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METAPOPULATION STRUCTURE AND MIGRATION IN THE BUTTERFLY *MELITAEA CINXIA*¹

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Abstract. We describe a spatially realistic metapopulation model and parameterize it for a metapopulation of the butterfly *Melitaea cinxia*, residing in a network of 50 discrete habitat patches within an area of 15 km². Parameter values that are difficult to estimate independently are obtained by fitting the model to patterns of patch occupancy and local density. There is no large “mainland” population, and the metapopulation appears to survive at an extinction–colonization equilibrium. Empty patches were smaller than the occupied ones, indicating the extinction proneness of especially small local populations; population turnover was 16% between 2 yr. Density in the occupied patches increased with decreasing isolation and with decreasing patch area, suggesting that migration plays an important role in local dynamics. Mark–recapture results confirmed that migration between local populations was common, in contrast to what is frequently assumed for butterflies with well-defined local populations in discrete habitat patches. The modelling results demonstrate that it is possible to have empty habitat patches in a metapopulation in spite of frequent migration, as we observed for *M. cinxia*. Colonization rate of empty patches may be low for several reasons, including difficulties in mate location at low density (not likely to be important here), conspecific attraction (possibly important), stepping-stone and other forms of nonrandom migration (likely to be important), and weak density dependence (likely to be important). Our results support the assumptions of structured metapopulation models, which demonstrate the possibility of alternative stable equilibria for metapopulations in which migration significantly affects local dynamics.

Key words: mark–recapture study; *Melitaea cinxia*; metapopulation dynamics; migration; northern Europe; population turnover; spatially realistic model.

INTRODUCTION

Large numbers of butterfly species in Europe and North America have been included in local and regional red books in response to alarming reduction and fragmentation of their distribution and dwindling local abundance over the past decades (Pyle 1976, Heath 1981, Ehrlich 1984, Heath et al. 1984, Thomas 1984, 1991, Rassi and Väisänen 1987, van Swaay 1990, Warren 1993). Detailed investigations have revealed that the declining trend can largely be attributed to deteriorating habitat quality, often due to various human activities (Thomas 1983, 1984, 1991, Ehrlich 1984, Thomas et al. 1986, Warren 1987b).

Shapiro (1979), Ehrlich (1984), and others have suggested that a “mosaic” pattern of population regulation, with an important role for local extinctions and recolonizations, is generally appropriate for many butterfly species. With a decreasing number of ever smaller patches of suitable habitat remaining for reproduction, the role of such metapopulation dynamics (Gilpin and Hanski 1991) is expected to become increasingly important (Ehrlich and Murphy 1987). A species failing to persist locally may persist regionally due to a balance between local extinctions and recolonizations (Hanski

1991); or the presence of a species in a larger region may hinge on migration from one or a few large “mainland” populations with a small probability of extinction (Harrison et al. 1988, Harrison 1991, Hanski and Gyllenberg 1993). Unfortunately, conservation biologists cannot take for granted that all species are “rescued” by metapopulation dynamics, and though the notion of metapopulation persistence of butterflies and other organisms in fragmented landscapes is intuitively appealing, we are only just beginning to assess the true significance of metapopulation dynamics in natural populations (Hanski 1994a, Harrison 1994, Thomas 1994).

Metapopulation dynamics have been examined with mathematical models (e.g., Nisbet and Gurney 1982, Hanski 1985, 1991, 1994b, Hastings and Wolin 1989, Adler 1991, Hastings 1991, Verboom et al. 1991, Gyllenberg and Hanski 1992, Nee and May 1992, Hanski and Gyllenberg 1993), but most models are not suitable for analysing specific metapopulations. In particular, there is an urgent need to develop spatially realistic metapopulation models (Hanski 1994b) that can be parameterized for particular metapopulations to generate quantitative predictions.

This paper has three aims. Firstly, we describe a relatively simple, spatially realistic metapopulation model with eight parameters and demonstrate how pat-

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terns of patch occupancy and local density in a metapopulation can be used to estimate parameter values that would be difficult to estimate independently. Secondly, we apply the model to a metapopulation of the Glanville fritillary, *Melitaea cinxia* (L.), in southwestern Finland. *Melitaea cinxia* belongs to a group of butterflies (Melitaeinae) that has received much attention in California by Ehrlich and coworkers (e.g., Ehrlich 1984). *Melitaea cinxia* and many related species are among the most threatened species of butterfly in many parts of Europe (Thomas and Simcox 1982, Rassi et al. 1986, Andersson et al. 1987, Warren 1987a, b, c, 1991, van Swaay 1990, Eliasson 1991, Väisänen 1992). In contrast to the much-studied situation in the Bay checkerspot butterfly *Euphydryas editha bayensis* (Harrison et al. 1988, Harrison 1991), there is no large "mainland" population in our *M. cinxia* metapopulation, which therefore may persist due to genuine extinction-colonization dynamics rather than by virtue of migration from a large and practically invulnerable reservoir population. Thirdly, we are particularly interested in migration in *M. cinxia* for two reasons. First, migration is required for recolonizations, and recolonizations are required for metapopulation persistence in the face of unstable local dynamics. Second, migration may affect the dynamics and the sizes of existing local populations. This second effect underpins the "rescue effect" (Brown and Kodric-Brown 1977), which may yield complex metapopulation dynamics with the possibility of alternative stable equilibria (Hanski 1985, 1991, Hastings 1991, Gyllenberg and Hanski 1992, Hanski and Gyllenberg 1993). A particular focus of this study was to quantify the effect of migration on local population sizes in *M. cinxia* at the scale of a few kilometres, the characteristic "metapopulation scale" for butterflies with small (<1000 individuals) and well-defined local populations.

A SPATIALLY REALISTIC MODEL OF METAPOPULATION DYNAMICS

The key criteria in constructing this model were the following. Firstly, the model has to be spatially realistic, incorporating information about the spatial locations and areas of specific habitat patches. Secondly, migration has to be modelled explicitly. And thirdly, the number of parameters has to be kept to a minimum to facilitate model parameterization for specific metapopulations.

Local growth in each occupied habitat patch was modelled with the discrete time logistic model,

$$N_i(t+1) = N_i(t)e^{r(1 - N_i(t)/\alpha_i)} \quad (1)$$

where $N_i(t)$ is population size in patch i in generation (or year) t ; r is the density-independent growth rate; $1/\alpha_i$ is the carrying capacity of patch i , defined as the equilibrium number of adult butterflies in the absence of migration; and θ sets the strength of density dependence near equilibrium (density dependence increases

with θ). Population sizes were truncated to the nearest integer value in each generation.

Emigration was assumed to be the density-independent, fraction c of individuals leaving their natal population in each generation. Immigration was similarly assumed to be density and patch size independent. The numbers of migrants from patch i were distributed to the other patches using the formula

$$D_{ij}(t) = cN_i(t)e^{-\tau d_{ij}} \frac{e^{-\tau d_{ij}}}{\sum e^{-\tau d_{ij}}} \quad (2)$$

where $D_{ij}(t)$ is the number of individuals moving from patch i to patch j in generation t . $e^{-\tau d_{ij}}$ is the fraction of individuals surviving migration over distance d_{ij} , and τ is a constant determining the shape of the distribution of migration distances (negative exponential). An empty patch was colonized in generation t with probability 0.5 if $\sum D_{ij}(t) > 0.5$, in which case the new population was started with $\sum D_{ij}(t)$ individuals, truncated to the nearest integer value.

The probability of local extinction in patch i in generation t was given by

$$P_i(t) = 1 - \frac{(1 - s_d)N_i(t)^2}{s_d^2 + N_i(t)^2} \quad (3)$$

where s_d is roughly the size of a population that has a 50% chance of surviving until the next generation, and s_e gives the asymptotic per-generation probability of extinction in large populations. s_d and s_e may be interpreted as reflecting the levels of demographic and environmental stochasticities, respectively. In reality, large populations typically become small ones before going extinct, which is not explicitly modelled by Eq. 3. We prefer the model of Eqs. 1 to 3 to a model with stochastic fluctuations in the sizes of local populations, because there is little information on which to base such a more complex model. However, we have also constructed such a stochastic model, which could be fitted to patterns of patch occupancy and local density equally well as the present model (as described below, in *Results: Parameter estimation*).

We describe parameter estimation, results of sensitivity analyses, and selected simulation results following a description of the metapopulation structure and migration in *Melitaea cinxia*.

MATERIALS AND METHODS

The study area, located on the main Åland island (970 km²) in the Baltic Sea, consists of 15.5 km² of heterogeneous countryside with small farms, cultivated fields, pastures, and meadows, as well as small woodlands, all surrounded by continuous coniferous forest and, on one side, by a lake (Fig. 1). It is reasonable to assume that migration to the study area from outside is very limited.

The entire study area was surveyed for habitat patches suitable for *M. cinxia* at the end of May and in early

June in 1991. We searched for the larval food plant *Plantago lanceolata* L., which is largely restricted to pastures and meadows in the study area, and which typically occurs in well-defined, small patches. The most favorable spots for *M. cinxia* were dry meadows on low rocky outcrops, typically located in the cultivated fields. The total number of habitat patches was 50 (Appendix).

In April and May 1991, larvae were searched for in one local population, called population A in this paper (Fig. 1; population number 1 in the Appendix). Larvae were found only on *P. lanceolata*, which is also the only food plant of *M. cinxia* in England (Thomas and Lewington 1991). However, in August 1991 about half of the larval groups in population A were found on *Veronica spicata* L., which is common at this site. It is unknown how important the presence of *V. spicata* is for *M. cinxia*, but because *V. spicata* is entirely absent in the majority of habitat patches with a local population of *M. cinxia*, the butterfly may clearly survive without *V. spicata*. We have only a few sporadic records of host plants other than *P. lanceolata* and *V. spicata*. All habitat patches had a range of flowers used by adult butterflies.

The area of each patch was measured in the field (small patches) or on the map (large patches). The areas varied from 12 m² to 4.6 ha (Appendix). Inevitably, there were a few cases in which it was questionable whether two patches should be considered separate or not. Generally, at least some tens of metres of unsuitable habitat separated two distinct patches. The coordinates of the central point of each patch were used to calculate their pairwise distances (in principle, interpatch distances could be measured more accurately between patch edges rather than centers, but the former is substantially more complicated to calculate and makes little difference when the patches are small relative to interpatch distances, as was the case here).

Other patch qualities that were measured apart from area included abundance of *Plantago lanceolata* (F, on a scale from 1 to 3), slope of the terrain (S, south-facing slope = 2, mixed = 1.5, no slope = 1, north-facing slope = 0.5), and the height of the vegetation (H, 1 = high, 2 = low; low is favorable for *M. cinxia*; Thomas and Lewington 1991; M. Kuussaari and M. Nieminen, *personal observations*). An index of habitat quality was calculated as the product FSH, which varied from 1 to 12 (values were truncated to the nearest integer; Appendix). Habitat quality was measured by M. Kuussaari and M. Nieminen in early summer 1991 after the larvae had pupated but prior to the beginning of the adult flight season. As larvae were studied in only one local population, habitat quality was measured prior to any knowledge of the presence of *M. cinxia* in the other habitat patches.

As there is no single measure of isolation that is necessarily superior to many others when applied to a system of many habitat patches such as the present one

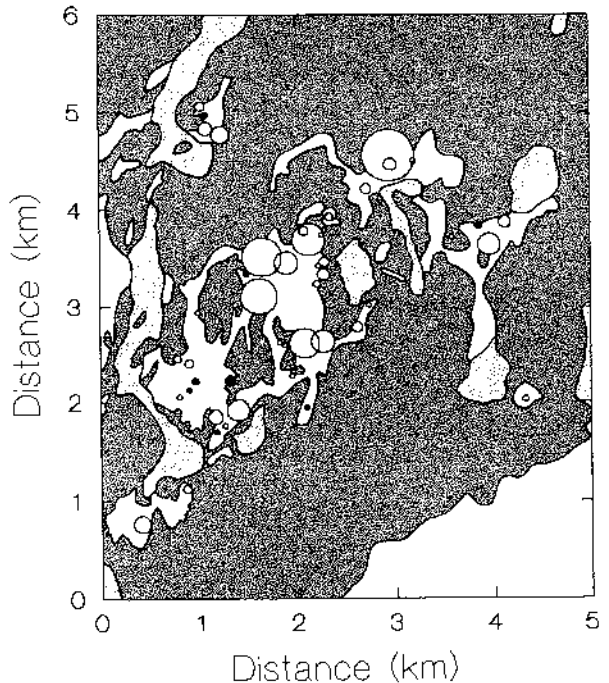


FIG. 1. A map of the study area indicating the relative sizes of the habitat patches and whether they were occupied or not in 1991 (O occupied, ● unoccupied). Dark shading indicates forest, light shading lakes, and unshaded areas are fields and pastures. The real sizes of the habitat patches (given in the Appendix) are smaller than shown here, hence the overlap between the patches.

(Fig. 1), we calculated several indices of isolation. The first two indices are the distance from patch i to the nearest occupied patch (I_{i1}) and to the average coordinates of all patches (I_{i2} ; this is justified because the study area is isolated, hence the central patches are less isolated than the peripheral ones). Three other indices, which are affected by all the neighboring patches/populations weighted by their distances from patch i , were defined as follows: $I_{i3} = -\sum \exp(-d_{ij})$, $I_{i4} = -\sum \exp(-d_{ij}) \cdot A_j$, $I_{i5} = -\sum \exp(-d_{ij}) \cdot N_j$, where d_{ij} is the distance between patches i and j in kilometres, A_j is the area of patch j in units of 100 m², and N_j is the estimated population size in patch j in units of 100 adult butterflies. I_{i4} is affected by the sizes of the neighboring patches, whereas I_{i5} is affected by the sizes of the existing local populations. Constants other than 1 could be used in the exponents, to give more or less weight to long distances. The value of 1 is a reasonable choice in our case on the grounds of the observed migration distances (see *Results: Migration*). Values for the different measures of isolation for each patch are given in the Appendix.

Butterflies were marked on their wings with a fine-point pen (Pilot SC-UF, permanent) and released immediately at the point of capture. A running number, not visible in flight, was written on the back of the hind wing. The sex of the butterfly was recorded.

Butterflies were marked and recaptured daily in population A, weather permitting, between 7 June and 8 July in 1991. These data allowed us to estimate daily population sizes, birth + immigrations, and death + emigrations using Jolly's method (Jolly 1965). The total number of butterflies in this population was estimated, separately for the two sexes, by multiplying the total butterfly-days by the average daily loss rate (deaths + emigrations; missing estimates of daily population sizes were calculated as suggested by Watt et al. 1977, and the [low] numbers before and after the study period were estimated by extrapolation).

Most of the other habitat patches were visited 3–4 times during the adult flight season in 1991. To estimate their total adult population sizes, we first multiplied the number of butterflies captured in population *i* in day *t* with the concurrent ratio of the estimated total over the captured number of butterflies in population A (this ratio appeared to vary somewhat in population A, hence we used four different estimates for different time periods). This calculation assumes that the same fraction of individuals was captured in all populations, which is a reasonable assumption as all the populations, when visited, were searched for butterflies using approximately the same effort per unit area. We then assumed that the seasonal development of numbers was the same in population A and in the other populations, and multiplied the estimated adult population size in day *t* in population *i* by the ratio of the seasonal maximum over population size estimate in day *t* in population A. Finally, the seasonal maximum was converted to total numbers of individuals during the entire flight season in population *i* using the respective ratio for population A. This calculation was repeated for every visit to population *i* and the several estimates thus obtained were averaged. The result is given in the Appendix.

To ascertain the breeding status/success of different local populations in 1991, all the 50 habitat patches were carefully searched for larvae in the spring 1992. As *M. cinxia* larval groups and even isolated larvae are conspicuous in early spring, we feel confident that our survey gave a reliable picture of the presence/absence of larvae in spring 1992.

All the 50 habitat patches were resurveyed for adult butterflies in the peak flight season in 1992. These results allowed us to examine local extinctions and colonizations between 1991 and 1992 based on the presence/absence of adult butterflies. Naturally, data for many more years would be needed to characterize population turnover in detail, but this is outside the scope of the present study.

RESULTS

Population A

The statistical model with which the mark–recapture results were analysed allows for death + emigration

and birth + immigration, and assumes that survival rates and capture probabilities are time dependent, but that survival rates are the same for individuals captured for the first time and for those captured subsequently. The model fitted the data well (females: $\chi^2 = 8.10$, $df = 6$, $P = .23$; males: $\chi^2 = 42.56$, $df = 46$, $P = .62$). Relaxing and varying these assumptions in various combinations resulted in models that did not fit the data well. We therefore conclude that survival rates and capture probabilities were time dependent, but that survival rates were not different for individuals caught for the first time and caught subsequently.

The average daily loss rate was 0.175 in both sexes. However, the numbers of females were so low before 18 June that the daily loss rate estimates for females prior to this date were very unreliable. We therefore estimated the average daily loss rates also for the period 21 June to 8 July, which were 0.312 for females and 0.247 for males. In the calculation of total population size, we used this latter estimate for females (0.312) but the earlier one for males (0.175), which were abundant already in the first part of the study period. This resulted in a population estimate of 2197 butterflies, consisting of 1046 females and 1151 males.

The higher daily loss rate in females than in males is at least partly due to a higher rate of emigration of females than males (see *Migration* below).

Metapopulation structure

The survey of habitat patches revealed 50 patches apparently suitable for *M. cinxia*, with the larval food plant present in nontrivial numbers. Of the 50 patches, adult butterflies were observed in 42 patches in 1991. Fig. 1 shows the locations and relative areas of the empty and occupied patches.

The empty patches tended to be small and have low habitat quality (Fig. 2). Area and habitat quality were uncorrelated (Spearman's rank correlation -0.01), and we analysed their effects on occupancy separately, using ANOVA on ranks. Both area and habitat quality had significant effects on occupancy (area, $F = 7.11$, $P = .01$; habitat quality, $F = 5.29$, $P = .03$); of the components of habitat quality, when analysed separately, abundance of *Plantago* had the greatest effect on occupancy, but not as great as the effect of the composite index FSH). In contrast, isolation had no significant effect on occupancy regardless of which measure of isolation was used. I_{15} had the highest F value in ANOVA, and the result was significant at the 5% level if one outlier was removed. However, in view of the many tests conducted, we conclude that there is little evidence for patch occupancy being affected by isolation in this metapopulation in 1991.

Turning to the occupied patches, we calculated the density of local populations by dividing the estimated total adult population size by patch area. Density increased with decreasing patch area and with decreasing isolation (Fig. 3). The effect of isolation was more sig-

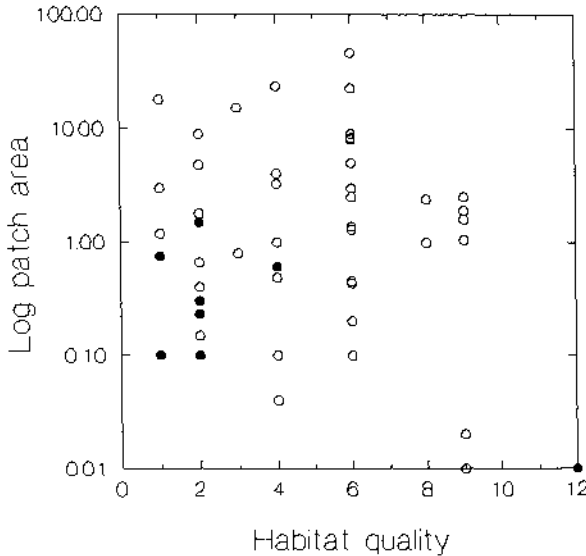


FIG. 2. Area and quality of occupied (○) and empty habitat patches (●). Patch area is given on a logarithmic scale and habitat quality is measured by the composite index.

nificant when measured by I_{15} ($P = .009$; Fig. 3), which takes into account the sizes of the neighboring populations, than when measured by the other indices of isolation.

To check that the effect of area was not due to statistical nonindependence, we also regressed population size against area using a second-order polynomial. The nine largest patches were omitted to stabilize variance. The second-order term was negative and significant ($P = .03$), consistent with decreasing density with increasing area.

Decreasing density with increasing isolation could reflect spatially autocorrelated habitat quality. In this case, habitat quality should be negatively correlated with our measures of isolation. But there was no such correlation in our material, consistent with the assumption that the isolation effect in Fig. 3 is due to population dynamics rather than the environment (discussed below, in *Discussion: Migration and metapopulation dynamics*).

Prior to the larval survey in spring 1992, three patches had been damaged by burning or otherwise, and these patches are omitted from the following analyses (Appendix). In the remaining 47 patches, larvae were found in 36 patches. The agreement between butterfly presence in 1991 and larval presence in 1992 was good, as there were only two patches in which larvae but no butterflies were found, and five patches in which butterflies but no larvae were found. These five patches had smaller adult population sizes in 1991 than the other occupied patches (means 110 vs. 270 individuals), though the difference was not significant ($P = .1$). It is of course possible that reproduction occurred in these patches in 1991, but no larvae survived until spring 1992.

We re-analysed the effects of patch area, isolation, and quality on occupancy based on the presence of larvae. The results were qualitatively the same as for adult butterflies, with the effect of area on occupancy being a little more and the effect of habitat quality a little less significant for larvae than for adult butterflies.

Population turnover

The habitat patches were resurveyed for adult butterflies in 1992. There was substantial turnover of local

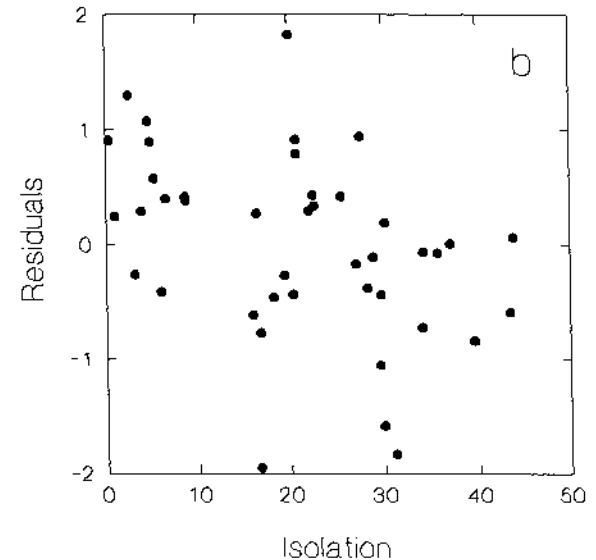
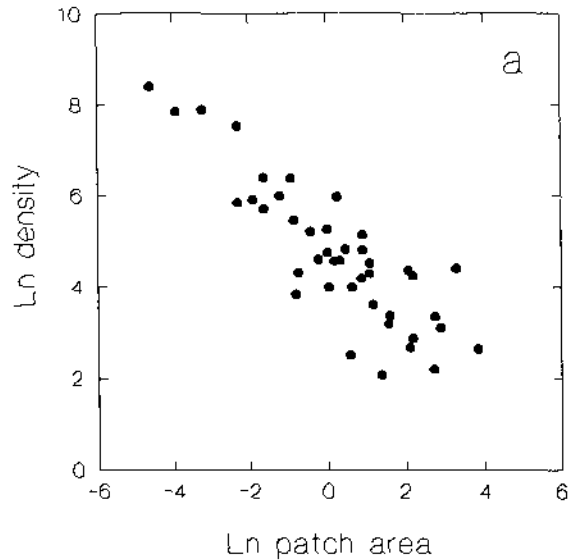


FIG. 3. Regressions of (a) log_e density against log_e patch area, and (b) the residuals from this regression against isolation (measured by I_{15}). Both regressions are significant (t values and their significance levels in a multiple-regression model: area -11.25 , $P < .001$, isolation -2.75 , $P = .009$; the full model: $F = 67.6$, $P < .001$, adjusted $R^2 = 0.78$).

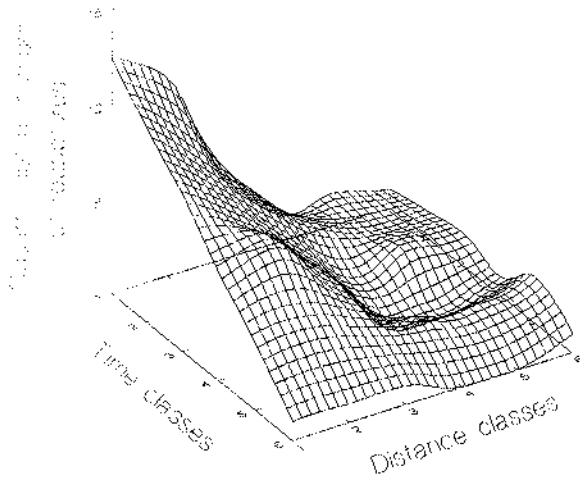


FIG. 4. Numbers of recaptures as functions of distance moved and time elapsed since the previous capture. Numbers of recaptures have been square-root transformed. The distance classes are <50, 51-150, 151-300, 301-500, 501-1000, and >1001 m. The time classes are 1, 2, 3-4, 5-7, 8-16, and >16 d.

populations between the 2 yr, with three extinctions and five colonizations. The number of occupied patches had thus increased from 42 in 1991 to 44 in 1992. All the turnover events had occurred in small patches with small local populations (Appendix).

With only six patches remaining empty in 1992, the power of the tests of patch area, isolation, and quality on occupancy is decreased. The results remained qualitatively the same as in 1991, but none of the three variables had a significant effect on occupancy in 1992 (for the effects of area and isolation see Table 3).

Migration

We accumulated 741 recaptures of marked butterflies, excluding repeated recaptures in the same day. Fig. 4 gives the distribution of recaptures as functions of the time elapsed and the distance moved since the previous capture. In both males and females, distances moved tended to increase with time (tests of independence between distance moved and time elapsed: $\chi^2 = 67.25$ and 35.97 , $df = 12$, both $P < .001$). The two sexes did not differ with respect to time since the previous capture, but they differed in terms of the distance moved (a significant interaction between distance and sex). Short-distance movements were more frequent in

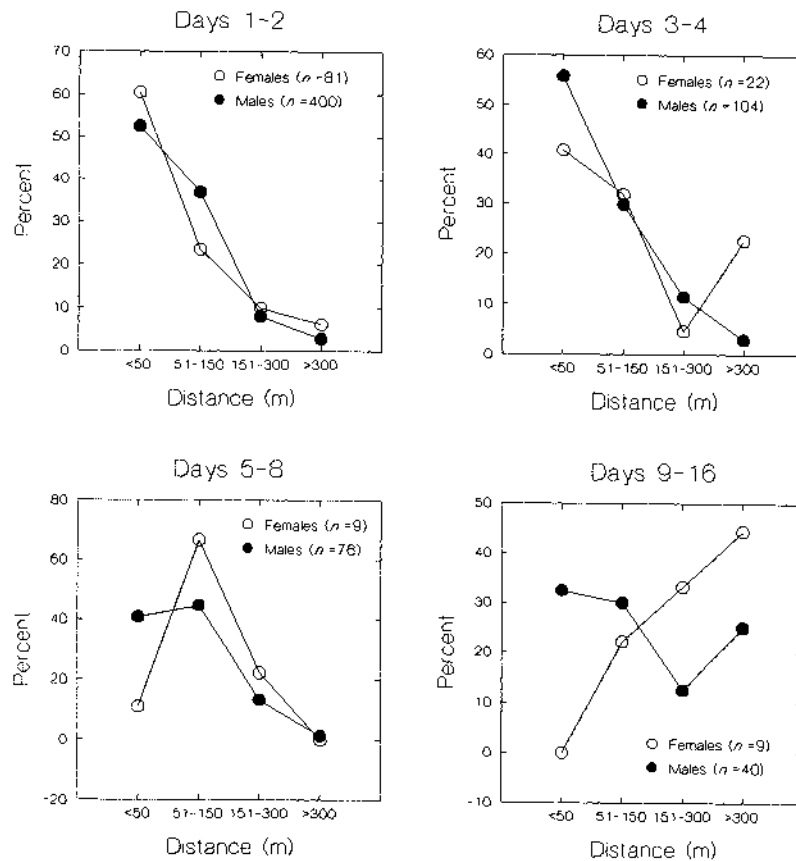


FIG. 5. Frequency distributions of distances moved for the two sexes and for different time periods elapsed since the previous capture.

TABLE 1. Numbers of males and females that were marked in population A and in the other populations and subsequently recaptured in the same (Res) vs. another population (Dis). The percentages of migrating individuals (%) were calculated from numbers corrected for sample and population sizes. Percentages in parentheses are based on <10 recaptures and are less reliable.

Period* (d)	From population A						From other populations					
	Males			Females			Males			Females		
	Res	Dis	%	Res	Dis	%	Res	Dis	%	Res	Dis	%
1	232	0	0	0	3	(100)	50	2	11	0	1	(100)
2	126	8	19	20	11	35	21	2	37	1	4	(61)
3-4	80	1	5	17	6	24	14	4	69	2	2	(47)
5-8	68	2	15	4	2	(25)	9	0	(0)	0	0	(...)
9-16	21	5	47	3	8	74	2	2	(79)	0	4	(100)
>16	0	1	(100)	1	1	(67)	1	0	(0)	0	0	(...)

* The time elapsed since the previous capture of the individual.

males than in females, but long-distance movements were more frequent in females (Fig. 5). In these analyses, we have treated separately six subareas of the large habitat patch occupied by population A (total area 2.66 ha; Appendix). "Short distances" in Figs. 4 and 5 mostly correspond to movements among the subareas in population A, whereas "long distances" consist of between-patch movements.

Table 1 summarizes the numbers of individuals that were recaptured in the same patch and that had moved to another patch since the previous capture. However, these figures do not give a true picture of between-population movements, because they are influenced by sample and population sizes, which were not constant. To obtain an approximate correction for these effects, we calculated the numbers of recaptures as the sum

$$C_{ji} = \sum N_{i,t} / S_{i,t}$$

This sum was calculated over all recaptures of individuals marked in population j and recaptured in population i ; $N_{i,t}$ and $S_{i,t}$ are the estimated population size and sample size, respectively, in population i in the day of recapture (t). For these calculations, we pooled all the populations other than population A into one "population," whose size in each day was taken to be 4.89 times the size of population A (which was the ratio of the estimated total adult population sizes). Nonetheless, a movement between two populations other than population A was still scored as migration.

We must first make one reservation about the results in Table 1. As the populations other than population A were visited only 3-4 times during the flight season, and not on consecutive days, the numbers of same-population recaptures with short durations are severely underestimated for populations other than population A. Results for population A are not similarly affected.

Three conclusions can be drawn from the results in Table 1. Firstly, movements between populations were frequent, with $\approx 15\%$ of the males and $\approx 30\%$ of the females being recaptured from another population in the course of 1 wk. Secondly, females moved more than males between populations (see also Fig. 5). And

thirdly, movements away from population A were less frequent than movements away from the other populations. As population A occupied one of the largest habitat patches, this difference may reflect differences in the sizes of the patches (with increasing patch size, the number of encounters with patch boundary probably decreases and thus emigration rate probably decreases).

Parameter estimation

We used the value of $10/A_i$ for α_i , where A_i is the area of patch i in square metres, and which corresponds to an equilibrium density of 0.1 butterflies/m² (the observed median value was 0.09 butterflies/m²). The estimates of c (emigration rate) and τ (migration distances) were based on the data reported in Table 1 and Fig. 4. A problem in using these results is that mortality during migration is unknown. We increased the value of c as deduced from Table 1 (≈ 0.2) to 0.3 to allow for migration mortality. Similarly, we used $\tau = 1$ to set migration distances, assuming that the observed distribution (Fig. 4) is steeper because of distance-dependent mortality. The density-independent growth rate r was set at 2, based on Warren's (1991) results for the related species *Melitica aethalia*.

We do not know of any data to estimate the values of the four remaining parameters, that is, μ , the distance-dependent mortality during migration; θ , the degree of density dependence near equilibrium; and s_d and s_e , the levels of demographic and environmental stochasticities. We estimated these parameters with the model by running several hundred independent simulations with different values of the parameter values (as explained in Table 2), using five criteria to evaluate the simulation results: the number of occupied patches and the effects of patch area and isolation on occupancy and local density in the occupied patches after 100 generations, when the predicted dynamics appeared to have settled to a stochastic equilibrium. The simulations were started with the pattern of occupancy observed in 1991. In these comparisons, the test statistic used was the absolute value of (Observed value - Predicted value)/(Observed value).

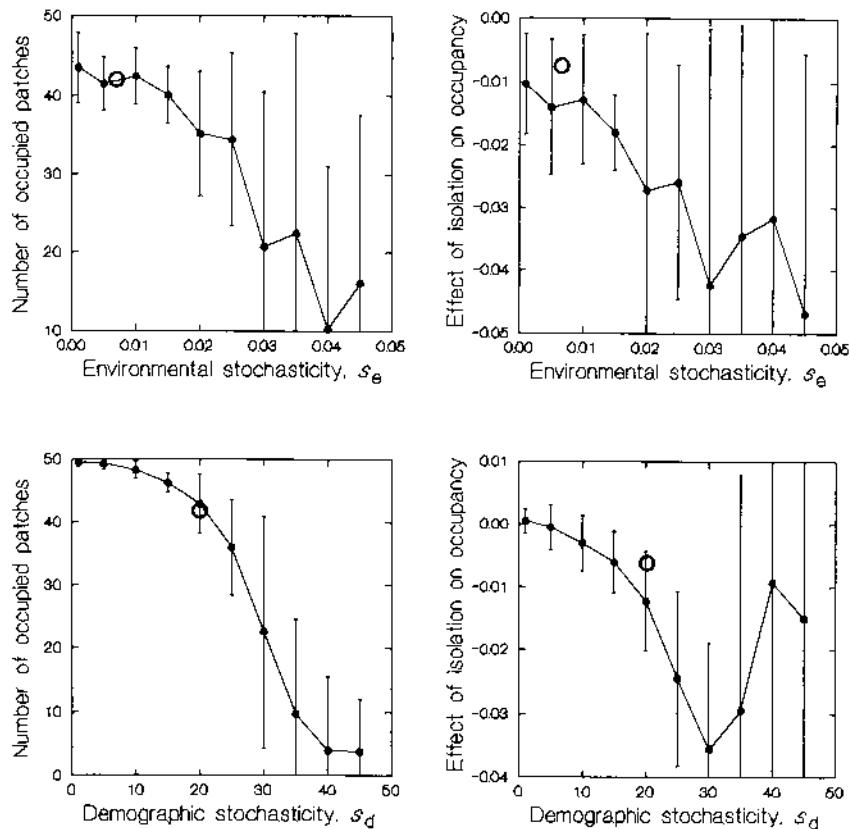


FIG. 6. Selected results of sensitivity analyses of the simulation model. The eight panels show the dependence of particular variables describing metapopulation patterns on the values of the four parameters that could not be estimated with independent data (s_e , s_d , θ and μ ; Table 2). The vertical axis gives the average value ± 2 SD of the dependent variable in 10 independent simulations (the value for each simulation run was the mean value for generations 91–100). Only one parameter was varied at the time, keeping the other parameters constant, at the values shown in Table 2. \circ = the observed values of the dependent variable (from Table 3) plotted against the “best” matching parameter values (from Table 2).

Sensitivity analyses

With a large number of parameters, it is possible that several different parameter combinations would lead to predictions that match the observations equally well. However, we found only one cluster of parameter values that yielded predictions closely matching the observations (Fig. 6). The “best” set of parameter values thus obtained is given in Table 2. These values are consistent with our informed guesses about the biology of *M. cinxia*. The good match between the predicted and observed metapopulation patterns (Table 3) is encouraging, and suggests that a relatively simple model may provide a good description of the dynamics at the metapopulation level.

Fig. 6 gives the results of sensitivity analyses, in which we varied the values of μ , θ , s_d , and s_e at a time while keeping the other parameters constant, at the values given in Table 2. Fig. 6 shows the result for those dependent variables that were most affected by variation in these parameters. In many cases the model outcome is very sensitive to variation in a particular parameter, for instance the number of occupied patches at equilibrium and the effect of isolation on patch oc-

cupancy both depend sensitively on s_d (demographic stochasticity) and μ (mortality during migration), whereas the effects of patch area and isolation on local density depend sensitively on θ , the strength of density

TABLE 2. The parameters of the simulation model, and the parameter values used to generate the results shown in Table 3 and Figs. 6 and 7.

Parameter	Value	Description
Parameters that were estimated independently		
α^{-1}	0.1	carrying capacity (individuals/m ²)
r	2.0	density-independent growth rate
c	0.3	emigration rate
τ	1.0	migration distances (unit 1 km)
Parameters that were estimated with the simulation model*		
θ	0.1	density dependence near equilibrium
μ	0.25	mortality during migration
s_d	20	“demographic stochasticity”
s_e	0.006	“environmental stochasticity”

* The following parameter values were combined in 625 independent simulation runs: θ , 0.1, 0.2, 0.4, 0.8, and 1.6; μ , 0.25, 0.5, 1, 2, and 4; s_d , 5, 10, 20, 40, and 80; and s_e , 0.003, 0.006, 0.012, 0.024, and 0.048.

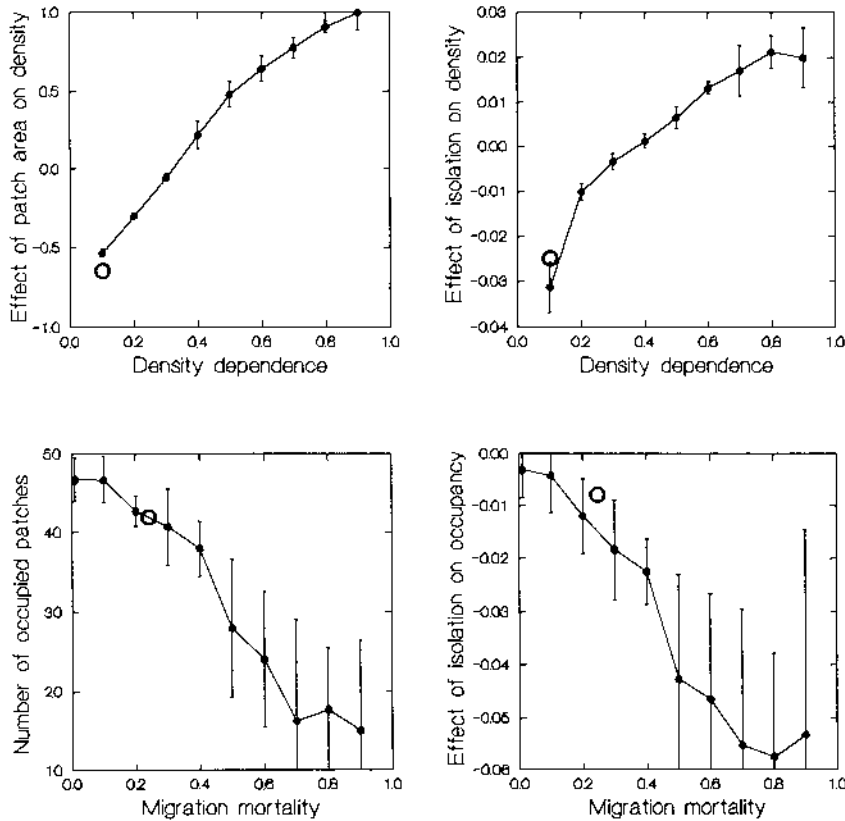


FIG. 6. Continued.

dependence near local equilibrium (Fig. 6). The small value of θ producing results matching the observations suggests that density dependence near equilibrium is weak. This result is consistent with Dempster's (1983) finding of weak density dependence in several species of butterflies. In our results, θ has a low value because the negative relationship between density and patch area requires weak density dependence in the model. Alternatively, the negative relationship between den-

sity and patch area could be generated by density- and/or patch area-dependent migration. We assumed density- and/or patch area-independent migration in the absence of contrary evidence, but this question needs to be re-addressed when more detailed information on migration becomes available.

The results of these sensitivity analyses suggest that estimating parameter values by fitting the model to metapopulation patterns is a useful approach in the

TABLE 3. Observed and predicted values of number of patches occupied (N) and of the relationships between patch occupancy and local density in the occupied patches against patch area and isolation (multivariate regression analyses). The predicted values were obtained using the simulation model with parameter values given in Table 2. The predicted regression coefficients and their t values are means for generations 91–100.

	N	Patch occupancy				Local density			
		Area		Isolation		Area		Isolation	
		Coeff	t	Coeff	t	Coeff	t	Coeff	t
Observed, 1991	42	0.06	2.49	-0.006	-1.28	-0.69	-12.84	-0.024	-2.31
1992	44	0.03	1.41	-0.006	-1.61				
Predicted	43	0.03	1.18	-0.011	-1.84	-0.54	-26.58	-0.030	-6.04
Prediction in a selected generation*	42	0.07	2.50	-0.008	-1.35	-0.52	-19.84	-0.028	-4.85

* The predicted results for a particular (selected) generation in the model output, in which the agreement with observations was especially good.

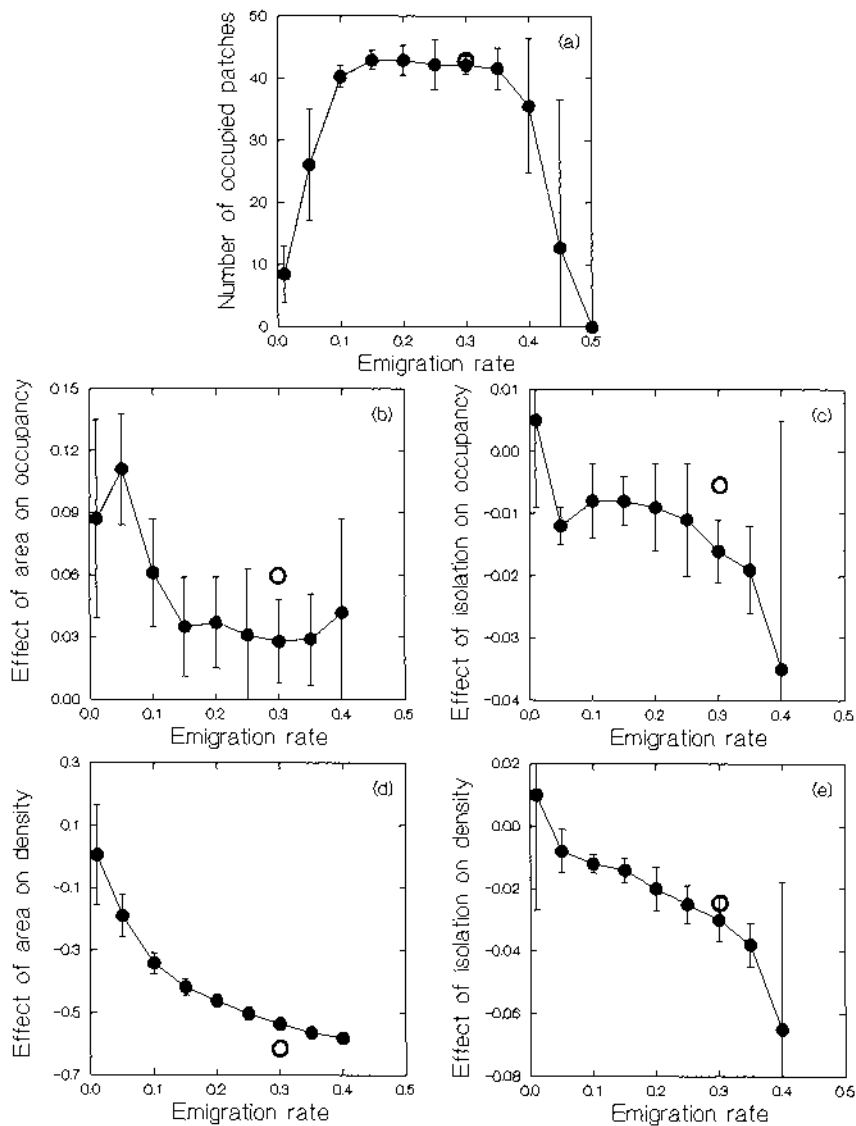


FIG. 7. Predicted number of occupied patches (a), and the effects of patch area (b and d) and isolation (c and e) on patch occupancy (b and e) and local density (d and e). The horizontal axis gives the emigration rate (c); other parameter values are as in Table 2. The vertical axis gives the average value ± 2 sd of the variable in 10 independent simulations (the value for each simulation run was the average for generations 91–100). The observed values (O) are plotted against $c = 0.3$.

case of parameters that are difficult to estimate independently.

Simulation results

Having estimated the parameter values, one can generate quantitative predictions about transient dynamics and about the dynamics of the species in some other network of habitat patches. For instance, one may ask whether a metapopulation would persist, and for how long, if certain habitat patches are removed. Such predictions should be of general interest in conservation biology. Hanski and Thomas (1994) give examples on butterfly metapopulations. We had data for two species of butterflies, *Hesperia comma* and *Plebejus argus*, to

test model predictions with independent data on transient and equilibrium dynamics from a metapopulation other than the one from which the parameters were estimated. The predictions were encouragingly successful.

A particular focus of the present study is the role of migration in the metapopulation dynamics of *Melitaea cinxia*. We used the model to explore the expected consequences of varying migration rate on metapopulation persistence. Fig. 7 shows the predictions for a range of emigration rates keeping the other parameters at the values given in Table 2. The match between the predicted and observed metapopulation patterns is best for emigration rates between 20 and 30%, in good

agreement with our mark-recapture results (Table 1). These simulation results suggest that effective emigration rate is definitely $\geq 10\%$ and $\leq 40\%$. It is noteworthy that "too much" migration can be as disastrous for metapopulation persistence as "too little" migration (Fig. 7). The former result is a generic feature of structured metapopulation models, in which the cost of migration is taken into account (Gyllenberg and Hanski 1992, Hanski and Gyllenberg 1993). Increasing migration rate increases mortality during migration, which has an adverse effect on metapopulation persistence.

In the model, the negative relationships between density and patch area and between density and patch isolation were generated by much migration (Fig. 7). The effect of patch area on local density was somewhat less steep in the model results than in our data (Fig. 7), suggesting that some factors not included in the model may have affected the empirical result. For instance, it is possible that the density of the larval food plant decreases with increasing patch area, which could steepen the density-patch area relationship.

DISCUSSION

Metapopulation structure in Melitaea cinxia

The *Melitaea cinxia* metapopulation that we have studied does not include a large "mainland" population, by virtue of which long-term persistence of the entire metapopulation would be ensured. The largest local population was just over 2000 individuals, a mere 0.2% of the size of the "mainland" population in the *Euphydryas editha bayensis* metapopulation studied by Harrison et al. (1988).

Several results support the hypothesis that long-term persistence in this *M. cinxia* metapopulation is based on genuine extinction-colonization dynamics as originally envisioned by Levins (1969, 1970), notwithstanding that there is spatial variation in the sizes of the habitat patches unlike the assumption made in the simplest models (for models with spatial variation in patch sizes see Hanski and Gyllenberg 1993).

Firstly, the largest local populations were within the size range in which local extinctions are expected to occur with a significant frequency. Harrison et al. (1991) reported that two local populations of *E. editha* fluctuated between 18 and 2000 individuals and between 40 and 7227 individuals over a period of 27 yr. *Melitaea cinxia* and *E. editha* have broadly similar biologies, and local populations of *M. cinxia* may well be as variable as these *E. editha* populations. In both cases, a major cause of population fluctuations is withering of host plants in dry years (Ehrlich 1984, Harrison et al. 1988; I. Hanski et al., *personal observations* for *M. cinxia*). The simulation model suggested that the risk of extinction is of the order of 1% to 0.1% per year in the largest habitat patches (the value of s_c in Table 2). This agrees well with Foley's (1993) recent analysis of the above-mentioned *E. editha* populations, which had

expected times to extinction from 50 to 300 yr, depending on model assumptions, and maximally ≈ 1000 yr, with the most favorable assumptions for persistence.

Secondly, population turnover was substantial between 2 yr, though not surprisingly, turnover was mostly detected in the smallest habitat patches. Empty habitat patches were significantly smaller than the occupied patches, supporting the notion about extinction proneness of especially small local populations (Williamson 1981, Diamond 1984, Schoener and Spiller 1987, Peltonen and Hanski 1991).

Thirdly, the good match between the observed and predicted metapopulation patterns demonstrates that the observed patterns are consistent with the processes included in the simulation model. In the model, the metapopulation persists in an extinction-colonization equilibrium.

Fourthly, *Melitaea cinxia* is most abundant on the Åland islands in regions where the density of suitable habitat patches is highest (I. Hanski and M. Kuussaari, *unpublished data*). *Melitaea cinxia* has gone extinct on the mainland Finland and on some relatively large islands (5–100 km²; I. Hanski et al. *unpublished data*), probably because of decreasing density of suitable habitat patches. An important point is that these regions still have habitat patches that are suitable for *M. cinxia*, as shown by successful introductions (I. Hanski et al., *unpublished data*). Metapopulation theories predict that long-term persistence of assemblages of unstable local populations is possible only in regions where the density of habitat patches exceeds a critical threshold value (Hanski 1991).

In summary, the *Melitaea cinxia* metapopulation described here is a likely example of a metapopulation persisting in a set of small habitat patches due to recolonizations compensating for the inevitable local extinctions. We are currently testing this hypothesis experimentally. In this respect this metapopulation contrasts with the *E. editha bayensis* metapopulation described by Harrison et al. (1988), which persists because it includes one very large local population in a very large habitat patch.

Migration and metapopulation dynamics

We estimated that 15% of males and 30% of females left their natal population and moved to another population in the course of their life. These figures may somewhat underestimate the true rate of emigration, because the calculations do not take into account mortality during migration. In any case, there is no doubt that a large fraction of individuals moved between habitat patches. The simplest metapopulation models, often called patch models (Hanski and Gilpin 1991), ignore the consequences of migration in the dynamics of existing local populations. These models predict that the probability of occupancy increases with patch area

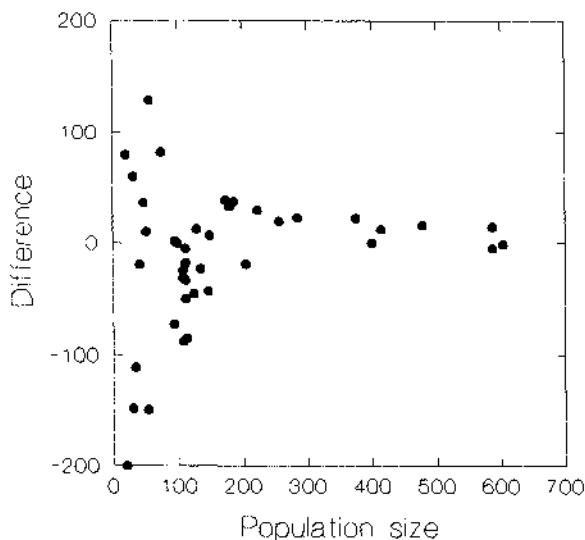


FIG. 8. The difference between population sizes predicted by the actual patch area and isolation (as in Fig. 3) and by the actual patch area and the median isolation for all patches, plotted against the observed population size. The difference on the vertical axis has been expressed as the percentage of the observed population size on the horizontal axis. Population A, which was larger than any other population (2000 individuals; Appendix), was omitted from this figure.

and decreases with increasing isolation, as we observed, but the patch models implicitly predict that local density is uncorrelated with area and isolation. In contrast, we found that local density increased with decreasing patch area and with decreasing isolation. While the former result has many possible explanations, the simulation model demonstrated that high rate of migration combined with weak density dependence can explain the observed patterns. The inverse relationship between isolation and local density has been previously reported for small mammals, in which it has been attributed to migration (Smith 1974, Gottfried 1979, Fahrig and Merriam 1985).

Fig. 8 demonstrates that the effect of isolation on local density (Fig. 3) can be very significant for small populations. In extreme cases, decreasing or increasing the observed level of isolation to the median value among all the patches is predicted to double the population size or to cause an immediate local extinction, respectively (Fig. 8). In other words, immigration to small but little-isolated populations may greatly enhance their persistence, while populations at similar but more isolated patches have a high risk of extinction. These results strongly support the significance of the "rescue effect" (Brown and Kodric-Brown 1977) in this metapopulation.

High rate of migration and many empty habitat patches are at first a paradoxical combination: if migration is so extensive that it affects the sizes of existing local populations, should it not lead to immediate colonization of all habitat patches? There are several rea-

sons why colonization rate may be relatively low in spite of much migration.

Firstly, the density of immigrants in a previously empty patch may need to exceed a critical level before the immigrants are likely to leave enough progeny to replace themselves. Such "Allee effects" are often attributed to low rate of insemination of females due to difficulty of locating a mate at low density. This is a potentially important factor in species in which mating occurs after migration, but not in species in which females migrate after mating. Melitaeinae butterflies belong to the latter category (Porter 1981, Singer and Thomas 1992; M. Kuussaari and M. Nieminen, *personal observations*), hence this factor is unlikely to be important here.

Another possibility is conspecific attraction (Ray et al. 1991), reduced emigration from and/or increased immigration to patches with many conspecifics. Conspecific attraction has been documented for many species (Smith and Peacock 1990). One plausible ultimate reason for conspecific attraction is avoidance of mate scarcity. Male butterflies should preferentially move to and stay in patches with many females, but it is less clear why inseminated females should do so, unless they use the presence of conspecifics to indicate the presence of suitable habitat. We found that habitat quality (as measured by us) was significantly correlated with patch occupancy but not with local density, which is consistent with the hypothesis of conspecific attraction.

A third possible explanation of many empty patches in spite of much migration is nonrandom migration: individuals are more likely to move short than long distances (Fig. 4), and for many reasons they are more likely to move between certain habitat patches than between some others. Migration is typically nonrandom in most organisms. Nonrandom migration may explain the presence of species even in tiny habitat patches, in which extinction rate must be very high: these patches may receive, because of their location, a disproportionate share of the migrants. In contrast, some other patches may receive very few migrants because of their location, prevailing environmental conditions during migration, etc.

Fourthly, immigration does not necessarily need to be massive to have a significant effect on local density. In the case of the smallest patches, say 100 m², even the progeny of a single female may give rise to high local density. Furthermore, how large the effect of immigration on equilibrium density is depends on the strength of density dependence in local dynamics, which operates to restore the equilibrium density in the absence of migration (assuming that there is a point equilibrium). If density dependence is weak, as the simulation model suggested for *M. cinxia*, even a relatively low rate of immigration may have a noticeable effect on equilibrium density.

In summary, we suggest that there are empty habitat

patches in the *M. cinxia* metapopulation in spite of substantial migration because of nonrandom migration and because of weak density dependence in local dynamics. Conspecific attraction may also be important, migrating butterflies being perhaps unlikely to settle in the often small habitat patches without conspecifics.

"Open" vs. "closed" populations of
butterflies

It has become widely accepted, especially among the butterfly biologists in Europe, that butterfly species with discrete local populations confined to well-delimited habitat patches show generally very low rates of migration (Thomas 1984, 1991, Warren 1993) and therefore form "closed colonies" (local populations). Species with less well-delimited habitat patches or scattered resources are thought to be "migratory" with an "open" population structure (Thomas 1984).

Several previous studies appear to support a dichotomy of species with "closed" vs. "open" population structures (Brussard and Ehrlich 1970a, b, c, Gall 1984, Warren 1987b). A case in point is Brussard and Ehrlich's (1970a) comparison between *Euphydryas editha* and *Erebia epipsodea*. *Euphydryas editha* has well-defined local populations, but "almost no exchange of individuals . . . between many small populations in close geographical proximity" (Brussard and Ehrlich 1970a: Table 2). Ehrlich (1984:34) further concludes that "during the 22 years of study of *E. editha*, it has been clear that . . . migration plays no immediate role in changes in population size." In contrast, *E. epipsodea* shows much migration but does not form discrete local populations, apparently because its habitat is more or less continuous in suitable regions.

Ehrlich (1984) has also emphasized the high level of variation that occurs in the spatial structures both within and between species of butterflies. Our results on *M. cinxia* provide a clear example of a species that does not form "closed" colonies (in our study area) in spite of discrete habitat patches with all the necessary resources for local populations.

The theoretical basis for the dichotomy of "closed" vs. "open" populations of butterflies is not entirely clear. It appears that discreteness of habitat patches has been considered to be significant, but this is unlikely to be so. More importantly, we could expect that migration rate is low in species/metapopulations in which mortality during migration is high (Comins et al. 1980, Levin et al. 1984, Klinkhamer et al. 1987, Fahrig 1990), though substantial migration may occur especially among small and unstable populations in spite of high migration mortality (Hamilton and May 1977). Generally, migration mortality may be expected to increase with increasing isolation of habitat patches. The contrast between the low migration rate in the *E. editha* metapopulation studied by Harrison et al. (1988) and the high migration rate in the present *M. cinxia* metapopulation most likely reflects a difference in the

type of metapopulation. The *E. editha* metapopulation is dominated by a large and isolated "mainland" population, whereas the *M. cinxia* metapopulation consists of many small local populations, no one of which is safe from extinction. Selection may reduce migration in the former case but elevate migration in the latter case.

A further complication is that there may be much between-year variation in emigration rate. *Euphydryas editha* shows substantial migration in dry years when the larval food plants are in danger of drying up (Murphy and White 1984, Ehrlich and Murphy 1987). High migration rate in our study cannot be explained by this factor, because summer 1991 was relatively wet and *Plantago lanceolata* showed vigorous growth.

CONCLUSIONS

The *Melitaea cinxia* metapopulation analysed here provides a contrasting example to the *Euphydryas editha* metapopulation reported by Harrison et al. (1988). Unlike the latter case, there is no large "mainland" population in the *M. cinxia* metapopulation, and its long-term persistence appears to depend on genuine extinction-colonization dynamics. In contrast to what has been reported for *E. editha*, we found extensive migration between local populations of *M. cinxia* occupying discrete habitat patches. We also found that migration substantially affected density in the existing local populations, as assumed in the structured metapopulation models (Hastings and Wolin 1989, Hastings 1991, Gyllenberg and Hanski 1992, Hanski and Gyllenberg 1993). These models have complex dynamics with the possibility of alternative stable equilibria (Hanski 1985, 1991, Hastings 1991, Gyllenberg and Hanski 1992). We suggest that the *Melitaea cinxia* metapopulation may be representative of many other butterfly metapopulations occupying networks of small and not very isolated habitat patches.

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APPENDIX

The 50 habitat patches in the *Melitaea cinxia* metapopulation, and their properties.

Patch no.	Area (m ²)	Patch quality*	Isolation measures†					Est. adult pop. size in 1991	1992 presence‡	
			I ₁₁	I ₁₂	I ₁₃	I ₁₄	I ₁₅		Larvae	Adults
1	27000	4	0.26	0.55	-15.3	-0.61	-29.9	2190	1	1
2	660	2	1.63	2.54	-3.6	-0.14	-6.2	120	1	0
3	430	6	0.23	2.22	-7.3	-0.32	-12.9	100	2	2
4	8300	6	0.23	2.00	-9.1	-0.37	-15.9	120	1	1
5	2400	8	0.24	2.22	-8.1	-0.34	-14.2	160	1	1
6	600	4	0.22	1.95	-9.4	-0.41	-17.3	0	0	1
7	480	4	0.39	1.66	-10.4	-0.47	-20.4	40	0	1
8	200	6	0.23	1.80	-9.7	-0.64	-24.5	120	1	1
9	46000	6	0.09	1.70	-10.7	-0.67	-27.5	650	1	1
10	2500	6	0.09	1.63	-11.3	-0.74	-29.2	430	1	1
11	3000	1	0.03	0.89	-15.6	-0.77	-41.3	280	1	1
12	1000	8	0.03	0.85	-16.3	-0.79	-43.5	190	1	1
13	1300	6	0.10	0.66	-16.9	-0.85	-47.4	510	1	1
14	18000	1	0.10	0.58	-17.6	-0.86	-49.1	400	1	1
15	9000	6	0.26	0.36	-17.4	-0.87	-49.6	630	1	1
16	150	2	0.26	0.71	-14.1	-0.61	-30.5	60	1	1
17	1900	9	0.26	0.67	-14.6	-0.60	-29.7	100	1	1
18	9000	2	0.19	0.54	-15.9	-0.66	-31.7	160	1	1
19	15000	3	0.19	0.51	-16.8	-0.69	-33.1	140	1	1
20	300	2	0.36	1.18	-12.4	-0.44	-21.1	0	1	0
21	12	9	0.10	0.85	-15.4	-0.57	-27.4	45	2	1
22	40	4	0.10	0.75	-16.2	-0.61	-29.2	110	1	1
23	100	6	0.06	0.54	-17.0	-0.69	-34.0	40	1	1
24	20	9	0.06	0.55	-17.2	-0.68	-33.5	50	0	1
25	800	3	0.12	0.20	-17.6	-0.81	-44.0	80	1	1
26	200	6	0.07	0.36	-18.1	-0.84	-46.9	60	1	1
27	1600	9	0.07	0.42	-18.0	-0.82	-46.1	200	1	1
28	2500	9	0.10	0.32	-18.0	-0.81	-44.7	310	1	1
29	16000	6	0.41	0.42	-16.4	-0.73	-41.2	440	1	1
30	100	2	0.24	0.59	-15.6	-0.78	-44.5	0	0	0
31	1400	6	0.24	2.17	-6.8	-0.30	-15.8	130	2	0
32	100	1	0.11	2.07	-8.1	-0.34	-18.4	0	0	0
33	5000	6	0.16	1.82	-8.9	-0.40	-21.7	150	1	1
34	3000	6	0.16	1.95	-8.5	-0.37	-19.8	220	0	1
35	300	2	0.52	1.06	-12.7	-0.52	-27.9	120	1	1
36	1500	2	0.32	1.15	-14.8	-0.50	-25.6	0	1	1
37	1200	1	0.13	1.34	-13.7	-0.45	-22.9	120	1	1
38	4000	4	0.36	1.63	-12.6	-0.38	-18.8	30	1	1
39	750	1	0.20	1.40	-14.1	-0.44	-22.2	0	0	1
40	230	2	0.12	1.51	-13.7	-0.42	-20.7	0	0	1
41	3300	4	0.13	1.55	-13.4	-0.41	-20.3	120	1	1
42	12	12	0.11	1.67	-12.6	-0.38	-18.6	0	0	1
43	450	6	0.13	1.57	-13.2	-0.40	-20.1	20	0	0
44	8000	6	0.21	1.37	-14.1	-0.45	-22.3	630	1	1
45	1100	9	0.58	2.32	-7.5	-0.22	-10.4	60	1	1
46	4800	2	0.58	2.87	-5.0	-0.15	-6.6	120	1	1
47	100	4	0.06	0.66	-16.6	-0.83	-45.4	190	1	1
48	1800	2	0.35	1.28	-12.8	-0.72	-33.3	20	1	1
49	400	2	0.06	0.72	-16.8	-0.82	-45.1	240	0	1
50	1000	4	0.13	1.42	-12.3	-0.41	-21.1	120	1	1

* On a scale from 1 (worst) to 12 (best).

† Described in *Materials and methods*.

‡ Survey of larvae and adults in 1992: 2, habitat patch damaged prior to the larval survey (but patches nos. 21 and 31 recovered prior to the butterfly survey); 0, larvae/adults absent; 1, larvae/adults present.