_{i,t+1} = 0] = (1 - \phi)^{E_{i,t}}$. As the number of egg groups ($E_{i,t}$) oviposited follows the Poisson distribution with parameter $Q_{i,t}/t_i^*$, we sum over this distribution to obtain $P[O_{i,t+1} = 0] = \exp(-\phi Q_{i,t}/t_i^*)$. We continue in Appendix B in a similar manner, by sequentially integrating, either exactly or approximately, over all of the intermediate states of the IBM, to obtain

$$P[O_{i,t+1} = 0] = \prod_j \left[1 + e_t \left(-1 + \exp \left[n_h^0 \left(-1 + \exp[-\alpha_{i,t} R_{ji}] \right) \right] \right) \right]^{N_{j,t}} \quad (1)$$

where $\alpha_{i,t} = (\phi T_i)/t_i^*$. In the SPOM thus derived, we replace $N_{j,t}$ with $\rho O_{j,t} K_j$, where ρ is a scaling constant to be estimated during model fitting and K_j is the carrying capacity of patch j , used as a surrogate of the respective expected population size. Most of the process model

parameters, including the random effects, are the same as in the IBM; thus the parameters of the SPOM can be interpreted at the level of individuals. We note, however, that the SPOM is over-parameterized, because some of the individual-level parameters (such as ϕ and t_i^*) only occur as combinations in the SPOM. Although such parameters are not identifiable (Luo et al. 2009), they can still be estimated in the Bayesian framework, in which the full joint posterior distribution will contain information on those parameter combinations that can be identified.

Before fitting the models to empirical data, we compared the behaviors of the IBM and the SPOM using simulated data for network #61. The results of this comparison (Appendix B) show that the two models predict very similar occupancy probabilities for individual habitat patches and a very similar distribution of metapopulation size at the quasi-stationary state. We therefore conclude that the SPOM of Eq. 1 is a good approximation of the underlying IBM. Ovaskainen and Hanski (2004a) have previously reported a similar result for a simpler version of the individual-based model.

Observation models

Mark-recapture data.—Following Ovaskainen et al. (2008b), the capture probability is defined as the probability of observing a butterfly when it is present at a site that is being searched. Because the capture effort was greater in one habitat patch than in the other patches (Hanski et al. 1994), we used two capture probabilities, denoted by $p_{MR,2}$ for the intensively searched patch and by $p_{MR,1}$ for the other patches.

Long-term survey data.—In the IBM we assume that the number of winter nests observed in a patch is distributed binomially as $N_{i,t}^o \sim \text{Bin}(N_{i,t}, p_{i,t})$, where $p_{i,t}$ is the probability of detecting a winter nest during the autumn survey. Given that weather conditions, patch characteristics, and the abilities of the field assistant are all likely to affect the detection of the nests, we allow for a different detection probability for each patch in each year through using a random effect model, in which the logit-transformed detection probabilities are assumed to be normally distributed, $\text{logit}(p_{i,t}) \sim \mathcal{N}(p_\mu, p_\sigma^2)$. We have no observation model for the spring nest count, because we assume that nests found in the autumn are seldom missed in the spring if they have survived (their location is known accurately). The numbers of nests that remain unobserved in the autumn and in the spring are denoted by $N_{i,t}^u = N_{i,t} - N_{i,t}^o$ and $S_{i,t}^u = S_{i,t} - S_{i,t}^o$, respectively.

In the SPOM we assume that an empty habitat patch is never misclassified as occupied, but that an occupied patch is misclassified as empty (a “false zero”) with probability z (Appendix A). Previous research has estimated z to be 0.1 (see Moilanen 2002). We assume a wide prior distribution for this parameter, with a mean of 0.1 (Appendix C).

Control data to estimate the detection probability.—In the IBM we use an observation model for the control

data similar to the previous model, with $N_{c,y,s}^o$ (the number of nests observed in control patch c in year y by field assistant pair s) being distributed binomially as $N_{c,y,s}^o \sim \text{Bin}(N_{c,y}, p_{c,y,s})$, where $N_{c,y}$ gives the “true” number of nests (based on the intensive survey) and $p_{c,y,s}$ gives the detection probability, which comes from the same random effect model as for the long-term survey data. For the SPOM we used an analogous observation model with $O_{c,y}^o$ being a function of $O_{c,y,s}$ and z .

Model-fitting strategy

We fitted the movement model to the mark-recapture data using the method of Ovaskainen et al. (2008b) and we used the posterior distribution from this analysis as the prior distribution of the movement parameters (D_1 , D_2 , m , k_μ) in the metapopulation models. We then fitted the metapopulation models (IBM and SPOM) to the biannual data from network #61 with 49 patches for the period from autumn 1993 until spring 2009. To parameterize the SPOM, we used only the autumn data converted to presence/absence of populations in the habitat patches. We fitted the models using Bayesian inference with Markov chain Monte Carlo (MCMC), with some updating strategies resembling sequential importance sampling (SIS), an alternative method for fitting SSMs (Newman et al. 2009). The prior distributions for the parameters are given in Appendix C and the technical description of the MCMC is in Appendix D.

Because the SSMs that we implemented are quite complex, we performed several tests to ensure that the computer code was free of errors. First, we declared all data as missing, in which case the MCMC should return the priors. This is what happened. Second, we conducted tests with simulated data with known parameter values, using a similar spatial configuration of habitat patches and missing data structure similar to that in the real data. In these tests, the posterior distributions were consistent with the true parameter values (Appendix E). The SSMs were coded in grid Mathematica 7 (Wolfram Research 2008).

Random effects and environmental factors

The model includes two year-specific random effects: the probability of overwinter survival (e_t) and the mean number of days it takes to oviposit one egg group (t_t^*). Having estimated these year-specific parameters, we tested whether they correlated with temperature and precipitation. It is plausible that monthly average temperatures from July to November, in January, and in the spring in March or April would influence e_t (January is used to represent the winter conditions, and the months prior to overwintering are tested because the environmental conditions in the previous summer may affect larval condition that affects overwinter survival). Similarly, we tested whether t_t^* was correlated with average temperature and precipitation in June, the adult flight season. Weather data were obtained from Ålands Försöksstation. In these analyses, we used the mean

(over the posterior distribution) estimates of e_i and t_i^* as the dependent variables.

In a similar manner, we asked whether the patch-specific habitat quality parameters ε_i correlate with empirically measured parameters of patch quality. The latter include the pooled abundance of the two larval host plants *Plantago lanceolata* and *Veronica spicata*; the percentage of the host plants that were dry (potentially affecting larval survival); the percent cover of nectar plants; the percentage of the habitat patch's total area that had been grazed; and the percentage of patch boundary bordering forest. All of these variables were averaged over the years for which data were available. Finally, we included in the analysis a binary variable denoting the presence of a road to the patch. The dependent variable was the mean (over the posterior distribution) estimates of ε_i . We started with a regression model in which all variables were included and used stepwise AIC model selection to find the most parsimonious model. The regressions were coded in R Version 2.6.2 (R Development Core Team 2008).

Influence of patch quality on movements and patch carrying capacity

In the metapopulation model, the patch quality parameter ε_i influences both larval survival (through the patch carrying capacity) and movements of adult butterflies (through habitat selection). The effect of patch quality is scaled differently for these two processes (by q_e and q_k , respectively; Table 1), and it is thus possible to conduct simulation experiments to ask whether patch quality is more important for movements or local dynamics. We consider a single focal patch and set its quality parameter to $\varepsilon_1 = 1$, meaning that it has quality that is one standard deviation higher than the quality of an average patch. To prevent the focal patch from going extinct and to model the consequences of immigration, we added another patch with a radius 50 m and of average quality ($\varepsilon_2 = 0$); this patch was set to have 20 larval groups in each autumn. Four scenarios were compared, in which q_k and q_e in the focal patch were set either to zero (no patch quality effect on movements or the carrying capacity, respectively) or to the model-estimated value. We ran 100 simulations for 50 years, in which all of the model parameters, apart from ε_i , q_k , and q_e , were sampled from the posterior. We recorded the fraction of years when the focal patch was occupied and its mean population size conditional on occupancy, and we computed the mean and standard error of these variables over the 100 simulations. To see how robust the results were, we repeated the analysis for a small (radius 10 m) and a large (radius 50 m) focal patch, and for a well-connected (distance 250 m from the second, permanent patch) and isolated focal patch (distance 1 km from the second patch). In the first year of the simulation, the large and small focal patches were set to have 20 and 4 nests, respectively.

Posterior predictive tests and cross-validation with independent data

The fits of the two models (IBM and SPOM) were assessed by creating simulated data sets (posterior predictive data sets). A single simulated data set was generated by drawing the entire parameter vector, including actual model parameters, random effects, and states, from the joint posterior distribution, and simulating the model with these parameters. The procedure was repeated to create multiple data sets, which can be compared with real data in terms of statistics of interest.

We first created simulated data sets for the focal network that was used for parameterizing the models. We initialized the model with the true numbers of winter nests in the first year ($N_{i,1}$) in the IBM and the occupancy state in the first year ($O_{i,1}$) in the SPOM. Although these values are not known in reality, their values are specified in the draw from the posterior distribution, as the true states are included in the parameters that were estimated. We then simulated through the entire time series using two methods. In Method 1, we used the actual parameter values for the random effects (e_i , t_i^* , and ε_i), whereas in Method 2 we randomized their values from the respective distributions (with the means and variances set to the values drawn from the posterior).

Comparing the simulated data with the real data that were used to estimate the parameters is a useful test of the validity of the structural model assumptions, but it does not evaluate the generality of the parameter values. To do the latter, we next generated simulated time series data simultaneously for all 75 patch networks in the Åland Islands. Because the data were generated simultaneously for all of the networks, unoccupied patch networks could become recolonized during the simulation by migrants from nearby, currently occupied networks. The state variables in the first year were drawn from the full conditional distribution based on the random effect model for the observation probability (with the mean and the variance set to the values drawn from the posterior), given the data in the first year. Patches with missing data in the first year were initialized by drawing randomly a value from the years when there were observations for the particular patch. In these simulations, we used year-specific values of e_i and t_i^* for the years for which the model was fitted to the data (autumn 1993 to autumn 2008) and randomized the values for these parameters from their random effects distributions while simulating to the future. The ε_i random effect values were randomized from their distribution because they were not available for all the patches. We ran 250 predictive simulations for 200 years from autumn 1993 to autumn 2193. We carried out cross-validation with empirical data from all of the 75 networks by simulating the observation process on top of the simulated time series for the years 1993–2008.

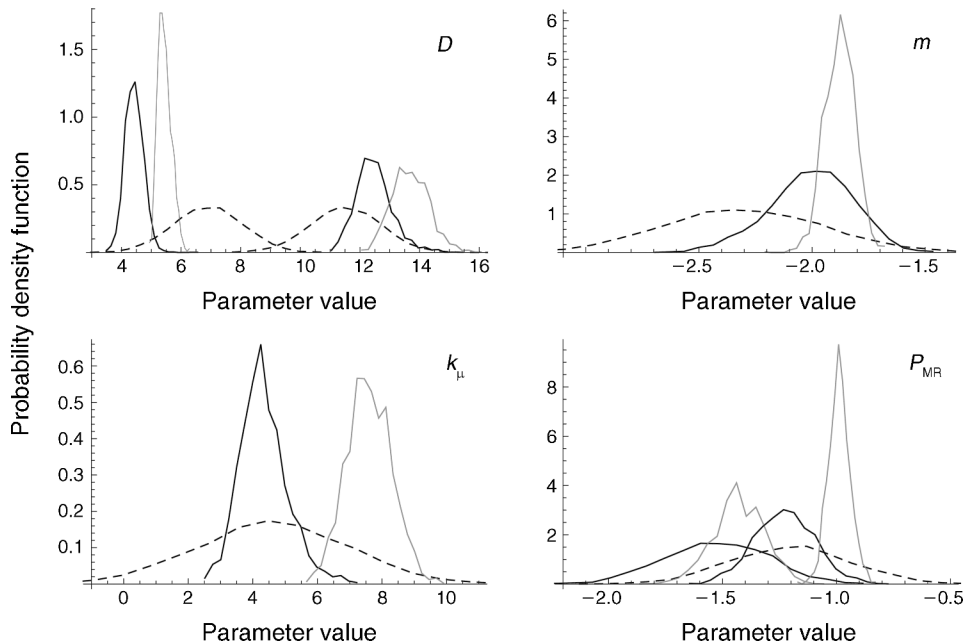


FIG. 3. Marginal prior (dashed black lines) and posterior distributions (solid black lines for females; gray lines for males) for the parameters of the movement model: D values are the diffusion coefficients (rightmost distributions for D_1 , diffusion in the matrix; leftmost for D_2 , diffusion in the habitat patches); m gives the mortality rate; k_μ gives the mean value in the equation for habitat selection; and p_{MR} gives the capture probabilities (leftmost distribution for $p_{MR,1}$; rightmost for $p_{MR,2}$). Distributions for the parameters show the logit-transformed values for the capture probabilities and the log-transformed values for the other parameters.

RESULTS

Adult dispersal

The diffusion model fits well the mark–recapture data (see Appendix C). The parameter estimates (Fig. 3) suggest that females move more frequently than males in the habitat matrix (smaller value of k_μ), but females have a lower movement rate both within the habitat patches (parameter D_2) and in the matrix (parameter D_1). There is no difference in the mortality rate (m) between the sexes. The capture probability is greater for males than females, leading to larger numbers of marked individuals and recaptures and hence to somewhat more concentrated posteriors in males. Because the demographic dynamics are primarily driven by females, we use the posterior distribution for females as the prior in the SSMs, approximated as a multivariate normal distribution (see Appendix C).

Parameter estimates and model fit to the focal patch network

The IBM is a complex model, and it was nontrivial to sample its posterior, i.e., to develop a MCMC scheme that would result in satisfactory mixing. After attempting a number of alternative methods (Appendix D), the best performance was obtained by combining particle filtering methods with MCMC, for which the mixing of the MCMC chains are assessed in Appendix F. Even

with this method, the computing time needed to fit the IBM was several weeks with a multicore computer.

Fig. 4 shows the marginal prior and posterior distributions for the main parameters of the metapopulation models. For both models, and in particular for the SPOM, many of the marginal posterior distributions resemble closely the corresponding priors, indicating that there is little information in the data to identify these individual parameters. However, the joint posterior distribution contains more information than the marginal posteriors through the correlations among the parameters (Appendix F). Particularly high posterior correlations occur between D_1 and k_μ (correlation coefficient $r = 0.93$) and q_μ and q_r ($r = 0.65$) in the IBM, and between D_1 and k_μ ($r = 0.92$) in the SPOM. As a result, the posterior distributions are much more concentrated than the prior distributions for integrated quantities such as model predictions. One unexpected result for the IBM is the low posterior mean of 1.2 days for the average number of days required to oviposit one egg group (averaged across all the yearly values), for which our a priori expectation was 3 days.

The IBM outperformed the SPOM in terms of both accuracy and precision when fitted to simulated data for which the true parameter values were known (Appendix E). Fig. 5 shows that this is also the case for the real data, using as test statistics the occupancy probabilities, numbers of extinction and colonization events, and the

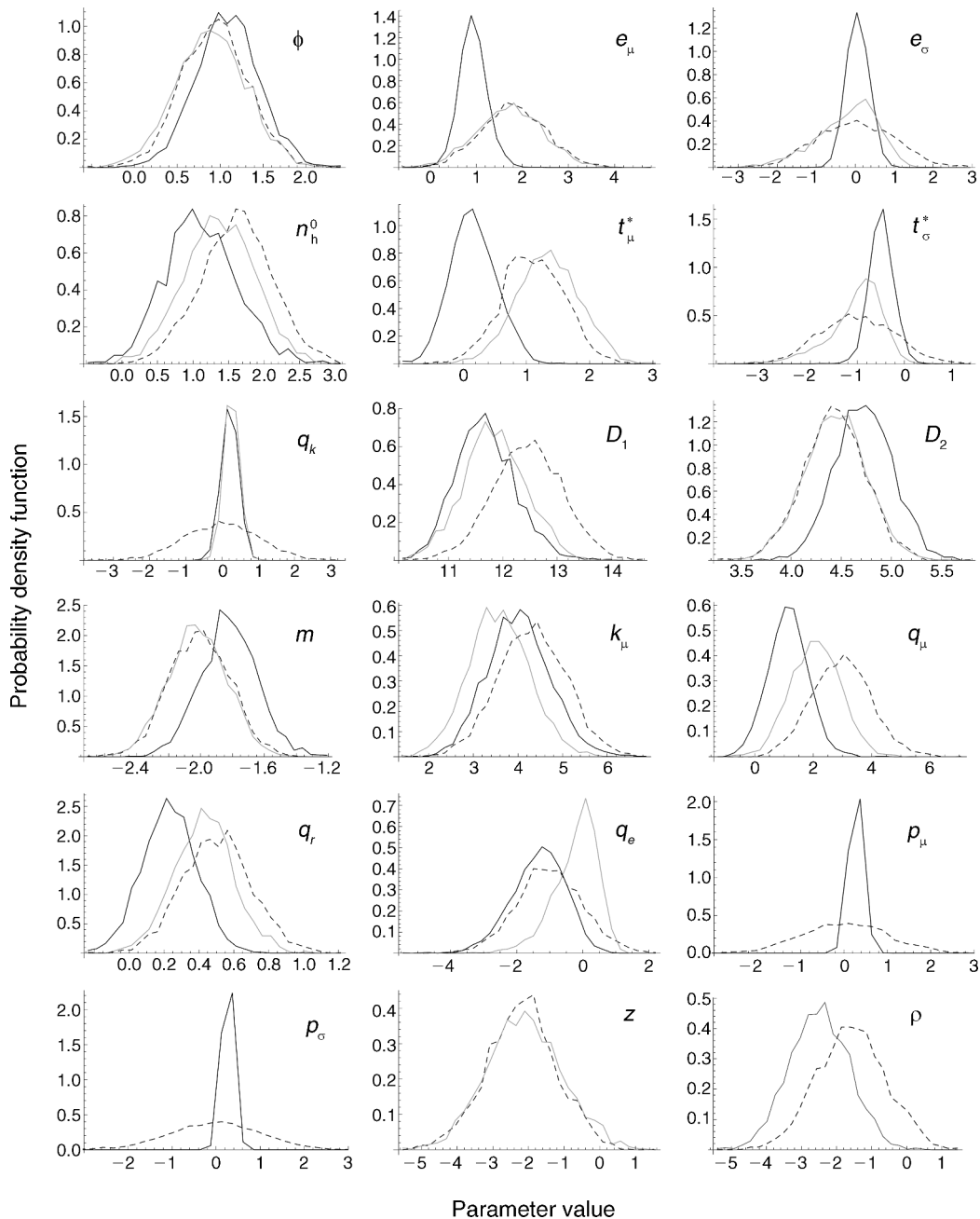


FIG. 4. Marginal prior (dashed black lines) and posterior distributions (solid black and gray lines for the IBM and stochastic patch occupancy model [SPOM], respectively) for the main model parameters. The distributions show the logit-transformed values for ϕ and z and the log-transformed values for all other parameters except those on the real scale (e_μ , t_μ^* , k_μ , q_μ , q_r , and p_μ). The parameter descriptions are given in Table 1.

size of the entire metapopulation. Fig. 5e, f shows that the models capture correctly the influence of patch size and connectivity on the probability of occupancy. The slight biases in the results, for instance the posterior mean for the occupancy probability being greater than the true value (Fig. 5a), are likely to be due to a mismatch between reality and structural model assumptions. Indeed, when the model was fitted to data that

had been generated by the very same model (Appendix E), there were no such biases.

Simulated trajectories and cross-validation with independent data

The parameterized model can be used to simulate dynamics at different spatial levels, from the level of individual habitat patches to the level of the entire

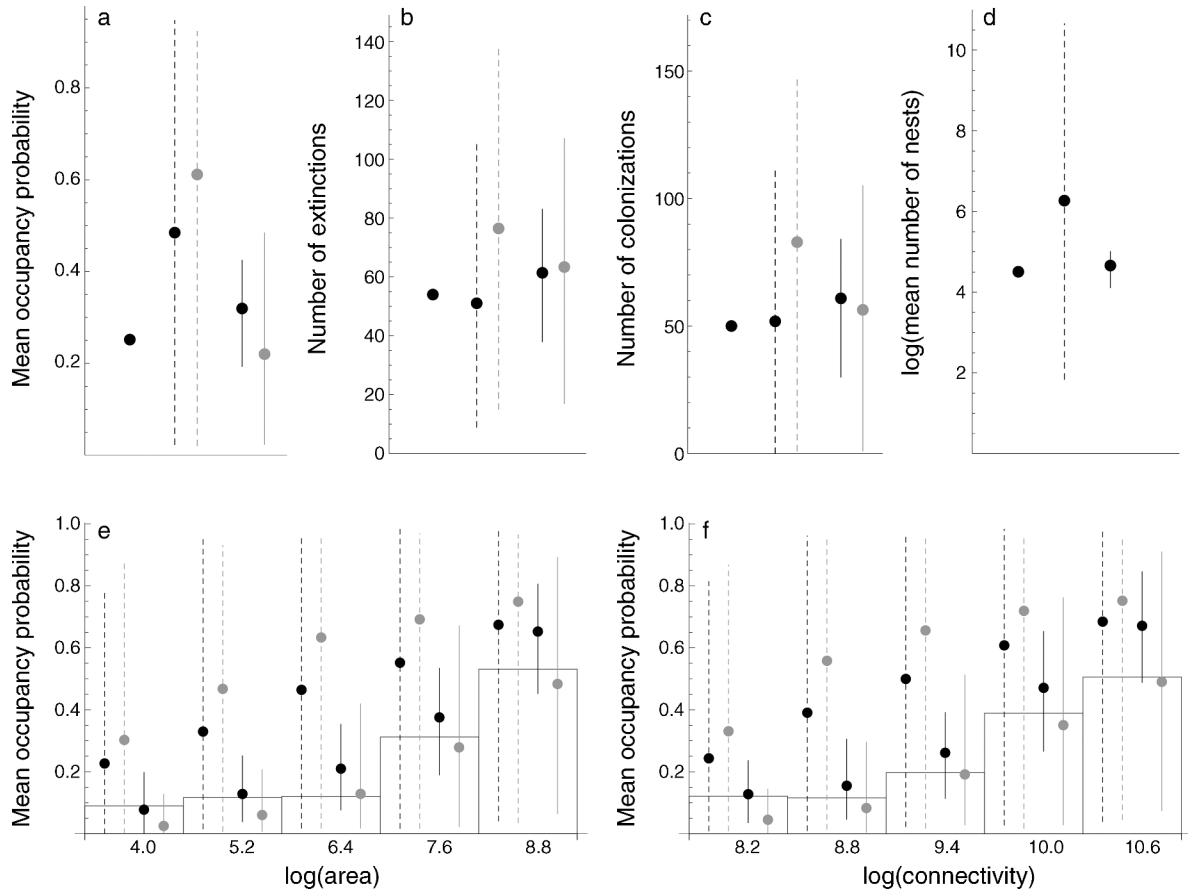


FIG. 5. Posterior predictive tests for the focal network for: (a) the mean occupancy probability across all years; (b) the number of extinctions; (c) the number of colonizations; and (d) the logarithm of the mean number of winter nests for the metapopulation. In each case the first dot shows the value from the real data, and the following dots and lines give the mean values and the 95% Bayesian credibility intervals for 250 posterior predictive data sets. Posterior predictive data sets were simulated from the priors (dashed lines) and the posteriors (solid lines) for both the IBM (black) and the SPOM (gray). In panels (e) and (f), the patches were grouped according to their areas, A_i , and connectivities, S_i , and the bars show the mean occupancy probability in the data. The connectivity was calculated as $S_i = \sqrt{A_i} \sum_{j \neq i} \{\exp(-\alpha d_{ij}) \sqrt{A_j}\}$ where $\alpha = 1$ and d_{ij} gives the distance in kilometers between patches i and j .

Åland Islands (Fig. 6). Small and isolated patches (Fig. 6, first row) remain unoccupied for long periods of time, whereas large, well-connected patches (Fig. 6, second row) are mostly occupied. At the network level, our focal network (Fig. 6, third row) has a high proportion of occupied patches, whereas small and isolated networks (Fig. 6, fourth row) are often unoccupied. Finally, at the scale of the entire Åland Islands, on average 50 of the 75 networks are occupied in any one year (Fig. 6, fifth row). In Fig. 6, results in the first three columns are based on different parameter values sampled from the posterior distribution. Variation among the results shows that even though we have used relatively long-term data to parameterize the model, there remains much uncertainty in predicting long-term dynamics. Based on the model prediction, the entire metapopulation in the focal network may occasionally go extinct (the third row of panels), but it is very unlikely that the entire Åland “megapopulation” (population of

metapopulations; Hanski 1999b) would go extinct (the fifth row of panels). This conclusion of course makes the assumption that the environmental conditions (patch quality and climatic conditions) will remain unchanged in the future. The simulated trajectories for the statistics that can be calculated for the SPOM (rows 3–5 in Fig. 6) give similar results but with greater variability (results not shown).

Turning to cross-validation with independent data, the prediction by the IBM explained a large part of the variation ($R^2 = 0.53$, slope = 0.68, $P < 0.001$) in the observed fraction of occupied patches among the 75 networks (Fig. 7b). Weighting the fraction of occupied patches by patch area further improved the result ($R^2 = 0.63$, slope = 0.74, $P < 0.001$). The SPOM explained a smaller proportion of the variation (fraction of occupied patches: $R^2 = 0.34$, slope = 0.43, $P < 0.001$; fraction of occupied area: $R^2 = 0.45$, slope = 0.50, $P < 0.001$). Both models somewhat overpredicted the fraction of occupied

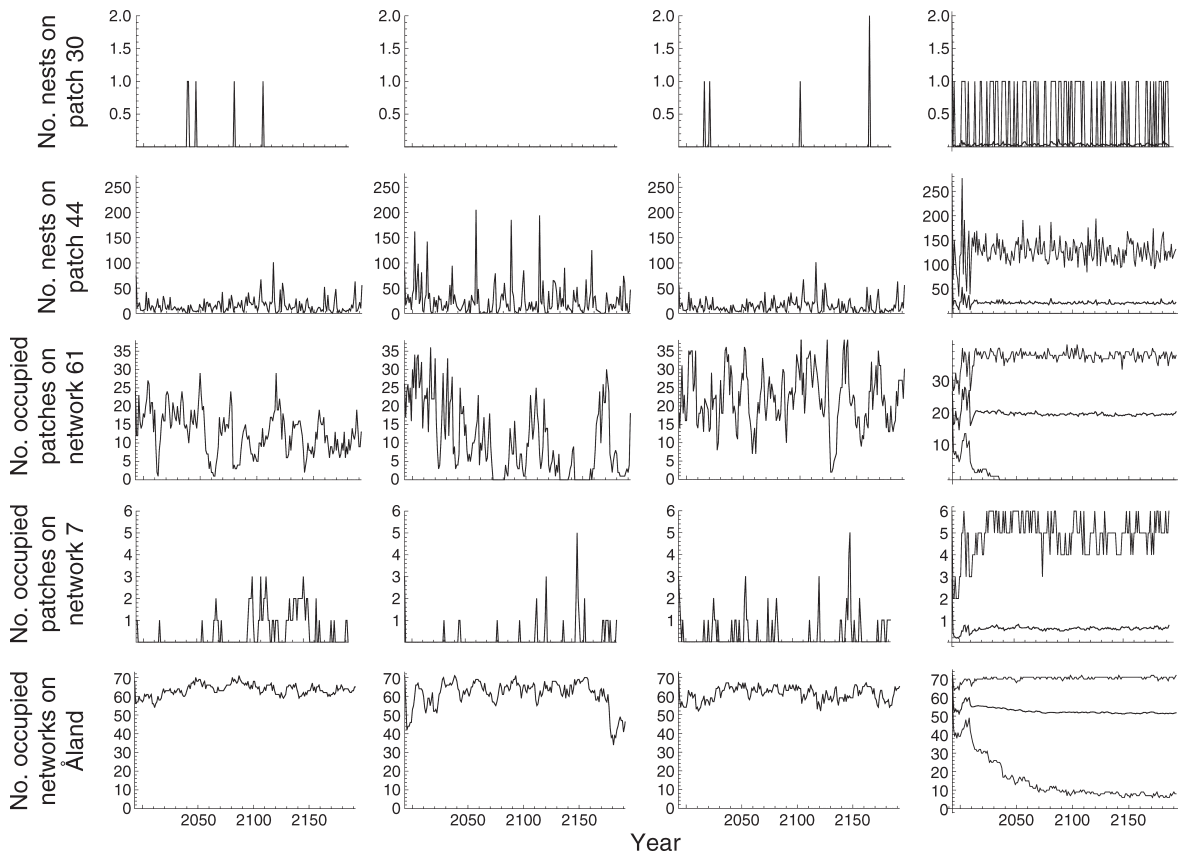


FIG. 6. Simulated trajectories based on the posterior distribution for the IBM. The first three columns give independent 200-year simulations, and the fourth column shows the mean (black lines) and 95% Bayesian credibility intervals (gray lines) for 250 simulations. The first and second rows show, respectively, the number of winter nests at the patch level for a small, isolated patch and for a large, well-connected patch in the focal network. The third and fourth rows show, respectively, the number of patches occupied at the network level in our focal network and in a small, isolated network. See Fig. 1 for network and patch locations. The fifth row shows the number of networks occupied among all the 75 networks on Åland Island.

patches, especially for networks occurring in the central Åland Islands (Fig. 7d). Fig. 7c shows that the models correctly reflect the influence of network size, measured here by metapopulation capacity (Hanski and Ovaskainen 2000), on the probability of occupancy, although with the overall positive bias previously mentioned.

Relationships between model parameters and environmental factors

We regressed the posterior means of the overwinter survival probabilities (e_i) and the number of days required to oviposit one egg group (t_i^*) against monthly weather variables (temperatures and precipitation). None of the regressions produced significant results for either the IBM or the SPOM. Using the original data, we regressed changes in population size from autumn to spring, $\Sigma_i S_{i,t}^o / \Sigma_i N_{i,t}^o$, and spring to autumn, $\Sigma_i N_{i,t}^o / \Sigma_i S_{i,t-1}^o$, against the monthly temperature and rainfall measures, but did not find any significant results.

The posterior means of the patch quality parameters ε_i were very similar for the IBM and the SPOM (linear

regression $R^2 = 0.83$, slope = 0.91, $P < 0.001$). Explaining the posterior means by empirically measured environmental variables yielded a model with $R^2 = 0.36$ that included four of the explanatory variables: the percent cover of host plants (slope = 0.73, $P < 0.001$), the percent cover of nectar plants (slope = 0.35, $P = 0.002$), the amount of grazing (slope = 0.30, $P < 0.001$), and the percentage of dry host plants (slope = 0.28, $P = 0.01$). Thus the quality of habitat patches as estimated by the metapopulation model is well correlated with external environmental variables (for the biological interpretation, see *Discussion*).

Given the relationships between the habitat quality parameter ε_i and the four environmental variables, we recalculated the posterior-predictive cross-validation test for all the networks in Åland using the expected ε_i for all the patches from the regression model. This modification somewhat reduced the level of overprediction but did not increase the amount of variability explained (IBM, fraction of occupied patches: $R^2 = 0.47$, slope = 0.88, $P < 0.0001$).

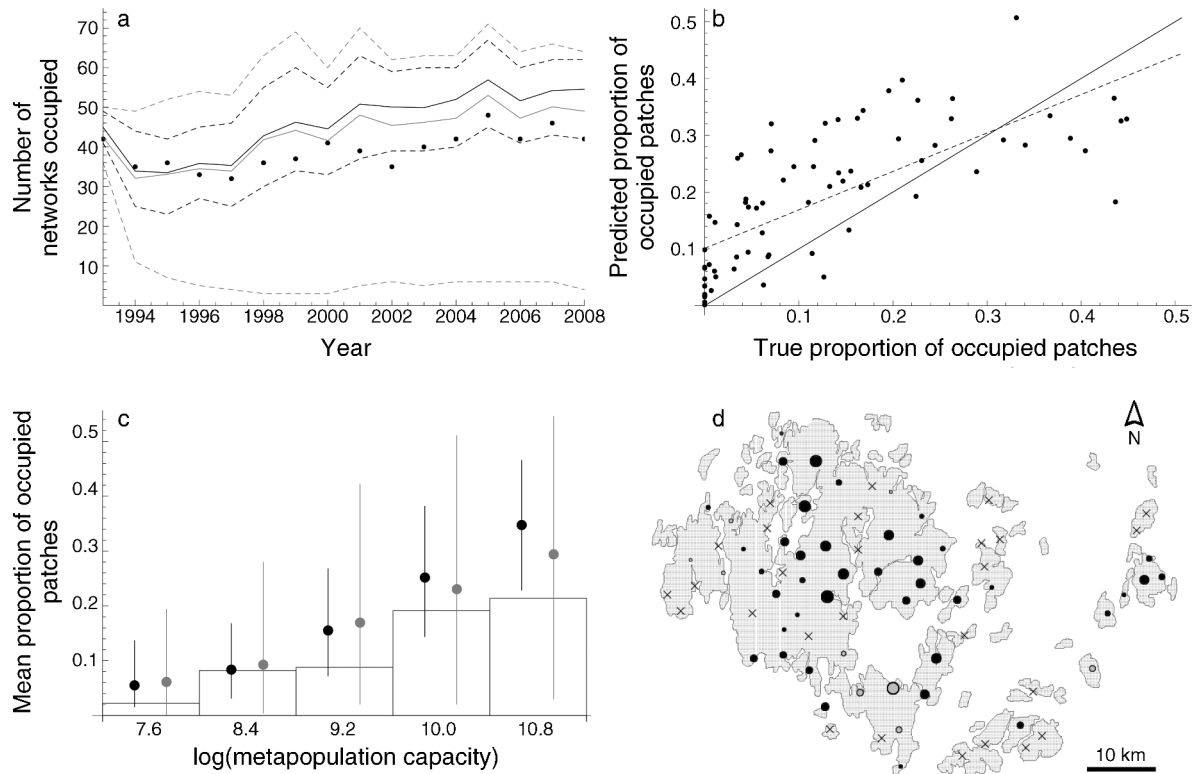


FIG. 7. Posterior predictive cross-validation tests for all the 75 networks on Åland. (a) Number of networks occupied during the study period as predicted by the IBM (black lines) and SPOM (gray lines). Solid lines show the mean predictions based on 250 simulated data sets; dashed lines show the 95% Bayesian credibility interval, and black dots show the true numbers from the data. (b) Mean proportion of patches observed as occupied, across all the years in each network, with the x -axis giving the true value and the y -axis the values predicted by the IBM. Each dot refers to one network. The solid black line gives identity, and the dotted line gives the fitted regression line. (c) Mean proportion of patches observed as occupied, averaged across all years in networks grouped according to their metapopulation capacity (λ_M). Bars show the true values from the data; black (IBM) and gray (SPOM) dots and lines show the mean and 95% Bayesian credibility interval, respectively, based on the simulated data sets. (d) Map showing overprediction (black dots) and underprediction (gray dots) for the match between true and predicted values shown in panel (b). The sizes of the dots are proportional to the amount of overprediction and underprediction. Crosses show the networks for which the absolute value of the difference between true and predicted values was ≤ 0.05 . The metapopulation capacities (λ_M) for each network were calculated as the leading eigenvalue of matrix \mathbf{M} with elements $m_{ij} = \exp(-\alpha d_{ij}) \sqrt{A_i} \sqrt{A_j}$ for $j \neq i$ and $m_{ii} = 0$, where $\alpha = 1$ and d_{ij} gives the distance in kilometers between patches i and j .

Influence of patch quality on movements and carrying capacity

Patch quality has a significantly greater effect on patch occupancy through its influence on movements than on carrying capacity (Table 2). In our model, patch

quality influences movements via the strength of edge-mediated behavior, which controls the rate of emigration, and thus the present results suggest that a major cause of low occupancy in low-quality patches is high emigration rate. Although variation in the carrying

TABLE 2. Comparison between simulations where patch quality was assumed to influence both movements and carrying capacity (models M, K), movements only (M), carrying capacity only (K), or neither of these (—).

Conditions for focal patch	Nest count, by model				Fraction of years occupied, by model			
	(M, K)	(M)	(K)	(—)	(M, K)	(M)	(K)	(—)
Well-connected large patch	15.62 (0.90)	10.69 (0.43)	4.70 (0.19)	4.23 (0.16)	0.92 (0.01)	0.87 (0.01)	0.72 (0.02)	0.66 (0.02)
Isolated large patch	10.82 (0.60)	7.75 (0.36)	3.46 (0.19)	3.33 (0.17)	0.75 (0.02)	0.67 (0.02)	0.38 (0.02)	0.35 (0.02)
Well-connected small patch	1.68 (0.05)	1.69 (0.06)	1.21 (0.04)	1.23 (0.04)	0.26 (0.01)	0.25 (0.01)	0.08 (0.01)	0.09 (0.01)
Isolated small patch	1.53 (0.07)	1.40 (0.06)	1.14 (0.05)	1.09 (0.04)	0.08 (0.01)	0.07 (0.01)	0.02 (0.003)	0.02 (0.002)

Note: Values are means (with SE in parentheses) over 100 simulations, each run for 50 years with the results for the first 10 years excluded.

capacity due to variation in habitat quality has a minor effect on patch occupancy, it does influence the mean population size in the occupied patches. A high emigration rate keeps the population size at low level, in which case the carrying capacity is largely irrelevant: the result for the K model is similar to that for the baseline model (Table 2). If individuals have a low tendency to emigrate, as they do in high-quality patches, the local population has a positive growth rate, in which case increasing the carrying capacity increases the mean population size: the model M,K has much higher population size than the model M (Table 2).

DISCUSSION

The major cause of worldwide decline in biodiversity is the anthropogenic destruction and fragmentation of natural habitats (Hanski 2005). As local populations become progressively smaller and more isolated from one another, their risk of extinction due to stochastic processes increases, but they may still survive as metapopulations in fragmented landscapes. It is therefore vital for conservation to develop a mechanistic understanding of spatial population dynamics and, in particular, of the conditions that allow the persistence of assemblages of extinction-prone local populations inhabiting fragmented landscapes. The Glanville fritillary metapopulation has served as one model system (Ehrlich and Hanski 2004) for acquiring such understanding (e.g., Hanski 1999a, Hanski and Ovaskainen 2000, Zheng et al. 2009).

A metapopulation consisting of tens or even hundreds of local populations connected by spatially restricted dispersal is a complex system, but it is not obvious how complex a model should be constructed to predict its dynamics. In particular, it is not obvious whether one needs to describe the dynamics of local populations at the individual level if the purpose is to predict the size of the metapopulation and its dynamics in terms of the numbers of local populations, a task that is relevant for conservation. In this study, we have tested the predictive abilities of models of dissimilar complexity by constructing an individual-based model (IBM) and a simplified stochastic patch occupancy model (SPOM), which include and ignore, respectively, the description of local dynamics.

Before discussing the results in greater detail, we summarize the conclusions as follows. First, the IBM and SPOM fitted the data used for parameter estimation equally well in the sense that the predicted probabilities of patch occupancy were nearly identical, although predictions made by the IBM contained much less uncertainty. The greater precision of the IBM was to be expected, because more information was used to parameterize it than the SPOM. Second, both models yielded comparable estimates for a parameter describing habitat quality, which was subsequently found to be correlated with particular empirically measured features of habitat quality. Third, in cross-validation tests, in

which model predictions were compared with independent empirical data, the IBM performed better than the SPOM, but both showed the same tendency to overpredict the fraction of occupied patches for most networks.

The fact that the SPOM performed almost as well as the IBM in predicting the dynamics of the metapopulation is a reassuring result, given that for many species, only patch occupancy data are available and are also significantly easier to collect than population count data. However, it should be recalled that the SPOM was constructed by carefully simplifying the IBM. When the life history of a species is well known, but only patch occupancy data are available, our results suggest that a SPOM derived from a realistic IBM can be a useful tool. Importantly, although the SPOM is a population-level model, it can shed light on the connections between individual behavior and large-scale population processes (DeAngelis and Mooij 2005) because the SPOM has parameters that relate directly to life history and movement behavior. A practical advantage of this model structure is that one may incorporate information from other sources, here specifically from the analysis of mark-recapture data, where the posterior distribution of the movement model provided the prior distribution for the relevant parameters in the metapopulation model.

Two drawbacks of the IBM are the technical challenges in constructing and parameterizing such a complex model and the large amount of data needed for the latter purpose. In a complex model, several parameters and states are likely to be correlated in the posterior distribution (as was the case here), which can make it difficult to construct a MCMC algorithm that efficiently searches the entire parameter space. The current models are very computer intensive and a significant amount of time was invested in the development and fine-tuning of the model-fitting procedure (see Appendix D for technical details). We would have liked to parameterize the model using data from all patch networks in the Åland Islands (with the inclusion of regional stochasticity; see Hanski 1999b), but this was not possible because of the prohibitively long computing time. We put considerable time and effort into optimizing the MCMC algorithm (Appendix D) and used a parallel grid Mathematica implementation that utilized five cores on a multicore computer, but the computing time to fit the IBM was about seven weeks.

Biological inferences

The reanalysis of the mark-recapture data of Hanski et al. (1994) using the diffusion model revealed that females tend to move more slowly than males both within and between habitat patches, but that females have a higher emigration rate. Thus females spend more time in the matrix and visit more patches than males. The latter result was obtained in the original analysis (Hanski et al. 1994), but questions concerning the movement rate would be practically impossible to

address using the conventional analyses of mark-recapture data. The difference between the sexes is likely to reflect the different functions of movements in the two sexes. Apart from nectar-feeding, females spend most of their time looking for host plants on which to oviposit and they are prone to disperse between habitat patches. In contrast, a fraction of males appears to be territorial (Wahlberg 2000, Niitepõld et al. 2011); these males are apt to perform rapid takeoff flights to search for females and to chase off competing males, whereas the remaining males tend to patrol over larger areas. These two types of male behaviors also have been reported for many other butterflies (Scott 1974, Wickman and Wiklund 1983). In both cases, males may be less likely than females to emigrate from the population.

The two factors considered to be most likely to cause spatial synchrony in population fluctuations are dispersal and spatially correlated weather effects (Kendall et al. 2000). Our models include both factors, although we assumed complete synchrony in environmental stochasticity across the network rather than a more spatially restricted correlated effect. A previous study on the Glanville fritillary (Hanski and Meyke 2005) found that for aggregate populations in 20 squares of 4×4 km located across the Åland Islands, changes in population size over the summers in the years 1998–2000 were negatively correlated with precipitation in August of the previous year and positively correlated with precipitation in June of the current year. We did not find such relationships, perhaps due to the fact that we fitted the models using data from one network only and hence compared different years rather than different regions, for which Hanski and Meyke (2005) had regional precipitation data obtained from weather radar. In any case, network-wide, relatively synchronous population fluctuations in our results (Fig. 6) are obviously driven by a large amount of environmental stochasticity in several parameters (Fig. 4).

Both the IBM and the SPOM detected strong spatial variation in patch quality measured by the patch-specific ε_i values. In both models, patch quality affects both movement behavior and local dynamics. We found that habitat quality affects patch occupancy more through its effects on dispersal rather than on local demographic dynamics (Table 2). The local carrying capacity, and hence patch quality affecting the carrying capacity, has no major role in determining patch occupancy, but it influences the mean size of populations with low emigration rate (due to large patch size or strong edge-mediated behavior) and hence high probability of occupancy. It was far from obvious, a priori, how patch quality influences population dynamics, and thus it is noteworthy that this question could be addressed by fitting a metapopulation model to the kind of data that were available for this study.

The model-estimated habitat quality (ε_i) was positively correlated with four environmental variables that were not used in parameter estimation: (1) the amount

of grazing; (2) the density of nectar plants; (3) the density of host plants; (4) the percentage of dry host plants.

Although the short-term effects of grazing and trampling must necessarily be negative (Hanski et al. 1996, Moilanen and Hanski 1998), other studies on butterflies have also found positive long-term effects of grazing (Murphy et al. 1990, Thomas and Jones 1993), apparently because grazing prevents secondary succession that would eliminate the appropriate microhabitats and even host plants for the butterfly. The disappearance of the Glanville fritillary from mainland Finland in the 1970s is thought to have been caused by dramatic decline in cattle and sheep grazing, causing meadows to become overgrown (Nieminen et al. 2004).

That nectar plant and host plant density had a positive effect on patch quality is not surprising, as these features represent the key resources for butterflies and tend to increase immigration to and decrease emigration from a habitat patch (Kuussaari et al. 1996, Moilanen and Hanski 1998, Nieminen et al. 2004). Not surprisingly, survival and growth of larvae are dependent on the density of host plants (Kuussaari et al. 2004). Our results indicate that habitat quality effects were largely mediated via dispersal, which suggests that the previously demonstrated nectar plant and host plant density effects on dispersal largely determined the overall effect of habitat quality on metapopulation dynamics.

That patch quality increases with an increasing percentage of dried host plants is a more surprising result, because withered host plants can cause widespread larval mortality (Nieminen et al. 2004). This result is likely to be due to variation in habitat type. The two host plants occur on dry rocky outcrops, meadows, pastures, and road verges. In most years, the dry rocky outcrops provide especially suitable habitat for the Glanville fritillary (Nieminen et al. 2004), but in exceptionally dry years, populations perform badly in these habitats. In fact, there is likely to be an interaction between temporal (year-to-year) and spatial (meadow-to-meadow) variation in habitat quality, although these interactions were not included in the models.

Cross-validations

Both models were successfully cross-validated in the sense that they explained a large amount of variation (roughly 50%) in the fraction of occupied patches among independent patch networks. However, both models tended to overpredict the occurrence of the butterfly in most parts of the Åland Islands, including the focal patch network that was used for model fitting. This is probably due to a mismatch between structural model assumptions and reality, although we could not clearly identify which model component should be revised to improve the match with the data. However, there are also alternative explanations of the overprediction, which highlights the fact that complex as our model already is, there are still likely to be other processes that

affect quantitatively the real dynamics. (1) The e_i and t_i^* values that we estimated may not describe well the environmental conditions across all the networks due to spatially correlated weather effects (Hanski and Meyke 2005). (2) We assumed that the type of the matrix habitat surrounding the habitat patches is the same within and between all networks. However, there is obvious regional variation in landscape structure in Åland, including barriers to dispersal (water bodies and more extensive forest areas; Nieminen et al. 2004). Therefore, “effective isolation” (Ricketts 2001) of the networks and patches within the networks may vary substantially, and our focal network that was used for parameter estimation may have been more favorable than the average network in this respect. (3) Interaction with the specialist parasitoid *Cotesia melitaearum* has been shown to cause local extinctions of the host butterfly and to cause regional differences in the occurrence of the Glanville fritillary (Lei and Hanski 1997). However, in the past decade the parasitoid populations have been at a low level and hence unlikely to have had a major effect on the host butterfly (Nieminen et al. 2004). (4) Previous research has shown an increasing risk of extinction with increasing levels of inbreeding in local populations (Saccheri et al. 1998). It is noteworthy that, in the present study, the model overpredicted the fraction of patches occupied, especially in those networks where a small fraction of patches was generally occupied (Fig. 7b). These networks have a small number of typically small populations, which is the situation in which inbreeding is most prevalent and likely to suppress fitness. This result highlights the potential importance of coupled demographic and genetic dynamics (Hanski 2011).

Given all these sources of additional complexity and uncertainty, which had to be omitted in the present models, we find it encouraging that the models nonetheless explained a large part of the variation in habitat occupancy among the networks. One interesting direction for future work would be to test whether the predictive power of the models could be improved by accounting for these factors. Doing so would require incorporating further hierarchical levels to the already rather complex model and fitting the model simultaneously to data from all patch networks instead of using a single network in parameter estimation, as done in the present study. This would call for the use of alternative approaches for model fitting, such as the Approximate Bayesian Computation, ABC (Csilléry et al. 2010) or MCMC methods that exchange information among models of varying complexity (Holloman et al. 2006).

In the present results, especially for the SPOM, some of the marginal distributions had posteriors that had not changed significantly from the respective priors (see Fig. 4), which implies redundancy in some of the parameters. Another interesting avenue for future research would be to use model selection, such as Bayesian Information Criterion, BIC (Schwarz 1978), to compare simpler

versions of the models in which some of the parameters and states have been integrated out. Another worthwhile extension would be to compare the performance of the present SPOM, derived from the IBM, with the performance of traditional SPOMs based on more phenomenological assumptions (Ovaskainen and Hanski 2004b).

Population models attempt to capture the essence of real population dynamics. However, the Earth's biota and environments are extraordinarily complex, and there is hardly any aspect of the interactions between the species and their environments that we can confidently describe with a mathematical equation (Lovelock 1989). In the words of Cormack (1968): “Even the most general mathematical model is a plaything relative to the complexities of an animal population.” Because reality is high dimensional (Buckland et al. 1997), no matter how rich our data sources are, the best we can ever do is to approximate reality. Here we have shown that a detailed model gives a better approximation of reality than a simpler model, but this comes with the costs of greatly increased data requirements and computational challenges. At the same time, the simpler model did not perform overly worse than the complex model, and our results support the notion that simple models play a key role in the development of ecological theory and in interpreting ecological data. An important point, however, is that we derived the simple model rigorously from the complex one, a step that should be generally useful and does not require quantitative data or extra computing.

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APPENDIX A

Additional model information for the IBM (individual-based model) and SPOM (stochastic patch occupancy model) (*Ecological Archives* M081-021-A1).

APPENDIX B

SPOM derivation and testing (*Ecological Archives* M081-021-A2).

APPENDIX C

Prior distributions and additional mark–recapture results (*Ecological Archives* M081-021-A3).

APPENDIX D

MCMC (Markov chain Monte Carlo) implementation (*Ecological Archives* M081-021-A4).

APPENDIX E

SSM (state-space model) results with simulated data (*Ecological Archives* M081-021-A5).

APPENDIX F

MCMC mixing and correlations between parameters (*Ecological Archives* M081-021-A6).

SUPPLEMENT

Focal network information, long-term survey data, and control data to which the SSMs were fitted (*Ecological Archives* M081-021-S1).