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Metapopulation structure and movements in five species of checkerspot butterflies

Abstract We studied the patterns and rates of migration among habitat patches for five species of checkerspot butterflies (Lepidoptera: Melitaeini) in Finland: *Euphydryas aurinia*, *E. maturna*, *Melitaea cinxia*, *M. diamina* and *M. athalia*. We applied the virtual migration (VM) model to mark-release-recapture data collected from multiple populations. The model includes parameters describing migration and survival rates and how they depend on the areas and connectivities of habitat patches. The number of individuals captured varied from 73 to 1,123, depending on species and sex, and the daily recapture probabilities varied between 0.09–0.52. The VM model fitted the data quite well. The results show that the five species are broadly similar in their movement rates and patterns, though, e.g. *E. maturna* tends to move shorter distances than the other species. There is no indication of any phylogenetic component in the parameter values. The parameter values estimated for each species suggest that a large percentage (80–90%) of migration events were successful in the landscapes that were studied. The area of the habitat patch had a substantial effect on emigration and immigration rates, such that butterflies were more likely to leave small than large patches and large patches were more likely than small patches to receive immigrants.

Keywords Mark-release-recapture · Migration · Metapopulation · Lepidoptera

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Introduction

Movement of individuals (migration) among patches of suitable habitat is a key process in metapopulation dynamics (Hanski and Simberloff 1997; Ims and Yoccoz 1997). Migration rate largely sets the rate of colonisation of empty patches, and migration may also influence the extinction risk of local populations through the rescue effect (Brown and Kodric-Brown 1977; Hanski et al. 1995b) and through increased risk of extinction of small populations when the emigration rate is high (Thomas and Hanski 1997; Hanski 1999). Patterns of migration among multiple populations have been studied using mark-release-recapture (MRR) methods in many taxa including butterflies (Thomas and Hanski 1997), but analysing such data is not straightforward. Standard methods for analysing MRR data have been developed primarily for single populations (Lebreton et al. 1992). The methods can be extended to several populations (Hestbeck et al. 1991; Lebreton et al. 1992), but they do not distinguish between mortality within a habitat patch from mortality during migration and they become exceedingly cumbersome as the number of connected populations increases.

While there are many published MRR studies on butterflies, comparing their results is not easy because they have been performed in different landscapes by different researchers in different years. Practically all studies on butterflies are concerned with single species, which further hinders comparisons. Most authors have developed their own ad hoc measures of migration rate to analyse movements of individuals in metapopulations (e.g. Scott 1973; Tabashnik 1980; Baguette and Nève 1994; Hill et al. 1996). The most common approach has been to simply record the distance an individual has moved between successive captures. The distributions of movement distances are usually highly skewed to the left, meaning that most individuals move short distances while a few individuals move a much longer distance (e.g. Hill et al. 1996; Brommer and Fred 1999; Gutiérrez et al. 1999). Most studies report that butterflies move

from 100 to 200 m on average (e.g. Scott 1975; Tabashnik 1980; Murphy et al. 1986; Warren 1987). The maximum observed movement distances are generally between 1–2 km, which usually corresponds to the maximum observable distance in the particular study area (e.g. Watt et al. 1977; Brown and Ehrlich 1980; Warren 1987; Baguette and Nève 1994). However, the average and maximum distances calculated from the raw data are influenced by sampling intensity and are thus not useful statistics. What is needed is an appropriate distribution of movement distances, the parameters of which can be estimated with the empirical data.

Several habitat patch-oriented metapopulation studies have attempted to calculate migration rates or probabilities among local populations (Baguette and Nève 1994; Hill et al. 1996; Lewis et al. 1997). The simplest index of "emigration rate" is the proportion of all recaptured individuals that are recaptured in a patch other than the patch where the previous capture took place. One may also attempt to estimate patch-specific emigration and immigration rates, again by calculating the proportion of emigrants and immigrants amongst all recaptures, but now separately for each patch. Using such an approach, several studies have discovered that patch area has a negative effect on emigration rate and that patch connectivity increases immigration rate in butterflies (Hill et al. 1996; Kuussaari et al. 1996; Sutcliffe et al. 1997; Baguette et al. 2000). However, these calculations do not take into account mortality during migration nor do they account for the detection probability which is less than 1. Clearly, basing inferences about movement rates and patterns on a clearly defined statistical model would be desirable.

One general pattern that has emerged from metapopulation studies is that the probability of an empty patch being colonised decreases with increasing isolation from existing local populations (Hanski 1999). Whether this is due to individuals simply not moving very far during their lifetime or to elevated mortality during migration is not clear. The difficulty lies in estimating mortality during migration. Migration mortality is one of the major costs faced by an individual when making the "decision" to leave its natal patch (Olivieri and Gouyon 1997). Being able to estimate the magnitude of this cost of migration would contribute to a better understanding of whether evolutionarily stable migration rates have evolved in different species inhabiting different landscapes.

A recent modelling approach proposed by Hanski et al. (2000), known as the virtual migration (VM) model, attempts to separate mortality within habitat patches from mortality during migration. The model requires data from many (≥10) local populations inhabiting habitat patches that differ in their areas and relative isolation. Using MRR data from such multiple populations, the model estimates parameters describing daily survival within a patch, the propensity to migrate from a patch, the effects of patch area on emigration and immigration, and the effects of patch connectivity on migra-

tion and mortality during migration. The latter is estimated on the assumption that the probability of dying during migration increases with increasing isolation of the source population from the other populations, which are the targets of migration.

Once we can estimate the parameters of migration and mortality in metapopulations, we can compare metapopulations of the same species and of different species to assess how conservative migration behaviour is. So far, the VM model has been used to compare the variation in migration behaviour among different years in one species of butterfly (Petit et al. 2001). Studying *Proclossiana eunomia* (Esper), the latter authors found that the rate of migration remained relatively stable over several years.

Extensive studies on *Melitaea cinxia* (L.) in Finland (see Hanski 1999 for a review) prompted us to ask whether related Finnish species would show similar metapopulation structures and movement patterns. We chose to study four species in addition to *M. cinxia* that all belong to the tribe Melitaeini (Lepidoptera: Nymphalidae): *Euphydryas aurinia* (Rottemburg), *E. maturna* (L.), *M. diamina* (Lang) and *M. athalia* (Rottemburg). Using the VM model of Hanski et al. (2000), we estimated the values of a set of parameters describing the movements of individuals in fragmented landscapes. We then used these parameter values to examine interspecific features of the rates and patterns of migration of these butterfly species.
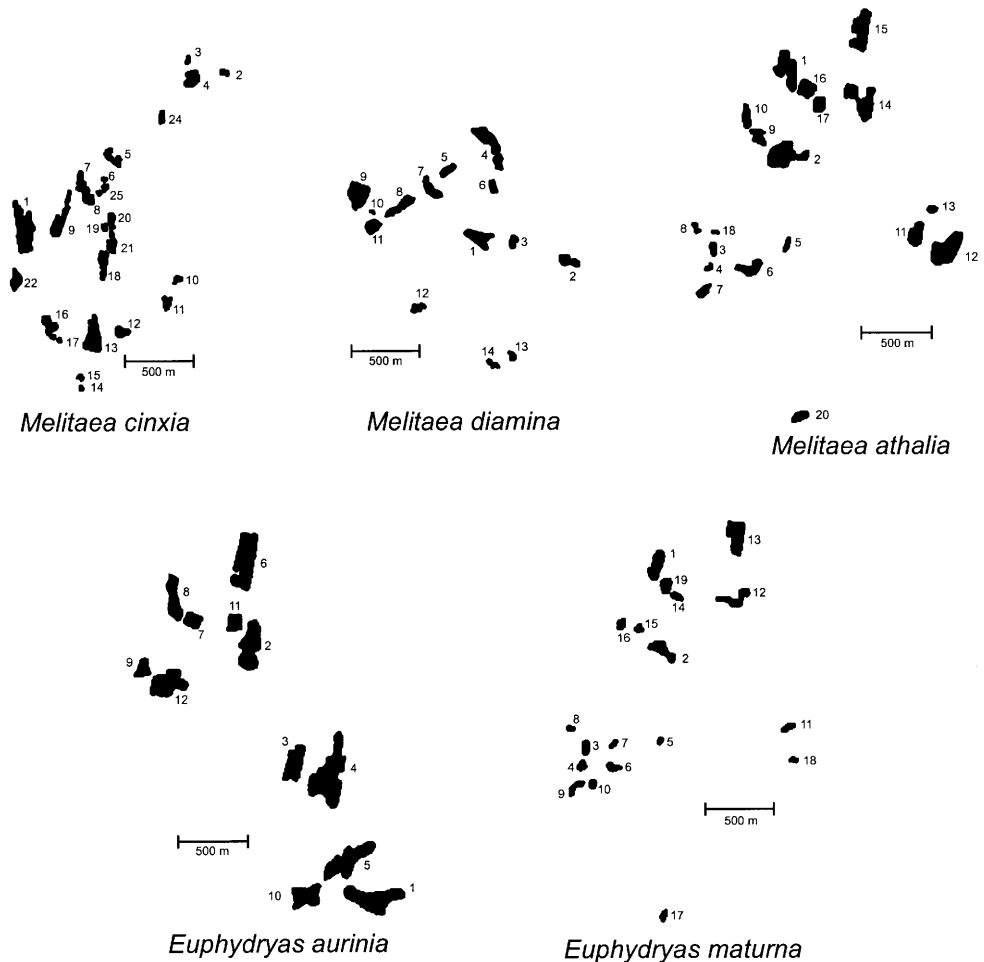
Materials and methods

The species

The five species studied here are ecologically fairly similar (Wahlberg 2000) and phylogenetically closely related (Wahlberg and Zimmermann 2000). Three species (*E. aurinia*, *M. diamina* and *M. cinxia*) are found on open meadows that are distinct habitats within the surrounding matrix of unsuitable habitat (Hanski et al. 1994, 1995a; Wahlberg 1997, 2000; Hanski 1999). The remaining two species (*E. maturna* and *M. athalia*) are found along forest edges and openings within forests (Wahlberg 1998, 2000, 2001). The adults of all five species can be found in flight in Finland from the beginning of June until the middle of July (Wahlberg 2000).

The conservation status of the five species is dissimilar. The three species found on open meadows are all endangered and highly localized in Finland and their population numbers have been declining in the past decades (van Swaay and Warren 1999). *E. maturna* is fairly common in south-east Finland, but in most of Europe it is considered to be highly endangered (van Swaay and Warren 1999; Wahlberg 2001). *M. athalia* is a common species throughout southern Finland and most of Europe (Tolman and Lewington 1997).

Mate-searching behaviour may influence movements of male butterflies. Mate searching behaviours have been classified into two types, known as the perching and patrolling tactics (Scott 1974). Perching males sit and wait on prominent pieces of vegetation or open ground and fly to investigate any passing insects. If the passer-by is a conspecific male, a spiral fight ensues, with the original perch owner returning more often than the intruder to the perch. If the passer-by is a conspecific female, the male attempts to court and mate with her. Patrolling males fly slowly through the habitat while searching for females, and they land next to any insect that has similar coloration and size to females. The perching

Fig. 1 The patch networks occupied by the five species of Finnish Melitaeini butterflies on which the mark-recapture studies were performed

Melitaea cinxia

Melitaea diamina

Melitaea athalia

Euphydryas aurinia

Euphydryas maturna

and patrolling tactics can be used interchangeably in some species, while others show only one or the other. Of our study species, *M. diamina* and *M. athalia* have been observed to use only the patrolling tactic in Finland (Wahlberg 1997, 2000), *M. cinxia* and *E. aurinia* use both the perching and patrolling tactics (Wahlberg 2000), and *E. maturna* males are strictly perchers (Wahlberg 1998).

The general biology, phylogenetic position and conservation status of the five studied species lead to different predictions about their movement behaviour. First, this is a set of closely related species of similar size, and thus they might be expected to have similar abilities in moving among habitat patches. Alternatively, the three endangered species might not migrate as readily as the two more widely distributed species, thus restricting the former to areas with dense networks of patches and potentially making them particularly vulnerable to habitat loss and fragmentation. Third, the behaviour of males may affect their rates of migration, such that genuine perchers move much less than patrollers. In this third case, the movement of females of the different species is expected to be more similar to each other than to movements of males in the respective species.

The study systems

The five species were studied using similar MRR techniques in three areas in southern Finland. *M. cinxia* was studied in the Åland Islands in south-west Finland (Hanski et al. 1994), *M. diamina* in the Tampere region in south-central Finland (Wahlberg et al. 1996) and the other three species were studied in the Joutseno region in south-east Finland (Klemetti and Wahlberg 1997; Selonen 1997). In all studies, we marked each butterfly with an individual number on the underside of the hindwing. We recorded the loca-

tion, wing wear (on a scale from 1 to 3: fresh, medium, worn) and the number of the individual for each capture and recapture. We studied all species within areas of circa 2×2 km², with the number of habitat patches within this area ranging from 12 to 20 (Fig. 1). *E. maturna*, *E. aurinia* and *M. athalia* were studied within the same 2×2 km² square. For *M. cinxia*, we use a subset of the data collected by Hanski et al. (1994), covering a similar area to that of the study areas for the other four species. For four species (except *M. cinxia*), the habitat surrounding the patches was mainly spruce forest. For *M. cinxia*, the matrix habitat was a mixture of open fields, gardens and woodlands.

The spatial configuration of the habitat patches in the landscape was known in advance for three of the species (*E. aurinia*, *M. cinxia* and *M. diamina*). In these cases, one patch with a central position in the network and with a relatively large local population was visited on every sampling day. The other patches were visited as often as possible, usually every other sampling day. For the other two species (*E. maturna* and *M. athalia*), we were unable to delimit habitat patches prior to the MRR study. Instead, we divided the study area into a grid with 10×10 m² cells and recorded the coordinates of each capture and recapture. Patches were defined a posteriori based on landscape features (meadows, forest edges) and the frequency of individual captures and recaptures (Selonen 1997). In each study, two or three researchers sampled butterflies daily throughout the flight season, except on rainy days (Table 1).

Analysis of MRR data

In this study, we were primarily interested in how the movement patterns of individuals are related to the structure of the fragment-

Table 1 Mark-release-recapture data for five species of Melitaeini in Finland

Species	Sampling period	Number of days sampled	Individuals captured		Individuals recaptured (total mumber of recaptures)	
			Males	Females	Males	Females
Euphydryas aurinia	10 June–10 July 1996	19	254	73	130 (217)	29 (38)
Euphydryas maturna	11 June– 15 July 1996	21	159	94	52 (76)	16 (16)
Melitaea cinxia	06 June–08 July 1991	24	1123	456	371 (616)	88 (116)
Melitaea diamina	16 June–14 July 1995	25	555	273	298 (710[a])	151 (317)
Melitaea athalia	11 June–15 July 1996	21	614	189	152 (190)	24 (33)

[a] Number of recaptures (1,301) reported in Hanski et al. (2000) is actually captures+recaptures, with some same-day recaptures included. These numbers were calculated from the original data file and do not affect the results reported in that paper in any way

ed landscape (Fig. 1). For this purpose, we estimated the parameters describing survival and migration of individuals using the VM model (Hanski et al. 2000) separately for males and females in each species. With this model, we obtain estimates of emigration and immigration rates and their scaling with patch area. An additional advantage of the VM model is that one can separate mortality within habitat patches from mortality during migration, based on the assumption that only the latter is affected by the isolation of the source patch. We describe only the biological model here; for details of the corresponding statistical model and parameter estimation see Hanski et al. (2000).

The model is based on discretised histories of individuals, with daily events occurring in the following order. First, the individual survives in the patch with probability ϕ_p until the end of the day or until it emigrates, whichever occurs first. The parameter ϕ_p is assumed to be independent of patch area. Second, if the individual survives and emigrates, it survives migration from patch j with probability ϕ_{mj}. Third, if the individual survives migration, it immigrates to some other patch during the same time interval (day). These events recur in the subsequent time intervals until the individual dies, either in some patch or during migration.

The patch-specific but time-independent probability ε_j of emigrating from patch j is assumed to scale to patch area A_j by the power function:

$$\varepsilon_j = \eta A_j^{-\zeta_{em}}, \tag{1}$$

where $\eta > 0$ is a parameter describing propensity to emigrate and $\zeta_{em} > 0$ is a parameter scaling emigration (subscript "em") to patch area. The connectivity of patch j is measured by:

$$S_j = \sum_{k \neq j} \exp\left(-\alpha d_{jk}\right) A_k^{\zeta_{im}}. \tag{2}$$

Here, d_{jk} is the Euclidian distance between patches j and k. Parameter $\alpha > 0$ determines the effect of distance on migration in this formula. Parameter $\zeta_{im} > 0$ scales immigration (subscript "im") to patch area A_k, such that different-sized patches "attract" individuals differently for a given d_{jk}. S_j as defined by Eq. 2 is analogous to the measure of population connectivity used in the incidence function model of metapopulation dynamics (Hanski 1994), but the role of the focal patch is here reversed. In the incidence function model, patch j is an empty patch, and S_j measures its connectivity to potential source populations. In the VM model, patch j is the source of migrants that may succeed in reaching other habitat patches.

The connectivity of patch j, as measured by S_j, is assumed to affect positively the probability ϕ_{mj} of surviving migration from patch j, i.e. mortality of emigrants is higher for the less connected patches. As ϕ_{mj} approaches 0 and 1 when S_j approaches 0 and ∞, respectively, we describe ϕ_{mj} as a sigmoidally increasing function of S_j:

$$\phi_{mj} = \frac{S_j^2}{\lambda + S_j^2}. \tag{3}$$

This formula adds one more parameter $\lambda > 0$ to the model. The parameter λ gives the square of the population connectivity (S, Eq. 2) for which the probability of surviving migration equals 0.5. λ thus determines mortality during migration, but note that since parameters α and ζ_{im} affect the value of patch connectivity, they also affect mortality during migration. The individuals that survive migration are assumed to be distributed among all the target patches in proportion to their contributions to the connectivity of patch j (Eq. 2). Thus the probability of an individual leaving patch j and reaching patch k is given by:

$$\psi_{jk} = \frac{\exp\left(-\alpha d_{jk}\right) A_k^{\zeta_{im}}}{\frac{\lambda}{S_j} + S_j}. \tag{4}$$

The probability of successfully migrating from patch j to patch k thus depends on the distance between the two patches, the area of the receiving patch k, but also on the number and areas of other patches in the neighbourhood of patch j. The latter dependence models "competition" among potential target patches for individuals migrating from patch j. Successful migration is assumed to occur within one time unit. The same individual may re-emigrate in the following time interval. The model has six parameters, ϕ_p, η, ζ_{em}, ζ_{im}, α and λ, which can be estimated using MRR data and knowledge of patch areas and locations.

To illustrate the consequences of the parameter values for the different sexes and species, we simulated the movements and survival of a cohort of butterflies in the respective patch network of each species using the parameter values estimated with the VM model. Daily population sizes were (roughly) estimated for the patches for which there were sufficient MRR data, using the Jolly-Seber method for open populations (Jolly 1965; Seber 1965; Pollock et al. 1990) as implemented in the program JOLLY (Hines 1990). We estimated the population size for the entire flight season following the method of Watt et al. (1977). For the other patches in the network, we estimated population sizes by multiplying the observed number of individuals by the ratio of population size estimate to the observed number of individuals in the patches for which we were able to estimate population sizes as explained above. Population size estimates for *M. cinxia* were taken from Hanski et al. (1994).

Results

Basic statistics

The ten data sets (5 species×2 sexes) show much variation and present challenging material for a comparative study. In general, more males than females were captured in all species included in this study (Table 1), reflecting the generally higher probability of capture of

Table 2 Basic results for observed migration events (*Migrants* number of individuals observed to migrate, *Proportion of recaptured individuals* previous columns expressed as proportions of all recaptured individuals, *Number of patch pairs* number of patch pairs between which migration was observed

Species	Migrants		Proportion of recaptured individuals		Number of patch pairs		Distance moved (m)			
							Males		Females	
	Males	Females	Males	Females	Males	Females	Mean±SE	Maximum	Mean±SE	Maximum
Euphydryas aurinia	22	2	0.17	0.07	12	2	645±69	1,300	467±43	510
Euphydryas maturna	23	4	0.44	0.25	11	1	238±33	640	141±0	141
Melitaea cinxia	44	20	0.12	0.23	16	15	438±57	1,700	573±89	1,700
Melitaea diamina	103	17	0.35	0.11	21	5	436±23	1,370	469±57	800
Melitaea athalia	58	7	0.38	0.29	35	6	498±53	1,676	555±148	1,204

males than females (see below). Otherwise, no two data sets are similar. Average patch sizes and connectivity measures varied between the landscapes (see Fig. 1). The numbers of individuals captured and recapture rates were different between species and sexes, with the fraction of individuals recaptured varying between 13–54% of the individuals marked (Table 1).

The basic statistics on migration show much variation, with the percentage of recaptured individuals observed in a new patch ranging from 7 to 44% (Table 2). The proportion of individuals that had migrated by this measure appears to be negatively correlated with the distance they were observed to migrate (Table 2). For example, 44% of recaptured *E. maturna* males had moved to a new patch, but only about 200 m on average, while 17% of recaptured *E. aurinia* males had moved to a new patch, located 650 m from the source population on average. This may largely be due to the differences in average patch areas in the different patch networks (see Fig. 1), i.e. an individual *E. aurinia* leaving a patch is more likely to move a longer distance than an individual *E. maturna*. The maximum observed movement distances were mostly over 1,000 m and largely reflect the maximum observable distances in the study areas. The exception is *E. maturna*, which apparently flew much shorter distances (maximum 640 m) than the other species. In summary, there appear to be real differences between the species, but these observed differences in the basic statistics may be greatly influenced by variation in the characteristics of the data sets. Comparisons should therefore be based on the parameter values of an appropriate model fitted to the data.

Parameter estimates

The estimated parameter values of the VM model and their associated 95% confidence limits are shown in Fig. 2. The quality of the data sets is reflected in the width of the confidence limits. In the extreme case, for female *E. aurinia*, all parameters related to migration had to be estimated based on two individuals that were observed to migrate between the patches, which was not enough to generate any confidence limits. For most of the data sets, we were able to obtain reasonable estimates for the six parameters. In the following, we compare the species and the sexes one parameter at a time. Because it is difficult to test whether two parameter values are statistically different when the confidence limits are asymmetrical, we consider parameter values to differ significantly only if their 95% confidence limits do not overlap.

The probability of daily survival within a patch (ϕ_p) ranged from 0.88 to 1.00 (Fig. 2). The data sets for females are small, and the model leads to an estimate $\phi_p=1$ for four species (Fig. 2), with very wide confidence limits (Fig. 2). The males of *M. cinxia* and *M. diamina* have a lower daily survival rate (around 90%) than the males of *E. maturna* and *M. athalia* (around 98%; Fig. 2). There is also an indication that *E. aurinia* males have a higher daily survival rate than the former two species (Fig. 2). It is worth noting that the summers of 1991 and 1995, when *M. cinxia* and *M. diamina* were studied, respectively, were warm compared to the summer of 1996, when the other three species were studied. Insect metabolism is faster at higher temperatures and this may decrease the expected lifespan of individuals.

The parameter η describing daily emigration propensity from a patch of unit area (1 ha) was mostly around 10% (Fig. 2). The actual emigration rate is also influenced by patch area and the scaling parameter ζ_{em} (see below and Eq. 1), but as 1 ha is a commonly occurring patch size for all species, we use it here as the basis for comparisons. The only difference between the sexes within a species is for *M. cinxia*, with females much more likely to emigrate than males ($\eta=0.38$ vs 0.12). The high rate of emigration by *M. cinxia* females sets it apart from all the other species, except female *E. maturna*, with overlapping 95% confidence limits. The parameter η is not correlated with the proportion of individuals recaptured as immigrants (Fig. 3a). The latter has been used as a measure of migration propensity in some studies (e.g. Baguette and Nève 1994). The parameter η also does not show any effect of the warm summers of 1991 and 1995 on the emigration propensities of *M. cinxia* and *M. diamina* compared to the cool summer 1996, during which the other three species were studied.

The parameter scaling emigration to patch area (ζ_{em}) varies greatly between the species and sexes, ranging
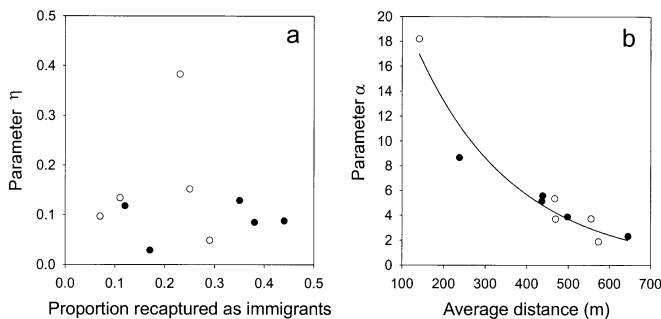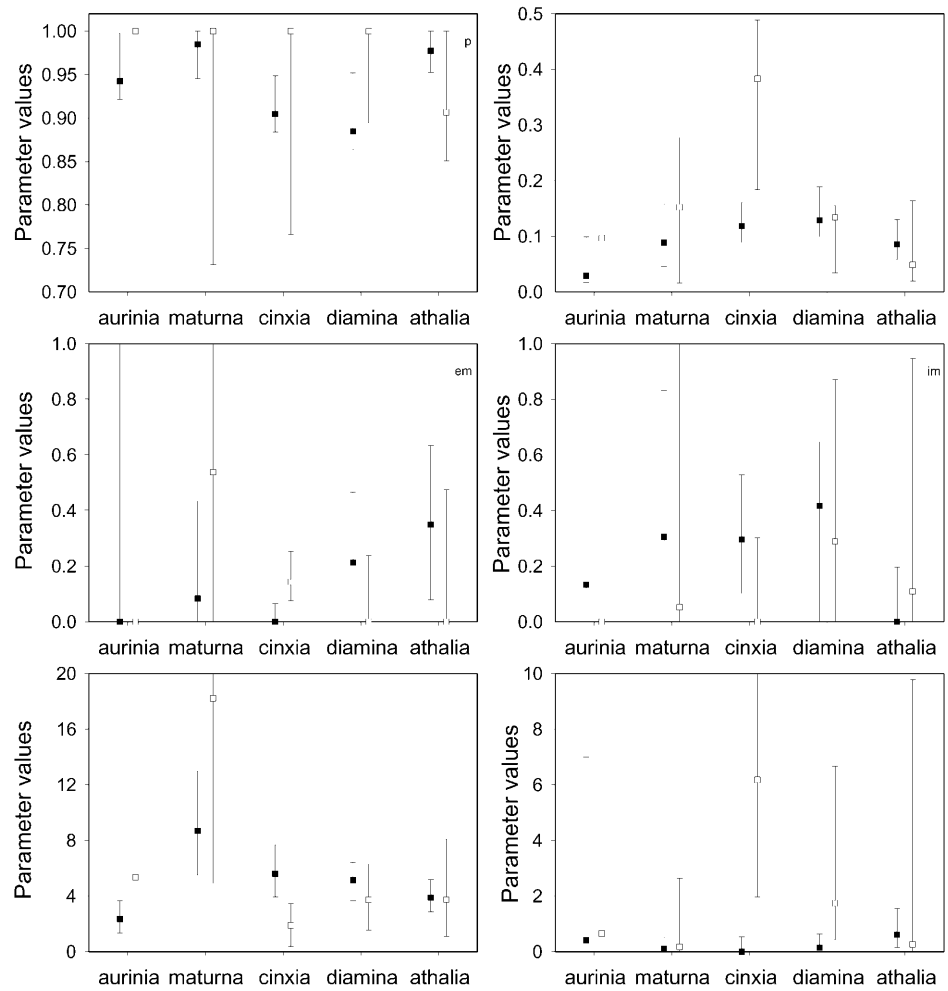
Fig. 3 a The value of parameter η plotted against the proportion of recaptures in a new patch (indicating migration) separately for different species and sexes (males *filled*, females *open symbols*). The value of η does not correlate with the proportion of recaptures following migration (Spearman rank correlation, $r_s = -0.100$, $P = 0.873$ for males and females). **b** The value of parameter α against the observed average distance moved by emigrating individuals in each species and sex (males *filled*, females *open symbols*). The value of α correlates well with the observed average distance moved (Spearman rank correlation, $r_s = -0.900$, $P = 0.037$ for both males and females). The line shows the fitted non-linear regression for the pooled data, where $\alpha = 30.94 \times e^{-0.004 \times \text{average distance}}$. Note that the model-predicted average distance moved is given by $1/\alpha$

from 0 (no effect of area on emigration) to 0.54. In general, however, the per capita emigration rate is higher in small than in large patches. The effect of patch area on emigration is significantly different only in a comparison of *M. cinxia* males ($\zeta_{em} = 0$) to *M. cinxia* females ($\zeta_{em} = 0.14$) and *M. athalia* males ($\zeta_{em} = 0.35$). The parameter scaling immigration to patch area (ζ_{im}) appears to be slightly higher on average than the previous parameter when comparing the two parameters within each species and sex. However, only the *M. cinxia* male data set has a parameter value that is significantly different from 0. There are no significant differences between the species and the sexes in this respect.

The parameter describing the effect of distance on isolation (α) varies from circa 2 (small effect) to over 10 (large effect) (Fig. 2). Note that α here describes the effect of distance on daily movements rather than on movements over the entire flight period (as reported in studies of yearly colonization rate: Hanski et al. 1994; Thomas et al. 1998a; Gutiérrez et al. 1999). The only significant difference between the two sexes within a species is in *M. cinxia*, where males tend to move shorter distances than females. In a comparison of different species, there is an indication that movements in *E. maturna* are more affect-

ed by distance than in the other species (Fig. 2). The α values for *E. maturna* males and females are significantly greater than α-values for *E. aurinia* males, *M. cinxia* females and *M. athalia* males. The α-values for *E. aurinia* males and *M. cinxia* females are also significantly smaller than those of *M. cinxia* males and *M. diamina* males. The estimated α-values are negatively correlated with the observed average distance moved (Fig. 3b). In parameter λ, the only significant difference is between *M. cinxia* females (with a large value) and males of *E. maturna*, *M. cinxia*, *M. diamina* and *M. athalia*.

For the females of all species except *M. athalia*, survival within a patch was estimated to be 1 and all mortality was placed in parameter λ (migration), with both λ and ϕ_p having very wide confidence limits (Fig. 2). This result is most likely due to a strong correlation among the parameters affecting mortality and small sample size for females (Table 1). The data for females are simply not sufficient to reliably tease apart mortality within habitat and mortality during migration.

Model goodness-of-fit

We tested how well the parameterised models fit the data using the goodness-of-fit test described in Hanski et al. (2000). In general, the model described well the numbers of residents, emigrants and immigrants for each habitat patch. As the goodness-of-fit tests were performed for each patch, species and sex separately, there are a total of 534 χ^2-tests, of which 23 were significant at the 5% level. Though 5% of the tests are expected to be significant when a large number of tests is performed, examining which patches failed the test is potentially informative. Most patches that failed the goodness-of-fit test had more observed events than was predicted, though in over half of the cases there was just 1 observation against a prediction close to 0, meaning that the test itself is very unreliable (*n*=14). The predicted number of resident captures differed significantly from the actual number of captures in two patches for *E. aurinia* males (too many predicted in one and too few in the other patch), one patch for *M. athalia* males (too few predicted) and one (different) patch for *M. athalia* females (too few predicted). Too few emigrants were predicted in one patch for *M. diamina* males, two patches for *M. athalia* males and one patch for *M. cinxia* females. Significantly less immigrants were predicted in one patch for *M. diamina* males, one patch for *M. athalia* males and two patches for *M. cinxia* females. None of these patches differed in patch area or connectivity from the patches for which the VM model successfully predicted the numbers of residents, emigrants and immigrants. We conclude that the model fitted the data well and the apparently significant deviations can be attributed to chance.

Population sizes and immigrant-days

We were able to roughly estimate daily population sizes for males of all species and for females of *M. cinxia* and

Table 3 Estimated size of the entire metapopulation and the average lifespan of adult butterflies (calculated as total number of butterfly-days/population size)

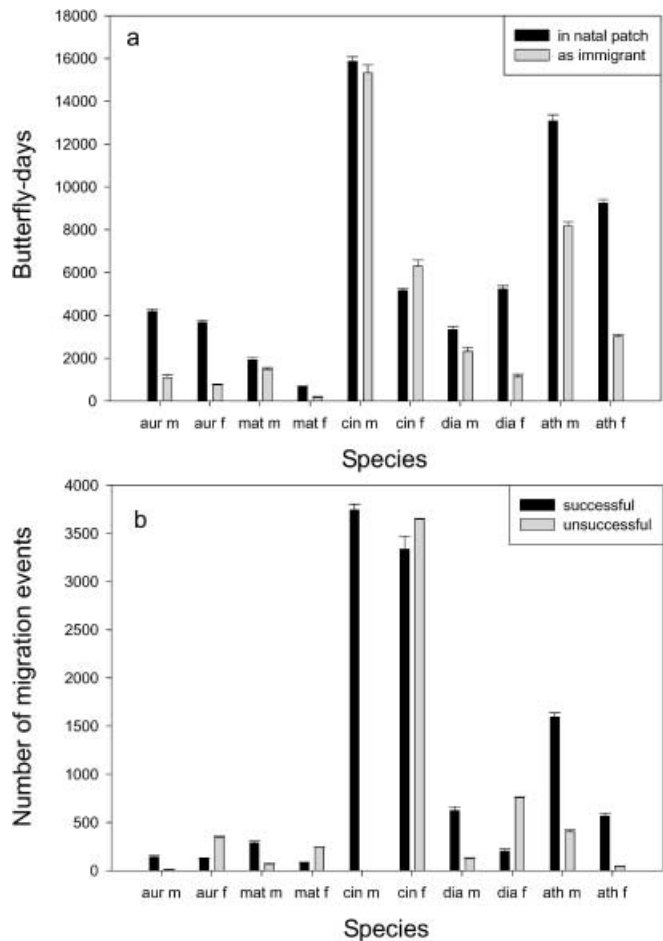| Species	Metapopulation size	Average lifespan (days)	
		Males	Females
Euphydryas aurinia	988	10.7	8.9
Euphydryas maturna	512	13.3	3.3
Melitaea cinxia	7,644	8.2	3.0
Melitaea diamina	1,886	6.0	6.7
Melitaea athalia	3,388	12.5	7.2

Fig. 4a,b Results of simulations for five species of Melitaeini in their respective patch networks. Each *bar* gives the average of ten simulations with 1 SD shown (*m* male, *f* female). **a** Total number of butterfly-days spent in the natal patch (*black bars*) and in a new patch following migration (*grey bars*). **b** Total number of migration events predicted to be successful (*black bars*) and unsuccessful (*grey bars*)

M. diamina. The sex ratio of all the studied species has been about 1:1 in rearings (N. Wahlberg and I. Hanski, personal observations) and thus we multiplied the population size estimate for males by 2 to arrive at an estimate for the entire metapopulation size (Table 3). While the numbers presented in Table 3 cannot be considered

accurate, they represent the correct magnitude of population sizes. The estimated metapopulation sizes ranged from about 500 individuals in *E. maturna* to more than 7,000 individuals in *M. cinxia*.

The simulation model described in Hanski et al. (2000) calculates the numbers of days individuals spend as residents, emigrants and immigrants for each patch separately, given the parameter values of the VM model and the total population sizes of each patch. Our results indicate that the majority of pooled butterfly-days are spent in the natal patch in most species and sexes (Fig. 4a). Dividing the total number of butterfly-days spent in the system by population size gives an estimate of the average lifespan (Table 3). In general, males are estimated to live longer than females. The two species that were studied during warm summers, *M. diamina* and *M. cinxia*, had shorter lifespans than the three other species studied during a cooler summer.

Females of *E. aurinia*, *E. maturna*, *M. cinxia* and *M. diamina* had estimates of within-patch mortality rate of zero and thus all mortality in the simulations occurred during migration. This is reflected in the high proportion of failed migration events (Fig. 4b). Conversely, for *M. cinxia* males, migration mortality was estimated to be zero and hence all migration events were successful (Fig. 4). Realistic values are shown by males of *E. aurinia*, *E. maturna*, *M diamina* and both sexes of *M. athalia*, with reasonably good estimates of parameter values (Fig. 2). In all these groups, 80–90% of migration events are predicted to be successful, and more individuals remain in the natal patch than migrate to new patches.

Discussion

We were able to successfully estimate parameter values related to individual movements among habitat patches and mortality within and between patches from data sets of varying quality. The parameter values obtained in this fashion are comparable, though one must keep in mind that, strictly speaking, they are specific to the landscape studied and the year of the study. Movement rates and patterns are known to vary temporally and spatially in butterflies (Gilbert and Singer 1973; Watt et al. 1977; White and Levin 1981; Ehrlich 1984; Petit et al. 2001). Nonetheless, the VM model parameter values are as informative for comparative purposes as any results based on observational field studies.

A realistic estimate of migration rate has been difficult to obtain using standard MRR techniques, since only individuals surviving migration can be recaptured, leading to a biased estimate of the true migration rate (Hill et al. 1996; Thomas et al. 1998b). The proportion of individuals recaptured as immigrants out of all individuals that were recaptured has been used as a measure of migration propensity (e.g. Baguette and Nève 1994). However, in our data sets, there is no relationship between the propensity to emigrate (parameter η) and the proportion

of individuals recaptured as immigrants (Fig. 3a). The result in Fig. 3a remained unchanged when emigration rate was calculated for a patch of 0.1 ha (Eq. 1). Other studies have calculated patch-specific immigration rates, taking into account mortality during migration without quantifying it (e.g. Hill et al. 1996; Sutcliffe et al. 1997), but these studies were not able to make any inferences about the emigration rates.

Patch size has an effect on emigration in several butterfly species (Hill et al. 1996; Kuussaari et al. 1996; Sutcliffe et al. 1997; Baguette et al. 2000; Petit et al. 2001), such that emigration rates are higher from small than from large patches. Our study shows the same effect for about half of the data sets (see Fig. 2), though the characteristics of the patch networks and especially the quality of the data sets clearly influence these results. For example, the range of patch sizes in *E. aurinia* may have been so small that the effects of patch size are obscured. The area effect makes intuitive sense, as individuals in a small patch are more likely to encounter the patch edge than are individuals in a large patch (Thomas and Hanski 1997).

The patches for which the model prediction did not match the observed numbers of residents, emigrants and immigrants did not seem to share any feature. Given the small number of significant differences and the generally small sample sizes (very small number of expected events), the deviations can perhaps be largely or even entirely attributed to chance. However, certain particular cases are suggestive of a biological mechanism. For example, patch no. 6 in the *M. diamina* network (Fig. 1) had a highly male biased sex ratio, with 14 males and only one female captured. Eight of the males are known to have emigrated, because they were recaptured in new patches. If there truly were very few females in patch no. 6, males in that patch would be expected not to stay but to migrate in search of females. Patch no. 6 was effectively not a patch for *M. diamina* males in 1995.

Checkerspot butterflies are generally fairly sedentary and tend to move short distances when moving between habitat patches (Ehrlich et al. 1975; Murphy et al. 1986; Warren 1987; Hanski et al. 1994). The species we have studied here are no exception, though we did find interspecific differences in the distances individuals moved during a migration event. The only species in which the sexes differed was *M. cinxia*, in which females were more likely to move further than males (see also Hanski et al. 1994). The three species studied in Joutseno are especially interesting to consider in this context, because they were studied in the same landscape in the same year. *E. maturna* and *M. athalia* had a similar migration propensity, while *E. aurinia* appeared to be less likely to leave its natal patch. The average patch size for *E. aurinia* was much greater than for the other two species (see Fig. 1), which may be related to the observed difference in emigration (though note that the parameter value η is not directly influenced by patch size). The individuals that do emigrate tend to move very short distances in *E. maturna*, long distances in *E. aurinia*, and intermedi-

ate distances in *M. athalia*. Mortality during migration was estimated to be higher for the two species that move further during migration. *E. maturna* is likely to immigrate into the neighbouring patch and stay there.

The VM model was apparently successful in separating mortality within patches from mortality during migration in five data sets (males of *E. aurinia*, *E. maturna*, *M diamina* and both sexes of *M. athalia*), though this result may be sensitive to model structural assumptions, which should be investigated in more detail. Emigration rates are around 10% per day from patches of 1 ha and decrease with increasing patch size. The exceptions are female *M. cinxia*, which had an emigration rate up to three times higher than in the other groups. This high rate of emigration was also found by Hanski et al. (1994) using ad hoc measures. For the five data sets with reasonable parameter estimates, the model predicted that 10–20% of migration events over the entire flight period lead to death.

A recent paper analysing the evolution of emigration rate with the help of the VM model parameterised for *M. diamina* males found that the value of η estimated empirically was very close to the predicted evolutionarily stable migration rate (Heino and Hanski 2001). This result may apply to the five species studied here, since the predicted mortality during migration is similar across the species. In particular, the five best-quality data sets discussed above gave rather homogeneous results despite the heterogeneity in the data sets themselves.

There appears to be no phylogenetic component in the parameter values. If there were, one would expect the two *Euphydryas* species to be more similar to each other than either is to the three *Melitaea* species and vice versa. None of the parameter values shows this kind of interspecific variation (Fig. 3). The absence of a phylogenetic component is not very surprising, because we have studied five closely related species of similar size and with similar ecologies. How broadly one must sample taxonomically to see a phylogenetic pattern (if there is one) is not clear at the moment. The only other butterfly species to have been studied using the VM model so far is *P. eunomia* Esper (Nymphalidae) (Petit et al. 2001), which is similar in size to the checkerspot butterflies, but has a different ecology. *P. eunomia* is not very closely related to checkerspots (it belongs to the subfamily Heliconiinae; Harvey 1991), yet it shows very similar parameter values (Petit et al. 2001) to the ones reported in this study. Other species which have been studied in fragmented landscapes are much more mobile, e.g. *Parnassius apollo* (L.) (Papilionidae) (Brommer and Fred 1999), or much less mobile, e.g. *Plebejus argus* (L.) (Lycaenidae) (Lewis et al. 1997; Thomas et al. 1998a). It is too early to say whether this is due to phylogeny (i.e. papilionids are more mobile than nymphalids and lycaenids are less mobile than nymphalids in general), or whether the observed differences are due to characteristics of the landscape (e.g. open versus closed habitat in the surroundings of the patches).

The mate-searching behaviour of males may affect their movement rates and the movement rates of females (Baguette et al. 1996, 1998), though the evidence from our study is scanty. Males in species using mainly the perching tactic (*E. maturna*, and to a lesser extent *E. aurinia* and *M. cinxia*) appear to have a lower migration propensity than females of the same species, while males in species using the patrolling tactic (*M. diamina* and *M. athalia*) have a similar or higher propensity to emigrate than conspecific females (Fig. 2). More data are needed to confirm such a possible pattern.

The parameter values of the VM model are not related to the conservation status of the five species in any way. All five species of checkerspot butterflies that we have studied in Finland have a fragmented population structure (Fig. 1). Three species survive in their respective patch networks as classical metapopulations in a colonisation/extinction balance: *M. cinxia* in the Åland Islands (Hanski et al. 1994, 1995a), *M. diamina* in the Tampere region (Wahlberg et al. 1996), and *E. aurinia* in the Joutseno region (N. Wahlberg, T. Klemetti, I. Hanski, unpublished data). These three species have restricted distributions in Finland, their current rarity is largely due to habitat loss, and none has a large mainland population that would be immune to extinction, unlike a well-studied metapopulation of the related *E. editha* Boisduval in California (Harrison et al. 1988). The other two species (*E. maturna* and *M. athalia*) are widespread and relatively common in southern Finland, but neither is known to have large mainland-type populations. Their habitat is naturally patchy and often successional (meadows and forest edges). These two species likely occur as large metapopulations within a relatively dense network of suitable habitat that is spread across most of southern Finland.

In conclusion, we have found that five species of closely related butterflies show similar movement patterns in their respective fragmented habitats. While the results are not surprising, they should not be assumed a priori, because even closely related species can differ substantially in their ecologies. Even within the checkerspot butterflies, there is evidence for higher mobility in a montane species (Schrier 1976). We have found the VM model to be a useful tool for analysing MRR data collected from multiple populations in highly fragmented landscapes. We suggest that more studies on a wide range of species using the VM model will facilitate the study of migration behaviour of insects inhabiting fragmented landscapes.

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