Extinction-Colonization Dynamics and Host-Plant Choice in Butterfly Metapopulations

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abstract: Species living in highly fragmented landscapes often occur as metapopulations with frequent population turnover. Turnover rate is known to depend on ecological factors, such as population size and connectivity, but it may also be influenced by the phenotypic and genotypic composition of populations. The Glanville fritillary butterfly (*Melitaea cinxia*) in Finland uses two host-plant species that vary in their relative abundances among distinct habitat patches (dry meadows) in a large network of ∼1,700 patches. We found no effect of host species use on local extinction. In contrast, population establishment was strongly influenced by the match between the host species composition of an empty habitat patch and the relative host use by larvae in previous years in the habitat patches that were well connected to the target patch. This "colonization effect" could be due to spatially variable plant acceptability or resistance or to spatially variable insect oviposition preference or larval performance. We show that spatial variation in adult oviposition preference occurs at the relevant spatial scale and that the other possible causes of the colonization effect can be discounted. We conclude that the colonization effect is generated by host preference influencing the movement patterns of ovipositing females. Migrant females with dissimilar host preferences have different perceptions of relative patch quality, which influences their likelihood of colonizing patches with particular host composition.

Keywords: classical metapopulation, oviposition preference, colonization, spatial dynamics, *Melitaea cinxia*.

Classical metapopulations persist in a balance between local extinctions and the establishment of new local populations at currently empty but suitable habitat patches

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(Levins 1969; Hanski 1999). Empirical studies of classical metapopulations have demonstrated that the probability of population extinction typically increases with decreasing population size (Schoener and Spiller 1987; Schoener 1991; Hanski 1999) or its surrogate, habitat patch area (reviews in Hanski 1994, 1999). The probability of colonization of an empty patch increases with connectivity to extant local populations (reviews in Hanski 1994, 1999). Apart from population size and connectivity, many other ecological factors have been reported to influence extinctions and colonizations (Simberloff 1994; Thomas 1994; Sjögren-Gulve and Ray 1996). In the case of the Glanville fritillary butterfly (*Melitaea cinxia*) in Finland, which provides an exceptionally well-studied example of classical metapopulations (Hanski et al. 1994, 1995; Hanski 1999), local extinctions are influenced by successional habitat loss (Hering 1995; Hanski 1999), drought and other adverse weather conditions (Hanski et al. 1996; Hanski 1999), demographic stochasticity (Hanski 1999), parasitism (Lei and Hanski 1997), emigration losses (Hanski 2001), and the rescue effect (Kuussaari et al. 1998, reduced extinction risk). Colonization probability is influenced by patch area, grazing (reduced colonization probability), and the quality and quantity of host plants (Hanski 1999, table 11.1). Furthermore, both extinction and colonization events are to some extent spatially correlated (Hanski 1999).

While the various ecological causes of population turnover are becoming increasingly well understood, there is much less information on possible effects of the phenotypic or genotypic composition of local populations on their turnover. In the case of the Glanville fritillary, the exception is the recent demonstration that inbreeding depression increases the risk of extinction of small local populations (Saccheri et al. 1998). The proposition that the genotypic composition of populations influences their turnover is not new, of course—this is the idea of classical group selection (Wynne-Edwards 1962; Levins 1970; Gilpin 1975).

In this article, we report a study on the Glanville fritillary butterfly conducted over a large set of distinct habitat patches in the Åland Islands in southwest Finland (for a

review of the study system, see Hanski 1999 chapters 11 and 12). Kuussaari et al. (2000) have previously reported that the butterfly shows spatial variation in the relative use of two host-plant species among habitat patch networks due to a tendency for ovipositing females to prefer the regionally more common host plant. At a smaller scale, use of the two host-plant species in a local population was influenced not only by the local abundances of the host species but also by the use of the host species in the surrounding populations in previous generations (Kuussaari et al. 2000). Here, we extend the results of Kuussaari et al. (2000) in two ways. First, we use long-term observational data to document extinction-colonization dynamics in habitat patches with known host-plant use. With these results, we demonstrate that regional host use influences the establishment of new butterfly populations but not the extinction of existing populations. Second, we establish which of several possible mechanisms is responsible both for this "colonization effect" and for the effect of regional diet on host-plant use in existing populations as documented by Kuussaari et al. (2000). Knowing the mechanism of the colonization effect is important for the understanding of its ecological and evolutionary implications. In this article, we address the five possible explanations of the colonization effect with the results of field and laboratory experiments on the oviposition host-plant preference of butterflies, on the movement patterns of butterflies with different preferences in response to the relative density of the host plants, and on spatial variation in the acceptability of the host plants to adult butterflies and in the performance of their larvae on these plant species. We show that the colonization effect is due to oviposition preference of migrating females influencing their movement patterns. The novel twist that these results bring to metapopulation ecology is the realization that, at least in some situations, habitat patch "quality" should be assessed for individuals rather than for populations or species.

Material and Methods

Long-term Data on Extinctions, Colonizations, and Host Use

In the Åland Islands in southwest Finland, suitable habitat for the Glanville fritillary is highly fragmented into small patches consisting of dry meadows with one or both of the two larval host plants *Plantago lanceolata* and *Veronica spicata*. The mean, median, and maximum patch areas are 0.13, 0.03, and 6.80 ha, respectively ($n = 1,502$; Hanski et al. 1995). The habitat patches are mostly so far apart that individual butterflies have no chance of sampling many patches, and females are lucky to locate a new patch if they accidentally or otherwise fly away from the natal

patch (Hanski et al. 1994; Kuussaari et al. 1996). The Glanville fritillary in the Åland Islands represents a prime example of a classical metapopulation containing no large extinction-resistant local populations and hence persisting regionally in a balance between local extinctions and colonizations (Hanski et al. 1995; Hanski 1999).

All the ~1,700 habitat patches known on the main Åland Island were surveyed for larval groups each autumn in 1993–1997. These surveys provided patch-specific data on extinctions and colonizations. The field methods have been described in detail elsewhere (Hanski et al. 1996; Kuussaari et al. 2000; M. Nieminen, J. Pöyry, and I. Hanski, unpublished data). It suffices to emphasize here that counting of the larval population sizes in hundreds of populations is possible because of the gregarious behavior of larvae, which live in sib groups, and because of the generally small size of local populations, often less than five groups (Hanski et al. 1995; Hanski 1999). The numbers of extant local populations varied from 320 to 515 in 1993–1997. During the 1995 and 1996 surveys, the covers of the two host plants *P. lanceolata* and *V. spicata* were also estimated (fig. 1, *top*; fig. 2*A*). The average value of these estimates was used to calculate for each habitat patch the relative cover of *Veronica*, denoted by A_v and varying between 0 and 1 (Kuussaari et al. 2000). The absolute host-plant density is low in the habitat patches, typically a few percentages of the total area (Kuussaari et al. 2000). The host plant of each larval group was recorded in the surveys in 1993–1997, allowing us to calculate the relative use of *Veronica* in each habitat patch as the number of larval groups found on *Veronica* divided by the total number of larval groups. In some analyses, we calculated the relative cover of *Veronica* for patch networks, which are defined as clusters of habitat patches within which butterfly movements are relatively frequent (see Hanski et al. 1996).

The focus of our analysis was on the influence of the regional host-plant use on local extinctions and colonizations. We therefore needed to define a measure that describes in an appropriate manner regional host-plant use. To do this, we first calculated, for each habitat patch i, a measure of "connectivity" to larval groups on host plant X (*Veronica* or *Plantago*) in the surrounding populations in year t as

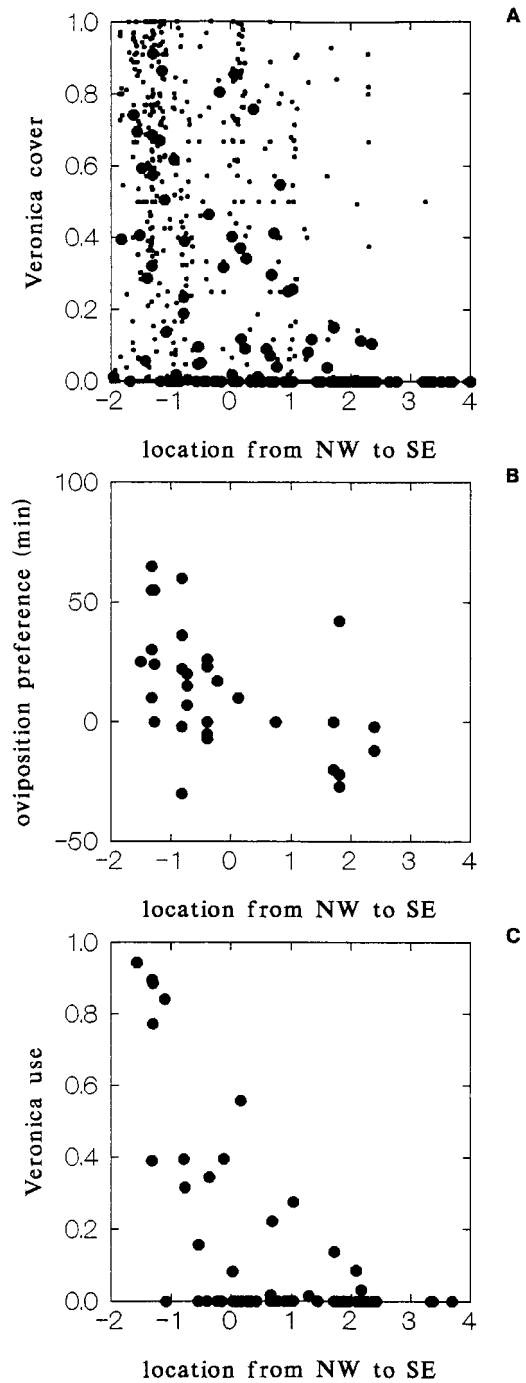$$S_{i,X}(t) = \sum_{i \neq j} \exp(-\alpha d_{ij})N_{j,X}(t), \qquad (1)$$

where d_{ij} is the distance between patches i and j, $1/\alpha$ defines the average migration distance (Hanski 1994), and $N_{j,X}(t)$ is the number of larval groups using host plant X in population j in year t. The value of parameter α was set to 1 based on previous mark-release-recapture studies (Hanski et al. 1994, 1996). A measure of overall connec-
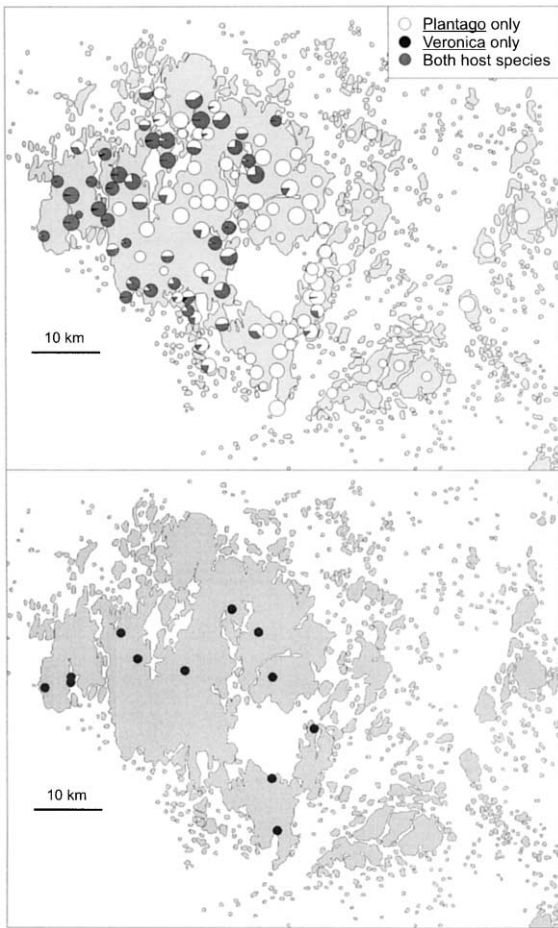
Figure 1: *Top*, map of the Åland Islands showing the relative abundances of the two host plants of the Glanville fritillary, *Plantago lanceolata* and *Veronica spicata*. *Bottom*, study populations used in the laboratory study of oviposition host-plant preference.

Figure 2: Gradients (*A*) in relative cover of *Veronica spicata*, (*B*) in female oviposition preference, and (*C*) in *Veronica* use in Åland Islands along an axis running from northwest to southeast. *A*, Relative cover of *V. spicata* of the pooled cover of *V. spicata* and *Plantago lanceolata* is given for individual habitat patches (*small dots*) as well as for patch networks (*large dots*). *B*, Data points are family means (*n* = 33) from 12 populations. Linear regression accounts for 24% of the variance in preference (slope, $t = -3.34$, $P = .002$; 36% without the outlier). *C*, Networks from which more than five larval groups were found are included.

tivity (inverse of isolation) of population i in year t is given by $S_i(t) = S_{i,V}(t) + S_{i,P}(t)$, and a measure of regional *Veronica* use in the neighborhood of population i is given by $R_i(t) = S_{i,V}(t)/S_i(t)$. This latter measure varies between 0 and 1. For some analyses, we need to divide the habitat patches into those that are dominated by *Plantago* versus those that are dominated by *Veronica*. The former are defined as patches with *Plantago* only, whereas *Veronica*-dominated patches are defined as those with relative cover of *Veronica* >70% (there are very few patches with *Veronica* only; fig. 1, *top*).

The relative use of the two host-plant species as measured by R_i varies spatially (Kuussaari et al. 2000; "Results" in this article). This variation can be due to (1) spatial variation in the relative abundances of the two host-plant species; (2) variable oviposition host-plant preference of females that influences the distribution of eggs; (3) variable

larval performance that influences the likelihood that larvae on different host plants would reach the age at which they are censused; (4) variable plant resistance due to plant acceptability to ovipositing butterflies (Singer and Parmesan 1993); and (5) variable plant resistance due to plant suitability for the early larval stages, thus affecting the likelihood that larvae would survive to be censused.

Any or all of these five factors could influence host use and the value of R_i. We know from a previous study (Kuussaari et al. 2000) that spatial variation in relative host abundances (hypothesis 1) does not suffice to account for spatial variation in relative host use. Therefore, spatial variation in the quality of either the plants or the insects, or both, must be invoked. Existing knowledge of oviposition preference (Kuussaari et al. 2000), larval performance, and plant suitability (S. van Nouhuys, M. Singer, and M. Nieminen, unpublished data; summarized in "Discussion") was here complemented with three additional experiments on oviposition preference, plant acceptability, and butterfly-movement behavior. The combination of prior knowledge and the results of the new experiments provides sufficient information for all the potential causes of spatial variation in R_i to be assessed.

Host-Plant Choice of Ovipositing Butterflies

The Glanville fritillary oviposits maximally one egg cluster per day under favorable conditions (Kuussaari 1998), and hence, very limited sample sizes of egg clusters can be obtained from individual females. Therefore, small differences among individuals in the probability of ovipositing on different host plants cannot be ascertained from differences in the proportions of eggs actually laid on those hosts, either naturally or in an experiment. For this reason, oviposition preference in the Glanville fritillary and related melitaeine butterflies has traditionally been tested by staged encounters between insects and plants, in which the readiness to oviposit is recorded but oviposition is not allowed to take place (Singer et al. 1992; Kuussaari et al. 2000). This technique allows one to gather more precise information from each individual than could be obtained from the distribution of a small number of egg clusters among host plants.

In a preference test, the butterfly is placed gently on each of two test plants in alternation at 10-min intervals, and its responses are observed (this can only be done while the sun is shining). This procedure is started before the female is highly motivated to oviposit, hence she begins by rejecting both hosts. Eventually, the butterfly accepts a plant by preparing to oviposit (curling of abdomen and extrusion of ovipositor). At this point, however, she is not allowed to oviposit, but she is removed from the accepted plant and 5 min later is placed on the other plant. If that

plant is also accepted, the insect is deemed to have no preference. If the second plant is rejected, the first plant is deemed to be preferred. Repeated staged encounters with the second plant are then used to estimate the length of the "discrimination phase," the time period during which the first plant would be accepted (if encountered) and the second one rejected. By this means, the strength of preference for the two plants can be measured as a quantitative trait, the length of the discrimination phase. This technique entails the assumption that the response of the insect to a particular plant at a particular time is unaffected by its prior encounters with hosts, an assumption that has been tested and supported in various ways (Singer 1983, 1986; Thomas and Singer 1987; Parmesan et al. 1995; Schöps and Hanski 2001).

Using this technique, we investigated spatial variation in oviposition preference. Unlike the previous study (Kuussaari et al. 2000), this work was focused in that part of the Åland Islands where both host species occur. We tested butterflies raised from eggs obtained from adults caught in 12 local populations in Åland in 1997 (fig. 1, *bottom*). All larvae were raised on *Plantago*, and adult preferences were tested in a greenhouse in Austin, Texas, in the spring of 1998, using plants grown from seeds collected in Åland (Jomala, where both host plants are used by larvae). We chose highly acceptable members of each plant species, as determined by prior tests with butterflies from Åland (these butterflies were not included in this experiment). Each data point was an estimated minimum length of the discrimination phase between *Plantago* and *Veronica* for an individual butterfly ($n = 47$). Data from sibs were combined to generate family mean preferences ($n = 33$), with positive signs attributed to preference for *Plantago* over *Veronica* and negative signs for preference for *Veronica* over *Plantago*.

Spatial Variation in Plant Acceptability versus Butterfly Preference

In June 1998, we randomly selected plant pairs, each comprising one *Plantago* and one *Veronica*, from four habitat patches in the central parts of the study area, where both hosts are used (mixed-use area), and from four habitat patches in northwest Åland, where *Plantago* is present but rarely used (*Veronica*-use area). The plants were carefully dug up with their roots, soil, and surrounding vegetation; placed in plastic plant pots; and transported to a single location (Husö Experimental Station) where they were placed outdoors. Using the technique described above and an experimental design developed by Singer and Parmesan (1993), we offered each plant pair to one butterfly captured from a *Veronica*-use patch and to one butterfly from a mixed-use patch. Each butterfly was tested on only two

plant pairs, one from the *Veronica*-use area and one from the mixed-use area. While being used in the experiment, each plant was covered with a net cage that admitted sunlight but prevented butterfly escape.

The test of each butterfly began with staged encounters between the butterfly and the four plants (two pairs), with the plants offered in rotation as follows: *Plantago* from patch X, *Veronica* from patch X, *Plantago* from patch Y, and *Veronica* from patch Y. In this experiment, we were interested only in the rank order of preferences, not in the strength of preference. Some tests rapidly generated such ranks within both plant pairs. If so, we considered the test of both the insect and the plant pairs complete. If the butterfly failed to discriminate within one or both plant pairs, it was allowed to oviposit and was retested on the plants that it had failed to rank (retesting begins immediately in order not to miss the point in time when the butterfly is again motivated to oviposit). We did this because failure to discriminate in a field experiment does not necessarily indicate lack of preference. For example, preferences are obscured by cold or cloudy weather, which was the norm in Åland in June 1998. Such obscuring of preference occurs when an insect begins by rejecting the test plants, then cannot be tested for an interval because of poor weather, and then accepts all the test plants as soon as the sun returns. We cannot tell from this result whether the insect would have expressed preference if the weather had permitted testing at regular intervals. Accordingly, we retested in such cases whenever the health of the butterfly permitted. In the data analysis, we ignored failures to discriminate and used only tests that generated a clear ranking of a plant pair by a butterfly. For this reason, we did not obtain exactly the same number of data points from the two classes of plant-pair origin. We used contingency table and Mann-Whitney tests to determine whether the proportion of expressed preferences for *Veronica* and *Plantago* depended on the origin of the plants, on the origin of the insects, or both.

Oviposition Preference and Movement Behavior

In order to establish a link between oviposition preference and colonization of new habitat patches, we examined the movements of butterflies with dissimilar preferences among patches with dissimilar host-plant composition. We reared larvae from one *Veronica*-preferring and two *Plantago*-preferring populations (Kuussaari et al. 2000), using *Plantago* as the larval host plant. We released 300 mated females at two release sites located ∼150 m apart on mainland Finland, close to the Tvärminne Zoological Station, in June 1997. These sites have no natural host plants, but we had placed 200 potted *Plantago* at one site and 200 potted *Veronica* at the other within areas of

∼30 × 30 m. Releases were spread over a period of 5 d. On each day of release, insects from both the *Veronica*-preferring and *Plantago*-preferring lines were divided equally between the two habitat patches. Insects were numbered on the upper side of the forewing with a marker so that the numbers could be recorded on resighting without disturbing the butterfly. Equal effort was expended in searching both sites for butterflies with weather permitting. Analysis was done by contingency table, with the expectation that the ratio of *Plantago*-preferring to *Veronica*-preferring insects seen at each site should be the same. Each insect was counted only once, at its last recorded location.

Results

Geographic Variation in Host-Plant Use and Preference

There is a distinct geographic gradient in the relative abundances of the two host-plant species in the study area (fig. 1, *top*), with the abundance of *Veronica* decreasing from northwest to southeast (fig. 2*A*), across a distance of 70 km. This gradient in relative host abundances is paralleled by a gradient in female oviposition preference as assessed in our laboratory experiments (fig. 2*B*). The preference cline shown here takes a form that could explain the known bias in the use of the two host plants toward the regionally more abundant species (fig. 2*C*; Kuussaari et al. 2000).

Figure 2*A* shows that there is a distinct geographic gradient in relative host abundances, but there is also much variation from one habitat patch to another around the geographic trend (fig. 2*A*). Thus, for instance, a butterfly that has left a *Veronica*-dominated patch may happen to move to a *Plantago*-dominated patch. The question thereby arises whether the observed oviposition preferences (fig. 2*B*) have consequences for the spatial dynamics of the species in this highly fragmented landscape.

The Colonization Effect

In this section, we analyze whether the rates of colonization and extinction in habitat patches with particular relative host abundances are associated with the regional host use around the focal patch, as measured by R_i ("Material and Methods"). In this analysis, we excluded patches located east of the longitude 20°12′E, where *Veronica* is practically absent (fig. 1, *top*). In the pooled data for the remaining study area, we recorded 317 colonization events out of a possible 2,356 events (13%) and 446 extinction events out of a possible 952 events (47%) in the years 1993–1997.

Results in figure 3 demonstrate that the colonization
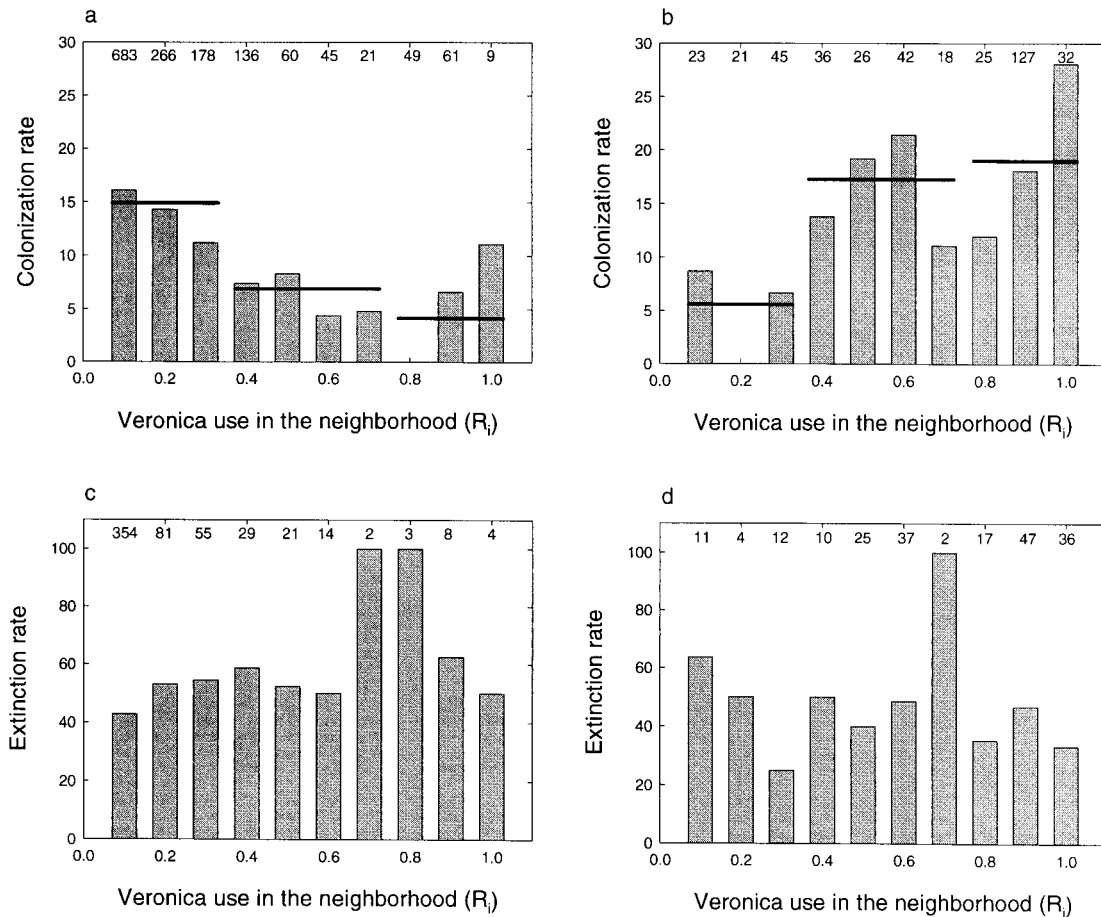
Figure 3: Colonization and extinction rates in habitat patches dominated by *Plantago* (*a* and *c*) and *Veronica* (*b* and *d*) versus *R*, the measure of regional host use. To test for the effect of *R*, we grouped the patches into three classes, as shown by the horizontal lines, $R < 0.3$, $0.3 \leq R \leq 0.7$, and $R > 0.7$. Test statistics (likelihood χ^2, df = 2) are as follows: *Plantago*, colonization (*a*) 24.27, $P < .0001$; extinction (*c*) 4.66, $P = .097$; *Veronica*, colonization (*b*) 9.93, $P = .007$; extinction (*d*) 0.94, $P = .63$. The values for sample size are shown above the bars. The data were pooled for the years 1994–1997.

of *Plantago*-dominated and *Veronica*-dominated habitat patches is associated with regional host use. The average annual colonization rate was around 5% when butterflies attempted to colonize patches containing the host species less used in the region, whereas when the dominant plant species in the empty patch was the one more used in the region, the annual colonization rate was 15%–20% (fig. 3). In contrast, there was no significant effect of R_i on local extinctions, although there was an indication of a slight effect in *Plantago*-dominated patches (fig. 3).

This analysis does not take into account any other variables that might influence local extinctions and colonizations. Because these other variables are not expected to be correlated with R_i, it is not likely that omitting them would seriously bias the results. Nonetheless, we per-

formed logistic regression analyses of the extinction and colonization events separately for each year, including overall population connectivity (S_i) and R_i as the explanatory variables in the colonization models and S_i, R_i, and population size in the previous year in the extinction models (population connectivity and size are the variables with the strongest effects on colonizations and extinctions, respectively; Hanski et al. 1995). As expected, higher connectivity consistently increased colonization rate, while connectivity and large population size reduced extinction rate (table 1). In these analyses, the effect of R_i was consistently negative on the colonization of *Plantago* patches and was significant at a 5% level in three of 4 yr, while the effect of R_i was significantly positive in *Veronica* patches in 1 yr and positive but nonsignificant in two more years.

Table 1: Logistic regression models for local extinctions and colonizations of empty habitat patches in 1993–1997

Turnover, patch, and variable	1994	1995	1996	1997
Colonization:				
Plantago:				
S	3.05 (.002)	2.91 (.004)	5.70 (<.001)	6.92 (<.001)
R	−3.04 (.002)	−1.94 (.05)	−1.21 (.23)	−3.33 (.001)
n	346	360	370	432
Veronica:				
S	2.35 (.02)	.49 (.62)	2.34 (.02)	2.14 (.03)
R	.79 (.43)	1.03 (.30)	2.41 (.02)	−.42 (.67)
n	89	113	101	92
Extinction:				
Plantago:				
N	−4.29 (<.001)	−2.94 (.003)	−3.90 (<.001)	−3.22 (.001)
S	−2.41 (.02)	−1.45 (.15)	−2.87 (.004)	−1.70 (.09)
R	1.91 (.06)	−.06 (.95)	−.26 (.80)	.80 (.42)
n	189	138	130	114
Veronica:				
N	−2.05 (.04)	−1.83 (.07)	−1.59 (.11)	−1.98 (.05)
S	−2.07 (.04)	.73 (.46)	−.92 (.36)	−1.61 (.11)
R	−1.58 (.11)	.88 (.38)	.15 (.88)	−.21 (.83)
n	69	31	34	67

Note: The explanatory variables are population size in the previous year (N), connectivity (S), and relative use of *Veronica* in the surrounding populations (R; see "Material and Methods" for definition). The values are t-tests of the regression coefficient and the P value (in parentheses); n is sample size.

The only significant ($P = .05$) extinction effect was detected in *Plantago*-dominated patches in one of 4 yr (table 1).

These analyses conclusively demonstrate that population establishment is related to the match between host use in the source populations of migrating females and the host-plant species composition in the target patch. We call this result the "colonization effect" for short. The remainder of our empirical work is directed toward understanding the mechanistic cause(s) of the colonization effect.

Spatial Variation in Plant Acceptability and Butterfly Preference

There was no indication that the relative acceptabilities of *Plantago* and *Veronica* would differ according to the origin of the plant pair (table 2). In contrast, butterflies originating from the mixed-use and *Veronica*-use areas showed strikingly different preferences (table 2). This latter finding is consistent with our previous results comparing more widely separated metapopulations of the Glanville fritillary in the Åland Islands (Kuussaari et al. 2000; fig. 2B), although in this experiment, butterflies from the mixed-use area were even more consistently *Plantago* preferring than in the previous experiments. The analysis of pooled data

in table 2 indicates that variation in insect preference rather than in host acceptability was the mechanism responsible for spatial variation in "electivity" within the set of eight patches that we studied. A Mann-Whitney test of the effect of butterfly origin on ranks of proportion of butterflies preferring *Plantago*, using just one data point per patch, is also significant ($U = 16$, $P = .02$). This result indicates that there was a general tendency in the system as a whole for oviposition preferences to differ between *Veronica*-use and mixed-use patches.

Oviposition Preference and Movement Patterns

In the field experiment in which *Veronica*- and *Plantago*-preferring butterflies were released on two nearby experimental patches with only *Veronica* or *Plantago*, our results showed a trend for the butterflies to assort themselves among the release sites according to their origin. With each insect recorded just once, at the site where it was last seen, the total numbers of *Veronica*-preferring females resighted at the *Veronica* and *Plantago* sites were 33 and 17, respectively, whereas in the case of *Plantago*-preferring females, the respective numbers were 18 and 23. This difference is significant at $P = .055$ (two-tailed) or $P = .028$ (one-tailed) by Fisher's exact test.

Consequences for Metapopulation Dynamics

Having demonstrated the colonization effect and having shown that it results from an influence of butterfly oviposition preference on patch colonization (see "Discussion"), we may ask about the broader implications of these results for ecological metapopulation dynamics and for evolutionary dynamics of oviposition preference and possibly other life-history traits. Here, we demonstrate that the colonization effect can have major consequences for the size and even the persistence of metapopulations. The evolutionary implications will be examined elsewhere (I. Hanski and M. Heino, unpublished data).

To examine the ecological dynamics, we use the previously parameterized incidence-function model (IFM; Hanski et al. 1996) to predict the size of the butterfly metapopulations in different networks of habitat patches in the study area. Hanski et al. (1996) divided the large Åland system into 127 semi-independent networks (for a map, see the original study). Here, we applied the IFM to the 53 networks that had both host plants and consisted of more than one patch. Metapopulation size is measured by the sum of patch-specific long-term probabilities of occupancy, obtained by iterating deterministic equations for the probability of patch occupancy until equilibrium (Hanski and Gyllenberg 1997; Hanski and Ovaskainen 2000). We contrast two different butterfly phenotypes, *Veronica*- and *Plantago*-preferring butterflies, that have a roughly threefold difference in the colonization rate of habitat patches that contain only the preferred versus the nonpreferred host plant (see fig. 3). To include the colonization effect into the IFM in as simple a manner as possible, we multiplied the patch-specific colonization probabilities (C_i in Hanski et al. 1996; Hanski 1999) determined by patch areas (surrogate for local population sizes) and connectivities by a factor of $(A_v + 0.5)/1.5$ for the *Veronica*-preferring phenotype and by a factor of $(1.5 - A_v)/1.5$ for the *Plantago*-preferring phenotype. The A_v variable is the relative cover of *Veronica* in the particular patch. With this modification, the colonization rate shows the empirically observed, maximally threefold difference in the probability of colonization depending on the match
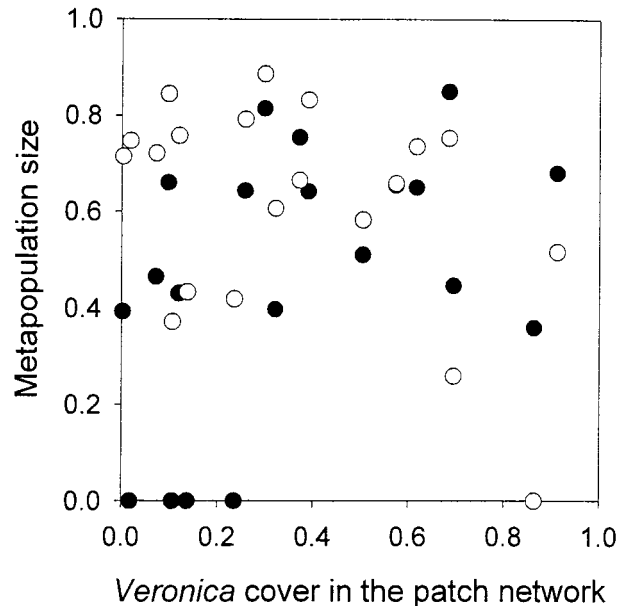
Figure 4: Model-predicted metapopulation size of *Plantago*-preferring (*open circles*) and *Veronica*-preferring (*dots*) butterflies in 19 habitat patch networks against the pooled relative *Veronica* cover in these networks. The results were obtained with the incidence-function model to which the colonization effect had been added as explained in "Consequences for Metapopulation Dynamics."

between the butterfly phenotype and the host-plant composition in the focal patch.

The results are shown in figure 4. Out of the 53 patch networks, the predicted metapopulation size was 0 for both *Veronica*-preferring and *Plantago*-preferring butterflies in 34 networks (these are typically small networks, not satisfying the deterministic threshold condition for persistence; Hanski and Ovaskainen 2000). In many of the remaining networks, the metapopulations of the two butterfly phenotypes have very different sizes. In the extreme cases (four networks), one phenotype is predicted to persist in the network while the other one goes deterministically extinct (fig. 4).

Table 2: Observed preference of females originating from mixed-use and *Veronica*-use areas in the Åland Islands when tested with plants from mixed-use and *Veronica*-use areas

	Butterflies from mixed-use area		Butterflies from *Veronica*-use area	
Origin of plants	*Veronica* preference	*Plantago* preference	*Veronica* preference	*Plantago* preference
Mixed-use area	2	9	11	1
Veronica-use area	1	17	10	1

Note: The origin of the plants has no influence on the preference exhibited by the butterflies, whereas the origin of the butterflies has a strong effect (pooled data, $P < .001$).

Discussion

The Colonization Effect and Its Causes

In this article, we have shown that an empty habitat patch containing mostly *Plantago* is more likely to become colonized if there is a history of high relative use of *Plantago* in nearby patches than if larvae have mostly used *Veronica* in the surroundings. Likewise, empty target patches containing principally *Veronica* are more likely to be colonized when larvae in the nearby patches have been found principally on *Veronica*. We term this phenomenon the "colonization effect." In a previous study (Kuussaari et al. 2000) on the Glanville fritillary in the Åland Islands, we demonstrated the "electivity effect," which is closely related yet distinct from the colonization effect; the relative use of *Plantago* and *Veronica* in the occupied habitat patches is influenced, as expected, by local host-plant density, but in addition, it is associated with the history of host use in the surrounding populations (Kuussaari et al. 2000). The data sets in these two studies were independent, consisting of the currently empty patches (this study) versus the occupied habitat patches (Kuussaari et al. 2000).

It is both parsimonious and probable that the electivity and colonization effects have a common underlying cause. In theory, both insect- and plant-based mechanisms may explain both effects. As an example of an insect-based mechanism of the colonization effect, a target patch containing mostly *Plantago* may remain uncolonized because migrating butterflies prefer *Veronica* or because larvae in the region are ill adapted to survive on *Plantago*. Exactly the same mechanisms could cause a patch that contains a butterfly population to have a lower proportion of larval groups on *Plantago* than expected from the relative local abundance of *Plantago* (the electivity effect). As an example of a plant-based mechanism, consider the possibility that the quality of *Plantago* is spatially autocorrelated and that habitat patches of low-quality *Plantago* tend to be surrounded by other patches with low-quality *Plantago*. Such a low-quality target patch would be less likely to be colonized, and larvae in nearby patches would have been found mostly on *Veronica*. These hypothetical examples illustrate that it is essential to understand at least the qualitative nature of the mechanisms that generate spatial patterns in plant-insect interactions (Singer 2000) before we can sensibly explain phenomena such as the colonization effect.

Relative host abundances necessarily influence host use (fig. 2*B*), but Kuussaari et al. (2000) have conclusively shown that one cannot explain patterns of host use in the Glanville fritillary solely by spatial variation in host abundances. We therefore reject hypothesis 1 in "Material and Methods" as the only explanation of patterns in host use. Note also that, even in principle, hypothesis 1 cannot explain the colonization and electivity effects, which can only be caused by spatial variation in the properties of butterflies or their host plants, or both (hypotheses 2–5).

Van Nouhuys et al. (unpublished data) describe spatial patterns in larval performance and host suitability for the Glanville fritillary. Working in habitat patches chosen for their disparate histories of host use, van Nouhuys et al. (unpublished data) staged encounters in the field between highly motivated butterflies and randomly chosen plants of each host species. They thereby caused females to lay eggs on undisturbed *Plantago* in regions where larvae had been frequently found on this host as well as in regions where larvae had been found entirely or almost entirely on *Veronica* despite high local abundance of *Plantago*. Eggs were deposited in like manner on *Veronica* in the habitat patches in which this host species occurred. Combined survival of eggs and young larvae until late summer was significantly lower on *Plantago* in the patches where it was commonly used than in the patches where it was rarely used, which is the opposite result from that expected if variation in survival on *Plantago* was responsible for the observed spatial variation in host use. In the patches where *Veronica* was the sole or principal host and *Plantago* bore few or no natural larval groups, survival of experimental larval groups on the two host species was not significantly different (van Nouhuys et al., unpublished data). This experiment thus indicates that spatial variation in R_i is not likely to be generated by larval performance or plant suitability, either acting alone or in concert. A series of independent experiments with crossed design using transplanted larvae and plants led to the same conclusion (van Nouhuys et al., unpublished data).

The results of van Nouhuys et al. (unpublished data) eliminate systematic spatial variation in either insect physiological performance (hypothesis 3) or in host suitability for larval growth (hypothesis 5), including host associations with natural enemies. This leaves insect oviposition preference (hypothesis 2) and plant acceptability (hypothesis 4) as possible causes of the colonization effect. In our crossed-design experiment, we preference tested female butterflies from sites with different host use on pairs of plants from sites with different host use, each plant pair comprising a single *Veronica* and a single *Plantago*. Which member of the plant pair was preferred depended entirely on the origin of the insect and not at all on the origin of the plant (table 2). Therefore, we conclude that, at least for the set of habitat patches in this experiment, variation in electivity (host use in proportion to host abundance) was due only to variation in the oviposition preference of the butterflies (hypothesis 2) and not to variation in plant quality (hypothesis 4). Spatially variable oviposition preference is therefore implicated as the principal cause of the electivity effect and hence also of the colonization effect.

Mechanisms of Spatially Variable Preference

Which mechanisms might cause oviposition host-plant preference to be spatially variable? Since our preference tests (fig. 2B) and those of Kuussaari et al. (2000) were performed with insects raised on a common host, a genetic basis for spatial variation in preference is likely. This conclusion is strengthened by a large difference in preference between two populations of the Glanville fritillary from Åland being maintained into the second laboratory generation in a common environment (Singer and Lee 2000). This explanation is also consistent with previous results on the closely related melitaeine butterfly *Euphydryas editha*. Estimated heritability of preference within a population of *E. editha* was 0.9, from a regression of the average lab-raised daughters' preference on maternal preference tested in the field (Singer et al. 1988). Reciprocal crosses among populations with consistently different preferences produced an F1 generation with intermediate preference, with no difference between F1 individuals with mothers from the different populations (Singer et al. 1991).

The frequency of encounters of butterflies with *Plantago lanceolata* and *Veronica spicata* must vary spatially, depending on the abundances of the two plant species. If encounters influence preference, such conditioning might contribute to the observed spatial variation in host use. Experiences of adult insects do often influence preference, but in Lepidoptera, the type of preference measured here, expressed after alighting, is generally unresponsive to prior host encounters (Thomas and Singer 1987), with a single documented exception (Cunningham et al. 1998). In particular, empirical results for the Glanville fritillary and other checkerspot butterflies have consistently failed to find evidence for learning in oviposition preference (Singer 1986; Thomas and Singer 1987; Parmesan et al. 1995; Schöps and Hanski 2001). Similarly, the once popular hypothesis that oviposition preference is influenced by prior larval feeding (Hopkins 1917; Thorpe 1930) has lost ground in the past 20 yr (Wiklund 1974; Futuyma and Peterson 1985; Jaenike 1990) and is currently unsupported by evidence for any herbivorous insect (Schoohoven et al. 1998, p. 214). We therefore consider it unlikely that learning or induced preference would make any significant contribution to the patterns of spatially variable preference documented here.

How Does the Genetically Determined Oviposition Preference Influence Colonizations?

Granted that genetically based preference comprises the principal mechanism of the colonization effect, how does it do so? It could operate by influencing the likelihoods that butterflies will immigrate to particular habitat patches, the lengths of time that they will remain in these patches, and the likelihoods of oviposition per unit time in the patches (for this latter possibility we lack data).

Five different studies have found evidence for a relationship between postalighting oviposition preference and movement behavior in melitaeine butterflies. Working with *E. editha*, Thomas and Singer (1987) marked and released butterflies in populations occupying large (>1 ha), adjacent habitat patches with different host plants. They then tested preferences of recaptured females, comparing those that had stayed in the same patch versus those that had moved. A strong association was found in the expected direction: females tended to stay or to leave depending on the presence of their preferred host species. In addition, females with no preference were more likely to emigrate than females that preferred the host used in their habitat patch. These results could indicate an influence of host preference on movement. Alternatively, they could stem from an effect of movement on preference, assuming that movements would affect host encounter, which would then affect preference. Thomas and Singer (1987) discounted the second possibility (that movements would affect preference) by showing that repeated staged encounters with particular hosts had no detectable influence on oviposition preference.

In the second study on *E. editha*, preferences were measured after a population extinction had occurred in one of the two populations studied by Thomas and Singer (1987). After the extinction, females that had immigrated to the now vacant habitat patch had significantly different oviposition preferences from butterflies that had stayed in the adjacent (source) population, strongly suggesting that nonrandom movement had been the cause of prior spatial variation in preference among the two populations (Singer and Thomas 1996). In a third study of the same system, Boughton (2000) found that immigration rate was not influenced by patch quality but that emigration rate was elevated in patches that contained only a low-ranked host species in terms of oviposition preference.

Fourth, I. Hanski, C. Breuker, K. Schöps, R. Setchfield, and M. Nieminen (unpublished data) compared strongly *Veronica*-preferring Glanville fritillary from Estonia with *Plantago*-preferring females from Åland. Observing the movement behavior of butterflies in habitat patches containing only *Plantago*, they found that the *Veronica*-preferring females had a significantly higher emigration rate and lower immigration rate than *Plantago*-preferring females. Finally, in the experiment described in this article, we released two lines of butterflies from Åland with dissimilar oviposition preferences. We found that their residence times within experimental habitat patches were different, depending on the match between the oviposition preference and the host species in the habitat patch. This

result, though not strongly supported statistically, is consistent with all the four previous studies summarized above. We conclude that the colonization effect is primarily caused by genetically based host-plant preference influencing the immigration and emigration rates of females as a function of the relative host-plant abundances in the habitat patches.

Lack of Extinction Effect

We found unambiguous evidence for the colonization effect but no evidence for a comparable extinction effect; that is, the risk of extinction was not significantly related to the use of the two host-plant species in the surroundings of the focal patch. By inference, the risk of population extinction was not strongly related to the regional oviposition preference in the butterfly populations. This result might be considered surprising because an insect-based mechanism of the colonization effect might also lead to an extinction effect in at least two ways. First, if there was local adaptation in larval performance at the same spatial scale and in the same direction as in oviposition preference (fig. 2*B*), larvae in a patch with a regionally rare host would be poorly adapted to that host, possibly increasing the risk of local extinction. However, as we have already described, a series of field and laboratory experiments has failed to find any trend for such local adaptation in larval performance of the Glanville fritillary in Åland (van Nouhuys et al., unpublished data). Because larvae from *Veronica*-use areas do not perform better on *Veronica* relative to *Plantago* than larvae from mixed-use and *Plantago*-use areas, spatial variation in adult oviposition preference cannot be explained by natural selection for adults to prefer the plant species to which the larvae are locally adapted. By the elimination of this possibility, the most likely explanation of the observed geographic cline in preference (fig. 2*B*) is an evolutionary response of adult butterflies to the gradient in relative host abundances.

The second way in which an extinction effect could be generated is by reduced probability of butterflies ovipositing in habitat patches dominated by the regionally uncommon host plant, either because they tend to emigrate or because they oviposit less often even if they stay. Apparently, any such effects are too small to be detected even in our large data set, possibly for two reasons. In the case of females emerging from a habitat patch with the regionally uncommon host plant, they might indeed be more likely to emigrate than females emerging in a patch dominated by the regionally common plant species, but because discrimination phases are usually much less than a day (Kuussaari et al. 2000), the former females would still have a large probability of laying their first batch of eggs in the natal patch, which would reduce the risk of population

extinction. Second, if the population would survive for several years, local selection would presumably operate to increase the match between local host-plant composition and local host-plant preference of butterflies. Host preference varies among females in the same population (Kuussaari et al. 2000), and we have detected small differences in preference in the expected direction among local populations in the same metapopulation (M. Singer and M. Kuussaari, unpublished data). Time available for evolution of local adaptation is limited, as most local populations survive only for a few years (Hanski et al. 1995; Hanski 1999). However, host preference of melitaeine butterflies is known to evolve rapidly, and dramatic changes have twice been observed to occur over only six generations in *E. editha* in response to strong directional selection (Singer et al. 1993).

Conclusions

The influence of gene flow on local adaptation is well established (e.g., Dias and Blondel 1996), including cases where gene flow has influenced butterfly oviposition preference (Singer and Thomas 1996). In this work, the strong and consistent effect of oviposition preference on the colonization of empty habitat patches with dissimilar host-plant species composition implies the reverse effect, namely that colonization of particular habitat patches and gene flow among local populations depend on the metapopulation-level adaptation of migrating individuals. This example demonstrates that the role of patch "quality" in metapopulation dynamics can be much more subtle than the mere existence of suitable versus unsuitable or "good" versus "bad" habitat patches. In the Glanville fritillary metapopulations, the relative quality of a particular habitat patch is dissimilarly perceived by individuals of different phenotypes, and the patches become effectively more or less suitable for colonization because of this perception. We have demonstrated in this article how such phenotype-specific perception of habitat quality has significant ecological consequences for the colonization of empty habitat (fig. 3) and for the dynamics of classical metapopulations (fig. 4). Fortunately, these results do not mean that the previous modeling work that has been done on this system (Hanski et al. 1996; Hanski 1999; etc.) would be seriously misleading. The butterflies show regional adaptation to their respective patch network, and, hence, the performance of metapopulations in their "own" network should be relatively little affected. The situation would be different if a new area would be colonized by butterflies adapted to a landscape with a dissimilar plant-species composition or distribution of host plants among the habitat patches (Singer 1994; Singer and Thomas 1996; Thomas et al. 1996). Therefore, a more fundamental and mechanistic

understanding of the ecological dynamics is obtained, and potentially more powerful predictive models can be constructed, if the colonization effect and other such phenotype or genotype-dependent effects would be included in the ecological models.

Acknowledgments

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