Metapopulation persistence of an endangered butterfly in a fragmented landscape

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We describe an extensive metapopulation study on the Glanville fritillary Melitaea cinxia, in a network of 1502 discrete habitat patches, comprising the entire distribution of this butterfly species in Finland. A thorough survey of the easily detected larval groups revealed a local population in 536 patches (dry meadows). We demonstrate that this system satisfies the four necessary conditions for a species to persist in a balance between stochastic local extinctions and recolonizations. Patterns of patch occupancy support several qualitative and quantitative model predictions. With decreasing regional density and average area of habitat patches, the butterfly occurs in a diminishing fraction of suitable habitat. To our knowledge, this is the first conclusive demonstration, based on a comparison of many conspecific metapopulations, of declining habitat occupancy and hence of increasing threat to survival caused by increasing habitat fragmentation.

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A metapopulation of many extinction-prone local populations may persist in a fragmented landscape in a balance between stochastic extinctions and recolonizations (Levins 1969, Hanski 1991a). The possibility of such metapopulation-level persistence has received much attention in population biology (Gilpin and Hanski 1991, McCauley 1993) and in conservation biology (Western and Pearl 1989, Falk and Holsinger 1991, Fiedler and Jain 1992), but the empirical evidence has remained controversial (Taylor 1991, Harrison 1994, Thomas 1994). We have little knowledge of how frequently species persist in fragmented landscapes due to metapopulation processes, in contrast to long-term survival of local populations.

Our purpose in this paper is to describe the most extensive metapopulation investigation conducted so far, on the Glanville fritillary Melitaea cinxia. We have surveyed the entire Finnish distribution of this endangered butterfly species within an area of 50 by 70 km², in a network of 1502 discrete habitat patches (dry meadows).

With these results, supplemented with the results of a more intensive study conducted in a 50-patch network during three years, we establish beyond any reasonable doubt that M. cinxia persists in Finland in a balance between stochastic local extinctions and recolonizations. We also demonstrate that the occurrence of this butterfly in its naturally fragmented environment is consistent with two qualitative predictions and one quantitative prediction stemming from metapopulation models.

Material and methods

Melitaea cinxia went extinct on mainland Finland in the late 1970s, and it now occurs in Finland only on the main Åland island and a few nearby, large islands (Marttila et al. 1990). Melitaea cinxia has two host plants on the Åland islands, Plantago lanceolata and Veronica spicata, of which the former is widespread but the latter occurs...
Fig. 1. A map of the study area, the Åland islands, with ca 1200 km² of land within an area of 50 by 70 km². Occupied and empty patches are shown by black and shaded dots, respectively. Small islands were not surveyed, but they do not generally have suitable habitat for *M. cinxia*. The shaded region in the northern part of the main island includes the subset of 50 patches which we have studied more intensively since 1991 (Hanski et al. 1994). The grid size is 10 x 10 km².

mostly in the northern part of the main island. Both host plants grow on dry meadows of various kinds, which are the potential habitat patches for the butterfly. The meadows are generally well delimited from the surrounding environment. Our observational and experimental knowledge of the butterfly’s habitat requirements (Kuussaari et al. 1993, Hanski et al. 1994, unpubl.) allows us to reliably identify the meadows which are suitable for breeding by *M. cinxia*.

Since 1991, we have studied a metapopulation of *M. cinxia* living in a 50-patch network in the northern part of the main Åland island. In the present paper, we refer to some published (Hanski et al. 1994) and some unpublished results obtained from this metapopulation in 1991–93.

In late summer 1993, we surveyed with 20 students the Åland islands within an area of 50 by 70 km² (Fig. 1). The aim of the survey was to locate all meadows which are suitable for *M. cinxia* and which are >25 m² in area, but additionally many smaller habitat patches (5–25 m²) were also recorded when discovered. The total survey time was 2660 h. Before the field work the students were trained to identify and describe the suitable kinds of meadows. Several attributes of the meadows were recorded, but the present paper only uses information on their areas and spatial locations.

During the survey, and following the description of the habitat patch, the presence and the size of a possible local population was established by counting the number of larval webs in the patch. Though the larval groups are relatively easy to detect because the larvae spin a conspicuous web (Thomas and Simcox 1982), not all groups were discovered during a relatively rapid survey. We estimate that 35% of the groups were actually discovered, based on a control census by all students of a carefully mapped 2-km² area. All meadows >0.1 ha and recorded as empty (no larvae) in the main survey were additionally re-surveyed after 1–2 weeks. In the re-survey, 17% of
these meadows were found to be occupied, usually by just one larval group. We conclude from these figures that the survey results reflect reasonably accurately the presence of the butterfly on the meadows.

A total of 1502 meadows were recorded, of which 536 were found to be occupied (Fig. 1). Most local populations were very small, with only 1 or 2 larval groups discovered (Fig. 2). The average number of larvae per group was 39 (in a sample of 381 groups from 78 meadows), which is a low figure in comparison with our previous results (ca 70 larvae per group in 1991, n=71). The small number of larvae per group, and the small number of groups per population, both reflect the general decline in the density of *M. cinxia* in 1992-93, which occurred due to two successive unfavourable summers.

We analysed the survey results by dividing the entire study area into 2×2 km² squares, which correspond in size to the movement range of the species (Hanski et al. 1994; next section). Our conclusions below about patterns of patch occupancy in these squares are conservative, as any patterns that emerge are observed in spite of the variable influence potentially exerted by populations located outside but in the vicinity of the focal square. We have also analysed the results by dividing the 1502 patches into 126 more naturally delineated, semi-independent patch networks. The results of the two forms of analysis were similar, and we report only the former results in this paper. Analyses based on the squares have the advantage that the size of the region (4 km²) is constant.

**Four conditions for metapopulation-level persistence**

To demonstrate that the persistence of a species living in a fragmented landscape is due to metapopulation dynamics, as opposed to local dynamics, one should establish the following: (1) that the habitat patches support local breeding populations; (2) that no single population is large enough to ensure long-term survival; (3) that the patches are not too isolated to prevent recolonization; and (4) that local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely. Fulfillment of conditions (1) to (3) eliminates the possibility of 'patchy populations' (Harrison 1994) without a distinct metapopulation structure, and the possibilities of mainland-island (Hanski 1991a, Schoener 1991, Harrison 1994) and non-equilibrium metapopulations (Harrison 1994), respectively.

**Condition 1: Population structure**

The dry meadows which are suitable for breeding by *M. cinxia* occur as discrete, small habitat patches. The mean, median and maximum patch areas on the Åland are 0.13, 0.03 and 6.80 ha (n = 1502). We have previously estimated that roughly 80% of butterflies spend their entire life-time in the natal patch (Hanski et al. 1994). We conclude that the discrete habitat patches support local breeding populations, though there is substantial migration among nearby populations and patches (Hanski et al. 1994). In this respect *M. cinxia* appears to be similar to several other species of fritillaries (Ehrlich 1984, Baguette and Névé 1994, Warren 1994).

Fig. 3. Comparison between local population sizes in June 1991 and in August 1993. The 1991 results refer to the numbers of adult butterflies (estimates from an intensive mark-recapture study; Hanski et al. 1994), whereas the 1993 results refer to numbers of larvae (estimates from a complete census of larval groups). Population sizes (N+1) were log-transformed. There is no significant correlation between the population size estimates in the two years. Multiple data points are indicated by numbers.
We conducted an intensive mark-recapture study of *M. cinxia* in the 50-patch network in 1991 (Hanski et al. 1991). In this study, 1731 butterflies were marked and released. We obtained 741 recaptures, of which 9% were from a new patch. The mean, median and maximum distances moved by the migrants between patches were 590, 330 and 3050 m, with 20% of the migrants having moved >1 km but only 3% having moved >2 km. Among the total of 1502 patches, the mean nearest-neighbour distance is 240 m (median 128 m, maximum 3870 m). Therefore, we may conclude that the patches are not too isolated to prevent recolonization (Fig. 1) and that this metapopulation does not exemplify the non-equilibrium type discussed by Harrison et al. (1991).

**Condition 2: Risk of extinction of the largest local populations**

In the autumn 1993, the largest local population had 69 larval groups (an accurate count), and only 68 populations had >20 groups (estimated on the assumption that 35% of existing groups were detected in the survey, as described in the previous section). Based on our unpublished results on larval mortality, we estimate that there will be ca 620 butterflies in the largest local population in 1994 (number of larval groups [69] times number of larvae per group [50] times overwinter survival [0.32] times survival from post-diapause larvae to adult butterflies [0.56]). Such populations are not safe from extinction. We have observed the extinction of a population of ca 650 butterflies in only 2 years (Fig. 3). Results for the related Bay checkerspot butterfly *Euphydryas editha* in California suggest an equally high risk of extinction (Harrison et al. 1991, Foley 1994). We conclude that all local populations in the present system are so small that they have a significant risk of extinction, hence the long-term persistence of the species cannot be understood at the level of isolated local populations.

**Condition 3: Recolonization**

We investigated the degree of isolation of the focal patches. The effective patch area was calculated for the 4-km² squares centred around the focal patch. The effective patch area is the average patch area in the square. In the case of extinctions, patch density was measured by the number of patches in a 4-km² square centred around the focal patch. The effects of patch area and density on the probability of extinction were tested with the logistic regression model, \( \logit(\text{extinction}) = \text{constant} + \text{area} + \text{density} \). Both effects were significant (area: \( p = 0.016 \) and 0.024; no significant interaction; deviance \( = 44.76 \), df \( = 39 \), \( p = 0.24 \)). The effects of average patch area and patch density on extinction probability \( P \) were tested with ANOVAs on ranks, using the 4 patch area and density classes shown in the table. Both effects were highly significant (area: \( F_{3,251} = 5.69 \), \( p = 0.001 \); density: \( F_{3,251} = 4.21 \), \( p = 0.006 \); no significant interaction).

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<th>Area (ha)</th>
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**Condition 4: Asynchrony**

The intensive study of the metapopulation in the 50-patch network has revealed largely asynchronous local dynamics in 1991–93 (Fig. 3), in spite of a general decline in density during this period, due to two successive unfavourable summers.

A degree of asynchrony among local populations of *M. cinxia* is maintained by at least two factors. First, there is an obvious interaction between the effects of weather and habitat quality in local dynamics. Thus, while the exceptionally dry and warm summer of 1992 caused much larval mortality on the driest meadows on rocky outcrops, populations occupying moister meadows survived better (unpubl.). In 1993, June was very windy and greatly restricted the flight activity of butterflies on open meadows, but wind had less effect on the more sheltered habitat patches. These observations are consistent with the more extensive body of data for the Bay checkerspot butterfly *Euphydryas editha* in California (Ehrlich and Murphy 1987, Weiss et al. 1993).

Second, *Melitaea cinxia* is attacked by two specialist parasitoids in our study area, *Cotesia melitaearia* (Wilkinson) and *Hyposoter horticola* (Grav.). These parasitoids impose substantial mortality on the butterfly, but the level of parasitism varies from one population to another (from a few per cent to >50%), because the parasitoids themselves exhibit distinct metapopulation dynamics and are often absent from host populations (G. Lei, unpubl.). Specialist parasitoids may generally have a strong impact on fritillaries (Porter 1983).

In summary, we have shown that *M. cinxia* in Finland satisfies the four necessary conditions for metapopulation-level persistence. We therefore attribute its long-term survival on the Åland islands to a balance between stochastic local extinctions and recolonizations. The significance of metapopulation dynamics in the occurrence of *M. cinxia* on the Åland is further highlighted by sup-

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Table 1. Effects of patch area and density on extinction rate between 1991 and 1993 and on patch occupancy in 1993. \( n \) is the number of occupied patches in the 50-patch network in 1991, of which the percentage given by \( \% \) went extinct by 1993. Occupancy was calculated for the 4-km² squares. \( n \) is the number of squares and \( P \) is the mean fraction of occupied patches in a square. In the case of occupancy, patch area is the average patch area in the square. In the case of extinctions, patch density was measured by the number of patches in a 4-km² square centred around the focal patch. The effects of patch area and density on the probability of extinction were tested with the logistic regression model, \( \logit(\text{extinction}) = \text{constant} + \text{area} + \text{density} \). Both effects were significant (area: \( p = 0.016 \) and 0.024; no significant interaction; deviance \( = 44.76 \), df \( = 39 \), \( p = 0.24 \)). The effects of average patch area and patch density on extinction probability \( P \) were tested with ANOVAs on ranks, using the 4 patch area and density classes shown in the table. Both effects were highly significant (area: \( F_{3,251} = 5.69 \), \( p = 0.001 \); density: \( F_{3,251} = 4.21 \), \( p = 0.006 \); no significant interaction).

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Effects of patch area and density on patch occupancy

A fundamentally important prediction of all metapopulation models (Levins 1969, 1970, Hanski 1991a) is that the fraction of occupied patches at a stochastic steady state, denoted by $P$, increases with regional patch density, because increasing patch density facilitates recolonization; and that $P$ increases with average patch area, because larger patches tend to support larger local populations with a smaller risk of extinction. We shall first demonstrate that the premises of these predictions are met by the present system, then test the predictions themselves.

Assumptions

In the intensively studied 50-patch network, we recorded 22 extinctions and 6 colonizations between 1991 and 1993. Extinctions exceeded colonizations apparently because of the general decline in density during this period. The smaller patches tended to have smaller populations of $M. \ cinxia$ (legend to Fig. 4), and as expected, the extinction rate was higher in the smaller patches (Table 1).

With only 6 colonizations between 1991 and 1993, we could not confirm the expected decrease in colonization rate with decreasing patch density (increasing isolation). But the effect of isolation on colonization rate is strongly implied by two other results. First and most obvious, the numbers of migrants originating from a particular meadow decline with increasing distance from the source population (Hanski et al. 1994), hence colonization rate must also do so. Second, the extinction rate increased with decreasing patch density (Table 1), apparently because local population size tends to be smaller in the more isolated habitat patches (Hanski et al. 1994; Fig. 4). These results support the rescue effect (Brown and Kodric-Brown 1977), which here operates at the metapopulation level (Hanski 1991a, Hanski and Gyllenberg 1993, Hanski and Zhang 1993): with decreasing $P$, the existing populations are smaller (Fig. 4) and are hence expected to have a higher risk of extinction.

Test of model predictions

The effects of average patch area and patch density on patch occupancy ($P$) were analysed using the 4-km² squares as replicates. Both effects were statistically highly significant (Table 1).

Two other model predictions

The core-satellite hypothesis

Metapopulation models incorporating the rescue effect predict that, for a range of parameter values, the distribution of the patch occupancy frequency $P$ is bimodal (Hanski 1982a, 1991a, Hanski and Gyllenberg 1993). Previous tests of the bimodal core-satellite distribution have used data from multispecies assemblages, which creates problems of interpretation, and the previous studies mostly deal with inappropriate spatial scales (Hanski 1982a, b, Gotelli and Simberloff 1987, Gaston and Lawton 1989). The spatial scale should correspond to the movement range of the species. Thomas (1994) has recently reported bimodal distributions of $P$ values in two
species of butterflies, at an appropriate spatial scale, but the number of patch networks (and hence $P$ values) in his study was very small.

The bimodal core-satellite distribution of $P$ values is generated by the rescue effect, which we have demonstrated to operate in $M. \text{cinxia}$ (Table 1). Additional support for the rescue effect is provided by a positive relationship between average size of local populations and the number of local populations in the 4-km$^2$ squares (Fig. 4). Of the four recognized explanations of positive abundance-distribution relationships (Hanski 1991a, Hanski et al. 1993, Lawton 1993, Nee et al. 1991), of which Fig. 4 is an example, all other explanations apart from metapopulation dynamics with rescue effect (Hanski 1991a) can be excluded in this case for the following reasons. First, the hypothesis of ecological specialization (Brown 1984) is not applicable because our study deals with only one species. Second, the hypothesis of varying average carrying capacity of patches (Nee et al. 1991, see also Hanski 1991b) among the squares can be excluded, because there was only a weak or no effect of average patch area on average population size (Fig. 4). And third, the hypothesis that the abundance-distribution relationship is a sampling artefact (Wright 1991) can be excluded, because our results are based on nearly complete population counts. In summary, the assumptions of the core-satellite hypothesis (Hanski 1982a) are met.

We tested the core-satellite hypothesis with the $P$ values calculated for the 4-km$^2$ squares, which correspond in size to the spatial scale of movements of the butterfly (previous section). As predicted, the distribution of the $P$ values in the 4-km$^2$ squares is distinctly bimodal (Fig. 5).

![Fig. 5. The frequency distribution of the patch occupancy frequency $P$ in the 4-km$^2$ squares. Standard deviations (lines) were obtained by repeating the calculations 100 times for grids displaced systematically at 200-m intervals in both main directions. While calculating the $P$ values, small patches <500 m$^2$ were omitted, because their occupancy is erratic (Table 1) and because the small populations have little influence on the dynamics of the metapopulation. Squares with <5 patches (≥500 m$^2$) were also omitted because the respective $P$ values are unreliable and are limited to a few possible values.](image)

![Fig. 6. Comparison between the predicted and observed patch occupancy frequencies $P$ in the 4 x 4 km$^2$ squares in the northern part of the main Åland island. (a) Predictions based on a logistic regression model, in which patch occupancy is predicted by patch area only. There is no relationship between the predicted and observed $P$ values ($R^2=0$). (b) Prediction based on the dynamic incidence function model (Hanski 1994a). There is a highly significant relationship between the predicted and observed $P$ values ($p=0.001$, $R^2=0.56$). In both cases, the horizontal lines give the standard deviation for 10 independent predictions. Both models were parameterized with data obtained from the 50-patch network in 1991, roughly corresponding to one of the 4 x 4 km$^2$ squares, in the northern part of the Åland island (Fig. 1; this square was omitted from the test). The parameter values of the incidence function model are reported in Hanski (1994a). Each patch was assigned an additional 5% probability of colonization per generation, when empty, to model long-range migration from outside the metapopulation (this is thought to be a realistic value, but we do not have actual data to estimate the value of this parameter).](image)
A quantitative incidence function model

Hanski (1994a, b) has recently described a new approach to modelling of metapopulation dynamics with a generalized incidence function, which allows one to make quantitative predictions about patch occupancy in particular patch networks. The model is described in detail by Hanski (1994a), who also reports parameter estimates for *Melitaea cinxia*, estimated from the intensively studied 50-patch network in the northern part of the main Åland island in 1991.

We used the incidence function model to predict the *P* values in 4×4 km² squares, instead of the 2×2 km² squares, to have a larger number of patches per square and thereby more reliable *P* values. Furthermore, to include the metapopulation dynamic effect of patches surrounding the 4×4 km² squares, the model was actually iterated for patches in 6×6 km² squares, though the result was recorded for the inner 4×4 km² square only. Model iterations were started with all patches occupied, and the results were obtained from generation 100, when the metapopulation had practically reached a stochastic steady state.

The incidence function model predicted with substantial success the *P* values in the northern part of the main Åland island (Fig. 6), around the 50-patch network from which the parameter values had been estimated. In contrast, a non-dynamic logistic regression model, which predicts occupancy on the basis of patch areas only, generated entirely unsuccessful predictions (Fig. 6).

The good news thus is that the model successfully predicted patch occupancy in the part of the study area from which the parameter values had been estimated in 1991. The bad news is that the model failed to predict patch occupancy in the southern parts of the Åland islands. This failure may be due to some environmental differences between the different parts of the Åland islands. For instance, the habitat patches in the northern part of the main island have both larval host plants, *Plantago lanceolata* and *Veronica spicata*, whereas only *P. lanceolata* occurs elsewhere. Alternatively, patch occupancy may not be very close to a stochastic steady state, and possibly metapopulations in different parts of the Åland islands have been perturbed at different times and to different directions. A more thorough analysis of these questions is in preparation (Hanski, Moilanen, Pakkala and Kuussaari unpubl.), but to resolve these issues conclusively may be impossible without data for several years.

Discussion

Our results demonstrate beyond any reasonable doubt that the long-term persistence of *Melitaea cinxia* in Finland is based on a balance between stochastic local extinctions and recolonizations. All local populations are so small that they have a substantial risk of extinction, and long-term survival is possible only in networks of habitat patches, in which the local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely.

This sort of situation appears not to be exceptional in butterflies. Warren (1992) has recently analysed the rate of extinctions of rare butterflies on nature reserves in the UK between 1960 and 1982. Even though many of the reserves have been managed for some particular target butterfly, extinctions have been rampant: all the 16 populations of *Lycaena dispar*, *Maculinea arion*, *Carterocephalus palaemon* and *Mellicta athalia* on nature reserves went extinct, and in *Hesperia comma* and *Lyandra bellargus* about one quarter of the populations on reserves went extinct. Thomas and Harrison (1992), Thomas and Jones (1993), Thomas (1994) and Hanski and Thomas (1994) review other data on British butterflies indicating the extinction-proneness of isolated populations, but also the persistence of butterflies in networks of favourable habitat patches. The clear message from these studies is that local populations of butterflies are not safe from extinction, not even on managed reserves, and not even for the modest period of 20 years. We suspect that similar conclusions will also apply to many other specialist, rare and endangered species, of which much less is known than about butterflies.

We found for *Melitaea cinxia* that the fraction of occupied habitat patches declines with decreasing patch area and with decreasing patch density, in agreement with model predictions (Levins 1969, Hanski 1991a, b). To our knowledge, this is the first study based on a comparison of many conspecific metapopulations to confirm these predictions. The extinction of *M. cinxia* from mainland Finland in the 1970s (Marttila et al. 1990) is most likely related to the decreasing density of suitable meadows on mainland Finland during the past decades (Päikäes 1993). Fortunately, dry meadows are still common on the Åland islands, where farmers have largely maintained their traditional land use practices.

The limited success of the quantitative incidence function model in predicting patch occupancy is both encouraging and sobering. We are clearly a long way from being able to predict the consequences of habitat fragmentation for the persistence of species in quantitative terms. One particularly worrying aspect is that the model predictions assume a stochastic steady state, which the real metapopulations in changing landscapes may never have time to reach (Hanski 1994c, 1995). Qualitatively correct predictions may be the best we can achieve, but even such predictions can be valuable for conservation biology, where the question often is to select the best option out of two or more alternatives.

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