

Population history and life history influence the migration rate of female Glanville fritillary butterflies

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This study examines the causes of emigration from small fragments of suitable habitat in a species that has a distinct metapopulation structure, frequent turnover of local populations, and substantial migration among local populations and currently unoccupied habitat fragments. We conducted a field experiment in which 727 individuals of the Glanville fritillary butterfly (*Melitaea cinxia*) originating from four regions were marked and released simultaneously in a natural environment. In three of the four source regions, larvae for the experiment were collected from dozens of small local populations, some of which had been established in the previous summer (new populations), whereas the remaining populations were older. In two of the source regions, female butterflies prefer a host plant (*Veronica spicata*) that is not present in the release area, where there is only *Plantago lanceolata*, the preferred host plant of females from the other two source regions. We found that migration rate of males was unrelated to any of the factors studied in this experiment. In contrast, two factors influenced the migration rate of females. First, *Veronica*-preferring females had higher emigration rate than *Plantago*-preferring females from the *Plantago*-containing release patches, demonstrating that the individual perception of habitat quality significantly influences the migration rate of females. Second, females from newly-established populations were more dispersive than females from older populations, supporting the notion that metapopulation processes (recurrent colonizations) select for increased migration. The observed migration rate was not correlated with any body size measurements, and thus the observed differences in migration rate were apparently caused by differences in the behaviour of female butterflies rather than in their flight capacity.

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Migration of individuals away from the natal population and among local populations in general is a fundamental part of the life history of most organisms with important consequences for metapopulation dynamics (for a comprehensive review see Clobert et al. 2001). Recently, increasing fragmentation of natural habitats and climate change have stimulated research on the possibility and consequences of rapid evolution of mi-

gration rate. Researchers have asked the following kinds of questions. Does increased extinction rate of local populations due to habitat loss and fragmentation select for increased, or decreased, migration rate in metapopulations (Thomas et al. 1998, Parvinen et al. 2000, Ronce et al. 2000, Heino and Hanski 2001)? Is the evolution of migration rate likely to be rapid enough to rescue species from extinction in landscapes

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fragmented by human activity (Leimar and Nordberg 1997, Heino and Hanski 2001)? Will increased migration rate at an expanding range boundary significantly facilitate the movement of species in response to changing climate and other environmental conditions (Hill et al. 1999a, b, Thomas et al. 2001)?

The Glanville fritillary butterfly (*Melitaea cinxia*) forms a large metapopulation in a network of more than 4,000 small habitat patches (dry meadows) in the Åland Islands in SW Finland. The turnover rate of the mostly very small local populations is high, and as there are no large populations with insignificant risk of extinction, long-term persistence of the butterfly in this metapopulation is based on classic metapopulation dynamics (Hanski et al. 1995). Migration occurs commonly up to 2 km from the source population, more rarely up to 4–5 km, but hardly ever further away (Hanski 1999, Wahlberg et al. 2001, van Nouhuys and Hanski 2002). Emigration rate from a habitat patch decreases and immigration rate to a patch increases with patch area (Kuussaari et al. 1996, Hanski et al. 2000).

A recent modelling study (Heino and Hanski 2001) suggested that spatial variation in habitat patch areas and connectivities in the Åland Island patch network is substantial enough to lead to regional variation in the optimal emigration rate. Heino and Hanski (2001) found that in a sparse patch network the evolutionary optimal daily emigration rate from a patch of 1 ha was 0.118, while in a dense network it was 0.104. Encouragingly, these predicted rates are in a broad agreement with the empirically observed rate, 0.130 (Hanski et al. 2000, Wahlberg et al. 2001), though data have not been available to specifically compare migration rate in Glanville fritillary metapopulations living in more and less fragmented networks.

Apart from the possible effects of the spatial configuration of patch networks on the evolution of migration rate, other studies on the Glanville fritillary in Åland have shown that the quality of habitat patches is likely to influence migration rate. Kuussaari et al. (1996) found that emigration and immigration were influenced by the density of nectar flowers and by the openness of the patch boundary, as well as by the density of butterflies themselves (inverse density dependence). The Glanville fritillary has two host plants in the Åland Islands, *Plantago lanceolata* and *Veronica spicata*, and females show geographic variation in their oviposition host plant preference, which variation is correlated with the relative abundances of the two host plant species (Kuussaari et al. 2000). Related to this observation, we have found that the match between the genetically-determined oviposition preference of immigrating females and the host plant composition of currently empty habitat patches significantly influences the rate of establishment of new populations in the empty patches (Hanski and Singer 2001). This “colonization effect” is

apparently due to the oviposition preference of female butterflies influencing the rate of settlement of immigrants in empty patches, oviposition rate following immigration, or both (Hanski and Singer 2001).

In this paper, we report on an experimental study of migration rate in the Glanville fritillary, which was stimulated by the previous findings and was conducted to test and answer four related predictions and queries. First, assuming that there is genetic variation in the traits influencing migration rate in the Glanville fritillary, butterflies in the newly-established local populations should be more dispersive than butterflies in older local populations, because the former populations are likely to have been established by more dispersive butterflies than the average butterfly in the metapopulation. Second, if there is such a difference between butterflies originating from the newly-established versus older populations, is the greater migration rate of the former correlated with morphological traits or with behavioural traits, or both? Third, are butterflies originating from a sparse patch network more dispersive than butterflies originating from a dense patch network, as predicted by the model of Heino and Hanski (2001)? And fourth, does female oviposition preference influence migration rate, as could be expected based on the “colonization effect” referred to above and demonstrated by Hanski and Singer (2001)?

In more general terms, this study examines the causes of emigration from small patches of suitable habitat in a species that occurs as a metapopulation in a highly fragmented landscape. The local populations are so small that the extinction rate is high, hence it is clear that a substantial amount of migration is necessary for long-term persistence (the model of Ronce et al. 2000 predicting low migration rate when extinction rate is high is not applicable here; see Heino and Hanski 2001). Our study is focused on the influence of the quality and the quantity of habitat fragments in modifying the rate of migration.

Material and methods

The experiment was conducted by sampling large post-diapause larvae from their natal populations, rearing them in a common environment, and releasing marked newly-eclosed butterflies in a natural environment, where observations on migration behaviour were made.

Source regions

Butterflies used in the experiment originated from four regions, three of which are located in the Åland Islands and one on the north coast of Estonia (Paldiski). Larvae from the four regions were collected in late April–early May 1999 at the penultimate larval stage.

Larvae were transferred to the Nåtö biological station in Åland, where they were reared in small outdoor cages using *Plantago lanceolata* as the host plant. Pupae were transferred to the island of Vårdö in eastern Åland Islands, where there is suitable habitat for the Glanville fritillary but where the butterfly has not occurred in 1993–99, apparently because the suitable habitat occurs too sparsely for a metapopulation of the Glanville fritillary to persist.

The Glanville fritillary has two host plants in Åland and Estonia, *Veronica spicata* and *Plantago lanceolata* (Kuussaari et al. 2000). Using the experimental technique developed by Singer (1983; see also Kuussaari et al. 2000), females from all four regions have been previously tested for their oviposition host plant preference. We thus know that butterflies from Paldiski in Estonia (region 4 in Table 1) prefer strongly *Veronica* (Schöps and Hanski 2001), while the Eckerö butterflies in western Åland (region 1) are weakly *Veronica*-preferring (Kuussaari et al. 2000). The remaining two Åland regions (2 and 3) have weakly *Plantago*-preferring butterflies (Kuussaari et al. 2000). The difference between the latter two regions is that in region 2 (Lemland, Lumparland, Sund) the density of local populations has

been higher in recent years than in region 3 (Geta, Saltvik, Hammarland, Jomala). This difference is reflected in the higher level of connectivity of the sampled local populations to other existing populations in region 2 than in region 3 (Table 1).

Larvae for the experiment were collected from *V. spicata* in Paldiski, mostly from *V. spicata* in region 1 in Åland, and mostly from *P. lanceolata* in the remaining areas in Åland. Previous experiments have shown no systematic difference in larval growth and development depending on the larval host plant used in rearings (van Nouhoys et al. in prep.), hence we do not expect that the switch in diet from *V. spicata* to *P. lanceolata* for some of the larvae would make any significant difference. This conclusion is indirectly supported by the Estonian butterflies being the largest in this experiment in spite of the switch in their diet (Table 2).

The Paldiski population (region 4) is a large and apparently isolated local population. In the three regions in Åland tens of local populations were sampled and adults were obtained from ca 50 populations (Table 1). In the experiment, an average of only 4–5 males and females per local population were released (Table 1), thus greatly increasing the quality of replica-

Table 1. Numbers of butterfly individuals and local populations from the four source regions included in this study. Connectivity to other occupied populations was measured by the *S* index (Hanski 1999).

Source region	Average connectivity	Host preference	Females		Males	
			ind.	pop.	ind.	pop.
1	5.0	<i>Veronica</i> (weak)	46	14	88	16
2	2.8	<i>Plantago</i> (weak)	76	16	116	21
3	1.6	<i>Plantago</i> (weak)	55	13	68	14
mean			4.1		5.3	
median			3		4	
4		<i>Veronica</i> (strong)	127	1	151	1

Table 2. Regional differences in body weight and wing size measurements.

Source region	Body weight			Forewing size		Hindwing size		
	Mean	sd	n	Mean	sd	Mean	sd	n
1 females	113.5	15.5	95	16.01	0.630	14.65	0.571	88
1 males	76.1	14.0	154	14.19	0.724	12.50	0.667	88
2 females	123.3	19.6	76	16.19	0.801	14.89	0.694	69
2 males	84.4	14.6	116	14.47	0.620	12.77	0.488	69
3 females	123.1	21.6	55	15.99	0.873	14.71	0.743	51
3 males	80.7	15.1	68	14.17	0.750	12.46	0.645	51
4 females	128.2	16.6	127	16.19	0.710	15.10	0.692	116
4 Males	86.8	16.6	151	14.53	0.573	13.04	0.596	116
females								
Mean	122.4	17.8	353	16.11	0.738	14.87	0.670	324
F/χ^2	12.49	10.55		1.69	8.33	8.66	5.59	
<i>P</i>	<0.001	0.014		0.167	0.040	<0.001	0.133	
males								
Mean	82.0	15.1	489	14.36	0.660	12.73	0.605	324
F/χ^2	14.18	4.84		8.91	10.44	23.58	11.13	
<i>P</i>	<0.001	0.184		<0.001	0.015	<0.001	0.011	

tion in the experiment. Based on our long-term data on the Åland populations (M. Nieminen et al. unpubl), we know that roughly half of the local populations sampled for this experiment had been established in the previous summer (1998), whereas the rest were older populations. In the case of the newly-established local populations, we thus used in this experiment the first generation offspring of the original colonizers.

Study area

There are several habitat patches suitable for the Glanville fritillary in the island of Vårdö, though they all have only *Plantago lanceolata* while completely lacking *Veronica spicata*. The experiment was conducted near the centre of a small village (Löfö) with one large (0.35 ha) and one small meadow (0.08 ha) with abundant *P. lanceolata*, separated by ca 150 m across a rocky outcrop area with a low density of small pine trees and no suitable habitat for the butterfly. Ideally, a small cluster of meadows would have been selected for the experiment but none was available. To increase the chance of recapturing the released butterflies, observations were also made along small roads with flowery roadsides and conveniently running in all four compass directions from the two meadows. The roadsides were censused up to a distance of ca 1.5 km from the meadows.

Release and recapture procedures

Pupae were kept either in shaded and hence cooler or in warmer conditions, as needed, to increase the synchrony of adult emergence, which nonetheless took place over a period of 13 days (10 to 22 June 1999). Following the emergence of a butterfly, it was weighed (accuracy 1 mg), photographed and marked, after which it was kept in shaded conditions until released in the same day. Initially, all butterflies were released in the evening, but when the numbers of emerging butterflies were highest another lot of butterflies was released at noon.

Each butterfly was photographed with a Nikon F801S (180 mm Sigma macro) under constant conditions. The photographs were replicated to obtain an accurate estimate of the measurement error (Arnqvist and Martensson 1998). The photographs were subsequently scanned in a standardized manner to obtain digital images for measurements, which were taken with SCION IMAGE (freeware from NIH, USA, 1998). We measured 4 landmarks on the forewing and 5 landmarks on the hindwing. Details on the choice of landmarks, methods and accuracy of the measurements are reported in Breuker et al. (in prep.). The coordinates of the landmarks can be used to calculate the centroid size

(the square root of the sum of squared distances from a set of landmarks to their centroid; Klingenberg and McIntyre 1998). The centroid size of forewing and hindwing will be used as a measure of the respective wing size (Klingenberg et al. 2001). Note that the centroid sizes of the forewing and hindwing are not directly comparable with each other because of differences in the spacing of landmarks and the different number of landmarks.

The butterfly was marked by writing a running number on the underside of the hindwing. We used four different colours for the four source regions. Butterflies were released on the two meadows, called release patch 1 (larger meadow) and 2 (smaller meadow). The released butterflies were divided on each release occasion roughly in the ratio 2.5:1 amongst the two release patches to standardize butterfly density. Butterflies from different regions and of the two sexes were released haphazardly as they emerged.

Butterflies were recaptured daily by systematically visiting the two release patches for several hours with equal recording effort per unit area. Additionally, all the roadside surveys were conducted either once or twice a day.

Analyses

The original study design called for the use of multi-patch mark-release-recapture models (Arnason 1973, Hilborn 1991, Hestbeck et al. 1991, Hanski et al. 2000) in data analysis. Unfortunately, only two release patches could be used, supplemented with recaptures from roadside surveys. As the numbers of observations from the patch in which a particular butterfly was not released were generally rather small, we analysed the data by dividing the recaptures into those that were made in the patch in which the butterfly was released versus those made outside that patch, whether in the other patch or along the roadsides. We parameterized a model with zero transfer rate from outside the release patch back to the release patch (the few observations made in the release patch preceded by an observation made outside the release patch were assigned as having been made outside the release patch). We used the program MSSURVIV (Brownie et al. 1993) to analyse the results, assuming time-independent parameter values. No more thorough investigation of more complex models e.g. with time-dependent capture probability was done because the material was limited. Models were parameterized separately for the four source regions and the two sexes. Additionally, separate models were estimated for the pooled material from the newly-established versus older local populations in regions 1 to 3.

A complementary analysis of migration rate was conducted with the binary variable “migrant”, which

Table 3. Survival and migration parameters (daily probabilities) for males from the four regions.

Parameter	Region			
	1	2	3	4
Survival in patch	0.801	0.838	0.804	0.843
95% conf. limits	0.749–0.852	0.799–0.877	0.743–0.864	0.795–0.891
Emigration	0.092	0.054	0.067	0.083
95% conf. limits	0.041–0.142	0.022–0.085	0.018–0.117	0.036–0.131
Surrounding	0.751	0.687	0.819	0.747
95% conf. limits	0.630–0.873	0.533–0.840	0.663–0.975	0.614–0.881
Capt. in patch	0.408	0.449	0.432	0.372
95% conf. limits	0.345–0.470	0.388–0.502	0.344–0.520	0.318–0.425
Capt. in surrounding	0.205	0.347	0.260	0.185
95% conf. limits	0.088–0.323	0.155–0.538	0.090–0.430	0.071–0.300
χ^2	64.1	99.4	37.6	113.2
df	50	51	39	52
P	0.118	<0.001	0.532	<0.001

has value 1 if the butterfly was recorded outside the release patch and value 0 if it was not recorded outside the release patch. We used logistic regression models to analyse the variable “migrant”, with the following independent variables: sex, date of release, release patch, time of release (noon or evening), source region of the butterfly (Table 1), history of the natal population (new versus old), and the measurements of body size explained above.

Results

Body size measurements

There were significant differences in body weight among the 4 source regions, butterflies from region 1 being the smallest while butterflies from region 4 being the largest (Table 2). In wing size measurements, butterflies from regions 2 and 4 were generally larger than butterflies from regions 1 and 3. In females, within-region variance in body weight was significantly smaller in regions 1 and 4, with the smallest and the largest mean values, than in regions 2 and 3. In males, within-region variance in wing measurements was largest in the regions (1 and 3) with the smallest mean values.

In summary, there are substantial and significant differences in the body size measurements of butterflies from the 4 source regions, up to 13% in the mean body weight and up to 5% in the mean wing size measurements.

Survival and migration from the release patch

Table 3 to 5 summarize the results on the rates of survival of butterflies in the release patch and in the surroundings as well as the results on emigration rate from the release patch to the surroundings. In males, the results are uniform across the data sets (Table 3 and

5). Daily recapture probability was around 0.40 to 0.45 in the release patch and lower outside the release patch, around 0.15 to 0.25. The latter estimates have wide confidence limits, reflecting the fact that some butterflies stayed in the patch to which they had migrated from the release patch while others, observed on roadsides, were searching for suitable habitat and were hence more mobile. The daily probability of staying alive in the release patch was estimated to be just over 0.80, while the estimated daily emigration rate was around 0.06 to 0.09. There were no substantial differences either among the 4 source regions (Table 3) nor between males from the newly-established versus older local populations (Table 5).

The results are more variable for females (Table 4 and 5). As is common in butterfly studies (Hanski et al. 2000, Petit et al. 2001), daily recapture probabilities in the habitat patch were somewhat lower for females (around 0.30 to 0.40) than for males (> 0.40). The daily emigration rate was around 0.07 for all 4 source regions (Table 4). The most deviating region was nr. 4, with low probability of staying and surviving in the release patch and especially low probability of staying (“surviving”) in the surroundings (Table 4). For the latter result, there is practically no overlap in the 95% confidence limits for region 4, with the point estimate of 0.35, and the other three regions, with point estimates ranging from 0.80 to 0.95 (Table 4). Given the low probability of staying in the surroundings of the release patch in the case of females from region 4, the low probability of apparent survival in the release patch itself for these butterflies (0.701 in Table 4) is very likely to be due to emigration: many of the region 4 females that emigrated were never found afterwards and hence there is little information to distinguish between mortality in the release patch and emigration. High emigration rate of region 4 females is indicated by another line of analysis described in the next section.

Comparing females from the newly-established versus older populations reveals a large difference in the emigration rate, which was twice as high amongst females from the newly-established than older populations (Table 5). Differences in the other parameters were small.

The MRR models did not fit all the data sets well (small *P* values in Table 3 to 5), but the limited material did not warrant the use of more complex models.

Recaptures made outside the release patch

The overall recapture rate was 0.59 for females and 0.66 for males. As expected, recapture rate declined significantly with release date both in males and females (logistic regression, males *P* = 0.005, females *P* < 0.001). In addition to this effect, we tested whether any other variable, such as source region, population history, release patch, release time of the day and body

size measurements would significantly explain variation in recapture rate. None of these factors had a significant effect on the recapture rate.

A butterfly was scored as a migrant if it was recorded outside the habitat patch where it was originally released. Fig. 1 shows the numbers of observations in the release patch versus elsewhere against the time since release. We used log-linear models to analyse the influence of time since release, source region and site of observation (release patch vs elsewhere) on the observations (this analysis should be interpreted with some caution, because many butterflies were observed two or more times during the study).

As expected, both males and females were initially (soon after release) relatively more numerous in the release patch than elsewhere (Fig. 1; interaction day × site highly significant in log-linear models). In addition, in females but not in males the interaction between release day and source region was highly significant when all the Åland regions (1 to 3) had been pooled together: Estonian females disappeared faster than

Table 4. Survival and migration parameters (daily probabilities) for females from the four regions.

Parameter	Region 1	2	3	4
Survival in patch	0.779	0.776	0.837	0.701
95% conf. limits	0.720–0.838	0.707–0.845	0.778–0.896	0.623–0.778
Emigration	0.067	0.069	0.064	0.068
95% conf. limits	0.023–0.111	0.019–0.199	0.018–0.110	0.000–0.153
Surrounding	0.957	0.849	0.804	0.350
95% conf. limits	0.838–1.000	0.716–0.982	0.629–0.979	0.006–0.694
Capt. in patch	0.384	0.302	0.334	0.377
95% conf. limits	0.302–0.467	0.213–0.392	0.250–0.419	0.293–0.461
Capt. in surrounding	0.169	0.247	0.316	0.413
95% conf. limits	0.068–0.270	0.095–0.400	0.113–0.519	0.000–1.000
χ^2	64.6	61.8	44.7	39.1
df	41	33	34	35
P	0.011	0.002	0.104	0.289

Table 5. Survival and migration parameters (daily probabilities) for females and males from newly-established and older populations in regions 1 to 3 (Table 1).

Parameter	Females new	old	Males new	old
Survival in patch	0.814	0.791	0.815	0.817
95% conf. limits	0.744–0.885	0.749–0.833	0.746–0.883	0.786–0.848
Emigration	0.109	0.051	0.084	0.067
95% conf. limits	0.043–0.176	0.024–0.077	0.016–0.152	0.041–0.094
Surrounding	0.919	0.846	0.729	0.753
95% conf. limits	0.814–1.000	0.730–0.963	0.554–0.904	0.662–0.846
Capt. in patch	0.401	0.320	0.465	0.416
95% conf. limits	0.303–0.499	0.263–0.377	0.385–0.545	0.373–0.459
Capt. in surrounding	0.166	0.290	0.198	0.276
95% conf. limits	0.070–0.262	0.160–0.419	0.032–0.364	0.174–0.378
χ^2	41.7	92.4	48.5	106.7
df	35	51	39	65
P	0.202	<0.001	0.141	<0.001

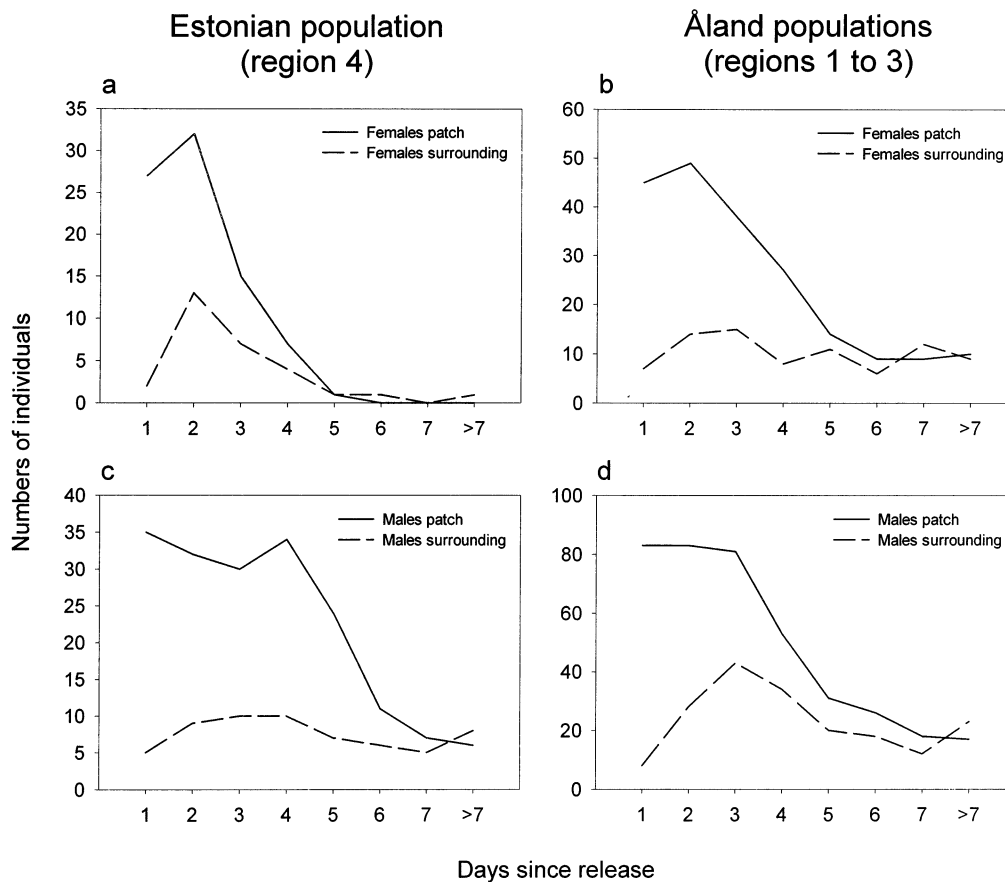


Fig. 1. Numbers of recaptures since the release of butterflies, shown separately for the release patch (continuous line) and the surroundings (broken line). Panels (a) and (b) are for females from Estonia (a) and Åland (b), whereas panels (c) and (d) are for males from Estonia (c) and Åland (d).

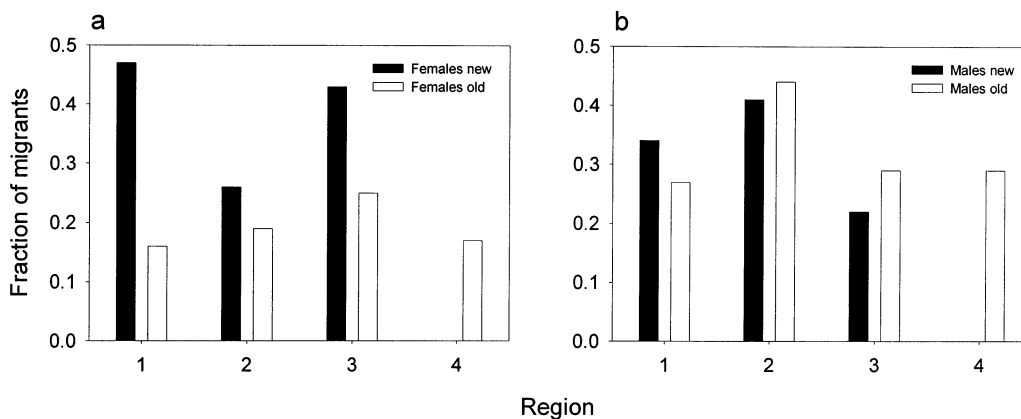


Fig. 2. Fraction of butterflies observed outside the release patch (“migrants”), shown separately for the four regions (horizontal axis), butterflies from new (black bars) and old populations (open bars), and females (panel a) and males (b). The fraction has been calculated out of released butterflies.

Åland females in the course of time (Fig. 1; model with day \times region interaction, likelihood $\chi^2 = 5.54$, $df = 8$, $P = 0.699$; model without this interaction, $\chi^2 = 37.08$, $df = 15$, $P = 0.001$). Analysed separately, there were no

differences among the three source regions in Åland in the rate of disappearance.

We next tabulated the data with respect to population history. Amongst the old populations, the fraction

of migrants was systematically higher in males than in females, but amongst the new populations there was no such difference (Fig. 2). In females, the fraction of migrants was systematically higher in new than old populations (Fig. 2).

Whether a butterfly was recorded as a migrant or not depended significantly on the release date: butterflies released earlier had more time to be recorded outside the release patch. We hence used the release date as a covariate in logistic regression models explaining the migrant status of butterflies. Adding the population history (new versus old population) to this model improved the model significantly (Table 6; change in deviance 4.59, $P < 0.05$). We next attempted to add to the model the following variables, but none improved the model significantly: release patch, release time of the day, body weight and wing measurements (the results for body weight and forewing size are nonetheless shown in Table 6). In short, the biologically significant result from these analyses is that females from the newly-established populations were more dispersive than females from older populations, consistent with the results in Table 5 and Fig. 2.

Comparing regions 2 and 3, where the primary difference is in the density of local populations (Table 1), the fraction of female migrants was higher in the sparse than in the dense habitat patch network, both in the case of newly-established and older local populations (Fig. 2). However, the sample size is relatively small (altogether 131 butterflies in this comparison), and the network type \times migration rate interaction does not make a significant improvement in a log-linear model (likelihood $\chi^2 = 6.66$, $df = 4$, $P = 0.16$ for a model without any interaction, $\chi^2 = 4.41$, $df = 3$, $P = 0.22$ with this interaction included).

The results were simpler for males. The release date had a marginally significant effect ($P = 0.04$) in a logistic regression model, but no other variables had an effect that would be even close to statistical significance.

Discussion

The results of this experiment may be summarized under five conclusions:

Migration rate of males was not related to any of the factors studied in this experiment

The results were uniformly negative for males. The movement rate of males showed no differences among the four source regions although there were significant differences in male morphology and female host plant preference among the regions; there was no difference between newly-established and old local populations; and the body size measurements explained no within-population variation in movement rate. These negative results for males are perhaps not that surprising, since the primary function of movements in male butterflies is to locate mates (Wickman 1992, Van Dyck et al. 1997), which does not need to have anything to do with female host plant selection nor the history of the population. Male flight behaviour might be influenced by morphology, but apparently this is not reflected in the rate of between-patch migration, not at least in this species and using the morphological measurements that were available in this study.

Host plant preference influences emigration and immigration rates of females

The strongly *Veronica*-preferring females from Estonia (region 4; Table 1) disappeared much faster from the release patches than did females from the three source regions in Åland (Fig. 1). The Estonian females also disappeared quickly from the roadsides that were surveyed (low "survival" rate in Table 4), and they showed an especially low transfer rate amongst the two release patches containing *Plantago* (below). All these results strongly support the notion that host plant oviposition preference influences migration rate in this oligophagous insect species: in the absence of the preferred host plant, emigration rate is elevated and immigration rate is lowered.

Females in source region 1 in Åland (Eckerö) also prefer *Veronica* to *Plantago* but much less strongly so than do the Estonian females (Kuussaari et al. 2000). There was a weak though non-significant tendency in our results for females from region 1 to migrate less among the release patches than did females from the *Plantago*-preferring regions in Åland, which is apparent

Table 6. Logistic regression model for the migrant status of female butterflies. The explanatory variables are the release date, the history of the source population (newly-established versus old population), body weight and forewing length.

variable	coefficient	sd error	coeff/se	P	change in deviance
constant	3.31	1.30	2.55	0.011	
release date	-0.244	0.082	-2.97	0.003	
history	-0.777	0.362	-2.15	0.032	4.59
deviance = 186.7, $P = 0.24$, $df = 174$					
body weight	-0.000	0.010	-0.01	0.996	0.05
forewing length	-0.029	0.039	-0.76	0.447	0.61

in the following figures. The fraction of individuals that were recaptured in the patch other than the release patch, out of the total number of recaptured individuals, was 8, 17, 24 and 8% in females from regions 1 to 4, respectively. Pooling the data in terms of female preference (regions 1 + 4 vs 2 + 3) gives a statistically significant result ($\chi^2 = 5.18$, $P = 0.02$), but the result is not significant if the Estonian females (region 1) are excluded.

Three previous studies on checkerspot butterflies have reported results indicating that female host plant preference influences emigration rate or immigration rate, or both. Thomas and Singer (1987) inferred elevated emigration rate of *Euphydryas editha* females from habitat patches with no preferred host plant, and they observed that females that colonized a previously empty habitat patch (following catastrophic extinction) had a biased preference in comparison with females in the source population. Working on the same species, Boughton (2000) found that immigration rate was not influenced by host plant composition in the habitat patch, but emigration rate was elevated in the patches that contained only a low-ranked host species in terms of oviposition preference. Thirdly, Hanski and Singer (2001) conducted an experiment with *Veronica*-preferring and *Plantago*-preferring females of the Glanville fritillary from the Åland Islands. They released the two kinds of butterflies in two nearby meadows with potted *Veronica* in one meadow and potted *Plantago* in the other meadow. After a few days, and following natural movements of the butterflies among the two meadows, there was a significant association between host plant species and oviposition preference in the occurrence of the butterflies in the two meadows. Our results are consistent with the findings of these previous studies. The present results provide the most clear-cut experimental evidence so far for the oviposition preference influencing migration rate in checkerspot butterflies.

There was no opportunity in the present study to do the reverse experiment, release butterflies in a landscape of habitat patches with *V. spicata* but no *P. lanceolata*. The “colonization effect” demonstrated by Hanski and Singer (2001) however strongly suggests that the influence of host plant preference on migration rate works similarly among *Veronica*-preferring and *Plantago*-preferring butterflies.

Females from newly-established populations are more dispersive than females from older populations

The most interesting result to emerge from the present experiment was the higher migration rate of females originating from newly-established versus old populations. Such a difference could be expected on the reasonable assumption that new populations are generally

established by females that are more dispersive than the average female in the metapopulation. In this manner, metapopulation dynamics (recurrent colonizations) would select for increased migration rate in the metapopulation as a whole (Olivieri and Gouyon 1997). A few previous studies on plants (Peroni 1994, Cody and Overton 1996), carabid beetles (den Boer 1970, Niemelä and Spence 1991), butterflies (Hill et al. 1999c) and bush crickets (Thomas et al. 2001) have inferred such a difference between new vs old populations based on variation in morphological traits, but such inferences are often problematic (below). As far as we are aware, this study provides the first demonstration of elevated migration tendency of individuals in newly-established populations based on direct measurement of migration rate under natural conditions.

Inconclusive result for butterflies from a sparse versus a dense patch network

In the present material, a fair though unreplicated comparison can be made between the two regions with *Plantago*-preferring females (regions 2 and 3; Table 1). As predicted by the evolutionary model of Heino and Hanski (2001), females from the sparse network were more dispersive than females from the dense network (Table 4, Fig. 2). The model-predicted difference in the emigration rate for two contrasting landscapes in Åland was 13% (Heino and Hanski 2001). In our results, the difference is substantially greater, 25% in the old and 62% in the new populations (Fig. 2), but there is so much variation in the results that the difference is not statistically significant. To empirically demonstrate the sort of difference predicted by the model would require a substantially larger sample size than was available for this experiment and/or a much more controlled experimental approach.

Body size measurements did not influence migration rate

None of the body size measurements that we employed in this experiment explained a significant amount of variation in the rate and pattern of migration observed. This conclusion applies both to the among-region comparisons as well as to within-region variation in migration behaviour. This conclusion is evident for males, whose migration behaviour could not be explained by any of the explanatory variables available, in spite of highly significant differences in the body size measurements among the four regions (Table 2). In females, the *Veronica*-preferring butterflies from region 4 and (to a lesser extent) from region 1 showed higher emigration and lower immigration rate than the *Plantago*-preferring butterflies from regions 2 and 3, even though

butterflies from region 4 were generally the largest and butterflies from region 1 were generally the smallest butterflies (Table 2). Apparently, behaviour related to host plant preference influenced migration of females more than differences in their overall size (body weight) and wing size measurements.

These results raise an important question about the use of body size measurements in observational studies of migration rate. Body size measurements are used because they can be taken relatively easily, whereas measuring the actual movement behaviour of individuals is more time-consuming and difficult. In the case of wing-polymorphic species, such as many carabids, waterstriders and crickets, it is clear that short-winged and long-winged individuals have a substantial difference in migration capacity, but in species with more continuous variation in the relevant morphological traits the interpretation of any morphological differences among populations in terms of migration capacity or migration tendency is problematic (Thomas et al. 1998, Hill et al. 1999b, c). A case in point is the study by Lewis and Thomas (2001) comparing a wild population of *Pieris brassicae* with a conspecific population that had been kept in captivity for at least 100 generations. Females of the captive population had substantially higher fecundity, as could have been expected, but there was no correlated reduction in relative thorax mass, which is often used as a measure of migration capacity. There was a significant difference in overall size, butterflies in the captive population being larger. Butterflies in the captive population need to fly to feed and to oviposit, which may be a sufficient reason for them to retain good flight capacity. Similar considerations apply to natural butterfly populations. Individuals in some populations/species may be very sedentary and only seldom fly outside their natal habitat patch, but they nonetheless need well-developed flight apparatus to feed, mate and reproduce. In two previous studies comparing relatively newly-established versus old populations, Hill et al. (1999b) found that individuals of *Pararge aegeria* were larger in the newly colonized than in old populations, whereas Hill et al. (1999c) found no such difference in *Hesperia comma*. Given our results and Lewis and Thomas's (2001) findings on *Pieris brassicae*, any conclusions about differential mobility based on overall size differences among populations seem unwarranted.

Two additional factors merit consideration. In our study we could not take measurements such as relative thorax mass, which would possibly be more relevant for assessing migration capacity or tendency than the measures that were available in this study. Second, we compared newly-established populations with older populations, but even the latter have an expected lifetime of less than 10 years (Hanski et al. 1995). Morphological changes might be detected in very isolated local populations that have nonetheless persisted for a long

period of time (Dempster et al. 1976, Dempster 1991). Ideally, one would like to have information on both the morphology and the behaviour of individuals.

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