

Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*

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Enfjäll, K. and Leimar, O. 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. – Oikos 108: 465–472.

Several factors might influence an organism's tendency or willingness to leave a given patch. One such factor is conspecific density, which may affect the per capita emigration rate. Some previous field studies on butterflies have reported positively density-dependent dispersal (emigration increases with population density) whereas the opposite, negatively density-dependent dispersal, has been found in other species. We investigated the effect of conspecific density on both the tendency to cross a patch boundary and within-patch mobility in *Melitaea cinxia*, by experimentally manipulating density in large outdoor cages divided into two habitat patches, separated by a barrier of unsuitable habitat. In contrast to previous results for *M. cinxia*, we found that the butterflies moved away from a patch at higher rates in high conspecific density (positively density-dependent emigration). The within-patch mobility, measured as the distance travelled per time unit, was however unaffected by butterfly density. A possible explanation for the seeming discrepancy with previous results could be that we used higher butterfly densities. For species with fluctuating population dynamics, such as *M. cinxia*, dispersal activity both at low and at high local density will be important for population phenomena such as fluctuations in distributional range over good and bad years.

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Several factors might influence a butterfly's tendency or willingness to stay in or to leave a patch. Some of these are individual characteristics, such as sex or age (Warren 1987, Hanski et al. 1994, Kuussaari et al. 1996), whereas others are properties of the habitat, for instance nectar and host plant density (Baker 1969, 1984, Odendaal et al. 1989, Shreeve 1995, Kuussaari et al. 1996) or the type of vegetation at the patch border and in adjacent matrix areas (Stamps et al. 1987, Gustafson and Gardner 1996, Ricketts 2001). Conspecific density can be viewed as a special kind of habitat characteristic, and it has also been suggested to influence dispersal activity (Dethier and MacArthur 1964). It is however not obvious how variation in conspecific density should affect an individual's tendency to leave a patch. In previous studies both negatively and positively density-

dependent dispersal in butterflies have been reported. Thus, there are some observations indicating that individuals disperse at a higher rate away from low density local populations, corresponding to negatively density-dependent dispersal (Gilbert and Singer 1973, Kuussaari et al. 1996, 1998), but in other cases the opposite has been found, so that individuals disperse at higher rates away from high conspecific density (Shapiro 1970, Odendaal et al. 1989, Baguette et al. 1996, 1998).

It has been argued that negatively density-dependent dispersal could result from mate scarcity (Hanski et al. 1994, Kuussaari et al. 1998), since the inhabitants of low density populations might leave their patch to find mates. Conspecific attraction is an hypothesis predicting higher immigration rates as well as lower emigration rates from high density populations (Ray et al. 1991,

Accepted 20 August 2004

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ISSN 0030-1299

Hanski et al. 1994). One possibility is that butterflies would be attracted to, and prone to stay in, areas with high conspecific density because the chance of mating would be higher there. This would be particularly likely for males, which seem to be attracted to areas of high female density (Odendaal et al. 1989). Gilbert and Singer (1973) suggested a different reason for conspecific attraction, arguing that conspecific density could be used as an indicator of suitable habitat for newly emerged adults, causing emigration from low density populations.

Positively density-dependent dispersal, on the other hand, has been suggested to be a consequence of social interactions among the members of a local population (Shapiro 1970, Odendaal et al. 1985, 1989, Baguette et al. 1996, 1998). In several species, males search out and pursue females to mate with them. Although already mated females may be reluctant to remate, they are nonetheless pursued and harassed by the males, and to escape this harassment they might disperse. Since male harassment ought to be more frequent in high density populations, females would consequently disperse at higher rates away from high density populations. Apart from species with male territoriality, where 'floaters' might disperse, it is less clear whether social interactions could also induce male dispersal, although a high conspecific male density and a low conspecific female density could have the effect of males moving away from an area (Baguette et al. 1998, Brunzel 2002).

Conspecific density might in itself affect the habitat quality in an area. It has been suggested that emigration will increase when the density exceeds the local carrying capacity (Dethier and MacArthur 1964). As vital resources become scarce, butterflies would suffer reduced habitat quality and, according to this theory, a migratory threshold could be reached (Baker 1984). When the threshold is exceeded, the dispersal rate will increase until the density declines and returns to below carrying capacity. The proximate factor causing migration might thus not be the population density as such, but rather density in relation to habitat quality.

Although there are a number of published hypotheses about density-dependent dispersal, there seem to be few really decisive empirical observations. To shed more light on the issue, we have investigated the influence of conspecific density and habitat quality on mobility in two field experiments with the Glanville fritillary, *Melitaea cinxia*. To be able to control butterfly density and habitat quality, we have kept the butterflies in large outdoor cages, and observed their movements from one end of a cage to the other. Compared to a more traditional mark-release-recapture study, our method has the advantage of greater control over the proximate factors that might induce dispersal, but there is of course a possible disadvantage of a relatively small spatial extent of the cages. Nevertheless, our study species

M. cinxia is fairly sedentary and therefore seems suitable to be studied in such cages.

Material and methods

Melitaea cinxia prefers open habitat such as dry slopes and hillsides and woodland clearings. It used to be one of the most common Melitaeini species in southern Sweden (Henriksen and Kreutzer 1982), but it is now only found on a few islands in the Baltic Sea and in some places along the Baltic coast. Its two main host plants are *Plantago lanceolata* and *Veronica spicata* (Henriksen and Kreutzer 1982).

Two experiments were performed, one in June 2001 and one in June 2002. The individuals used in the first experiment were collected from the island Munkö in the Stockholm archipelago. Of these butterflies, the individuals used in trial number 1–4 were collected as larvae in April 2001, while the ones used in trial 5–7 were the offspring from wild caught females collected in June 2000. The individuals used in the second experiment were collected as larvae in April 2002 on the island Öland in the Baltic Sea. All butterflies were reared in the laboratory.

Experimental set up

Both experiments were performed in two large outdoor cages (manufacturer: Serres de France S.A.; w × l × h: 8 × 30 × 4 m), placed in an open pasture at Tovetorp field station, 100 km southwest of Stockholm, Sweden. Each cage consisted of 16 arches, separated by a distance of two meters. Referring to the area between two adjacent arches as a section, each cage was divided

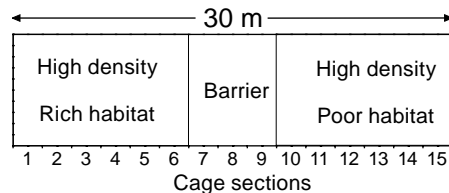


Fig. 1. Illustration of the experimental set-up in the first experiment. Two outdoor cages were placed parallel to each other along an east–west direction, with 5 m in between. The butterflies were kept at low density in one cage and at high density in the other. Both cages were divided into three parts: two parts of open habitat (sections 1–6 and 10–15) with a third, shady part in between (sections 7–9). In each cage, one open part contained rich habitat (high density of potted host and nectar plants) while the other contained poor habitat. The shady part lacked larval host plants and nectar resources and was considered as non habitat. When the eastern cage part contained rich habitat in one cage, it contained poor habitat in the other cage, and vice versa. During the course of the experiment, low and high density treatments were altered between the cages and rich and poor habitats were exchanged.

into 15 sections (Fig. 1). The cages were covered with a fine-meshed net that reduced the solar radiation by approximately 25%. The middle, shady part of each cage (Fig. 1) was arranged by covering the cage roof over that part with camouflage nets. To also reduce the view through this shady part, small camouflage nets were hung inside the cage. This decreased the free sight through the middle cage part by approximately 20%. In a previous study it was found that *M. cinxia* is reluctant to cross a shady cage part (Norberg et al. 2002), implying that it could fill the role of a dispersal barrier.

First experiment

The butterflies were kept at two different densities, referred to as high and low density. The aim was for a high-density cage to contain seven females and seven males in each open part ($0.175 \text{ ind. m}^{-2}$) and for a low-density cage to contain one female and one male in each open part ($0.025 \text{ ind. m}^{-2}$). Most butterflies were observed every day. A butterfly that was not observed for two days, or that was found dead, was replaced with another individual of the same sex. This produced approximately constant densities throughout the study.

To control the habitat quality inside the cages, grass and other vegetation was mowed. Nectar resources (wild flowers plus artificial flowers sprayed with honey solution) and larval host plants (*P. lanceolata*) were kept in pots and placed in the open cage parts in two different abundances (Fig. 1). A rich habitat contained approximately ten times as many resources as a poor habitat. No nectar or larval host plants were placed in the shady part of a cage. For each trial, the habitat qualities were exchanged between the open cage parts, by moving the potted plants. This ensured that there was no correlation between the compass direction of the cages (east or west; Fig. 1) and the direction of increasing habitat quality.

The experiment consisted of seven trials. For every second trial, the density treatments were exchanged between the two cages. For each trial, the particular individuals occurring in the low-density cage were exchanged with randomly chosen individuals from the high-density cage, in a way that a given individual could occur in low density during at most a single trial. The reason for this was to avoid the possibility that an accidental selection of four especially mobile (or especially sedentary) individuals could bias the result. Between trials 4 and 5 all butterflies were replaced by individuals that had been reared at lower temperatures and therefore emerged later.

To map each individual butterfly's position, the 15 cage sections were used (Fig. 1). An inventory was performed two to three times daily, during which the sections of all observed butterflies were recorded.

To disturb the butterflies as little as possible, the observer walked very slowly through the cage and used binoculars to read individual markings at a distance. The data on the locations and times of observations of individuals were then used to estimate mobilities. For each individual and trial, we computed the number of traversals through the middle, shady part of the cage, and the number of hours available for movement (a day was taken to last from 08:30 to 17:30).

Second experiment

The aim of the first experiment was to detect movements between cage parts, and the duration of inventories was no longer than needed to map the positions of the butterflies at that time. Particularly for the low-density treatment, this had the consequence that an individual was often observed only once during an inventory. Since movements between cage parts might be related to overall movement activity, we were also interested in short term mobility within an open cage part. The aim of the second experiment was to look for an effect of density on such short term mobility.

Movements within a cage part occur much more frequently than traversals across the shady barrier. For this reason, within cage part mobility was measured as the distance travelled during a 15 min session of observation in a cage part. Three sessions of observations were performed per cage part and trial. To map positions more accurately, each cage section was divided into four pieces (marked by strings), which resulted in a grid of $2 \times 2 \text{ m}$ squares. During a session of observation, the time and grid position of observed individuals were continually recorded as the observer walked slowly through an open cage part. For individuals observed more than once during a session, the distance moved was then calculated by summing the distances between the centres of successive grid squares where they were observed, and the corresponding time was set as the interval from the first to the last observation. The total distance and total time for each individual were obtained by summing over the sessions.

The high and low densities used were the same as in the first experiment, but the habitat was kept at the same (high) quality in all open cage parts. To make sure that most of the movements would take place within the open parts, the free sight through the middle parts were reduced somewhat more than in the first experiment. The experiment consisted of three trials. Between trials, density treatments were switched between cages and a different random set of individuals was selected for the low-density treatment.

Data analysis

One possibility for statistical analysis would be to compare individual butterflies with themselves when occurring in high and low density, but this has the drawback that some days are warmer than others, potentially making an individual more mobile on these days. Another possible procedure, which was used in our analysis, is to compare the group of individuals that took part in the low-density treatments with the distinct group of individuals that only took part in high-density treatments. This approach, where an individual is the unit of observation, has the advantage of fairly high statistical power (large sample size). Nevertheless the data were also analysed using trial as unit of observation, because the trials were devised to achieve statistically independent replicates of the experimental treatments (density and habitat quality). A trial-level analysis may be less sensitive in detecting effects, but results from such an analysis should carry more statistical weight.

If an individual has a given probability per time unit to move between cage parts, the number of traversals over a period of time will follow a Poisson distribution. For this reason generalized linear models (McCullagh and Nelder 1989) with Poisson distributed response (and log link function) was used for the statistical tests of traversal rates. In these models, the time available for movement was taken into account by using the logarithm of this time as so-called offset variable (this is analogous to a covariate; McCullagh and Nelder 1989). For individual-level analysis, the total number of traversals of the shady cage part (summed over the trials the individual took part in) was used as the response variable, the logarithm of the corresponding total number of hours available for movement for that individual was the offset variable, and the sex and density treatment of the individual were the factors. For trial-level analysis, we obtained the response variable by summing the number of traversals during a trial over the individuals of a given sex and density treatment, and we used the logarithm of the corresponding summed hours available for movement as offset variable. The procedure GENMOD in SAS Systems Release 8 (SAS Institute, Inc.) was used for these tests. For analysis of the distance moved within an open cage part (in the second experiment) the SAS procedure GLM was instead used, with the time available for movement as a covariate.

Results

First experiment

A total of 2 016 individual butterfly observations were obtained during the first experiment. Taking into account replacements, 35 females and 41 males took part in the

study. A total of 14 butterflies died and were replaced, resulting in an average mortality rate of 0.014 per day and individual.

Density-dependent traversal

Male butterflies had a higher traversal rate in high than in low density for all seven trials. The females had a slightly higher traversal rate in low than in high density in trial number five but a clearly higher traversal rate in high density in the remaining six trials (Fig. 2a). Since male and female traversal rates in a trial are two different measurements from the same cage, separate statistical analyses were performed for the two sexes (instead of including sex as a factor). In addition, trial was used as factor, corresponding to a within-trial comparison of the effect of density on traversal. The analysis showed that both males and females traversed across the barrier at a significantly higher rate in high than in low density (Table 1). It is also clear that the traversal rates differed between trials (Table 1), a result that might be explained by variable weather conditions.

No differences were found between male and female traversal rates when testing at the trial level (paired t-tests; high density: $t=0.6$, $n=7$, $p=0.56$; low density: $t=0.87$, $n=7$, $p=0.42$; Fig. 2a). Fitting a generalized linear model to individual traversal produced a highly significant effect of density on dispersal ($\chi^2=14.8$, $df=1$, $p<0.001$), but again showed no effect of

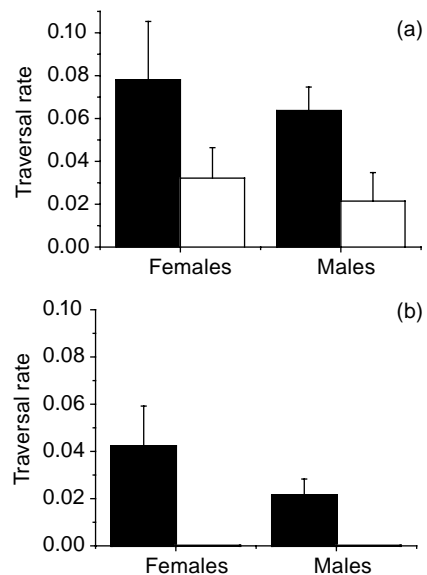


Fig. 2. Traversal rates (number of movements between open cage parts per individual and hour during a trial) in high and low density. Panel (a) gives the results from the first experiment ($\bar{x}+se$ for $n=7$ trials) and the black bars refer to high density and the white bars to low density. See Table 1 for statistical analysis. Panel (b) gives the result from the second experiment ($\bar{x}+se$ for $n=3$ trials). Note that there were no traversals in low density in this experiment.

Table 1. Analysis of deviance for a generalized linear model* fitted to the total number of dispersals in a given density during a trial, separately for females and males, for the first experiment. The degrees of freedom are 6 for trial and 1 for density in each analysis and the χ^2 -statistics derive from type III likelihood ratio tests.

Response variable	Effect	χ^2	p
Female dispersal	trial	48.2	<0.001
	density	4.43	0.035
Male dispersal	trial	26.2	<0.001
	density	8.50	0.004

*Poisson distribution with log link function and an offset given by log total time available for dispersal in a given density during a trial.

sex ($\chi^2=0.32$, $df=1$, $p=0.57$) or any sex by density interaction ($\chi^2=0.44$, $df=1$, $p=0.51$).

Habitat quality and compass direction

Classifying the traversal events during a trial as either from poor to rich habitat or from rich to poor, no statistically significant differences were found at the trial level between the frequencies of the two types of traversal (paired t-tests; high density: $t=1.56$, $n=7$, $p=0.17$; low density: $t=1.33$, $n=7$, $p=0.23$). However, it could be that a tendency of the butterflies to move towards the east or towards the west interfered with a tendency to move towards rich habitat (at the location of the cages used in the first experiment, there was good morning sunlight but more shade from trees in the west during late afternoons). Pooling the traversal events over the entire study, there were in fact considerably more movements from poor to rich habitat than from rich to poor and also considerably more towards the east than towards the west (Table 2), suggesting that both habitat quality and the direction of the sun may have influenced dispersal.

Second experiment

During the second experiment, which lasted three days, 684 individual observations were made. Seventeen individuals of each sex were used and three butterflies died and were replaced during the experiment. The aim was to investigate if density would influence mobility within

a cage part, since this type of mobility might lie behind movement between cage parts. Considering the three trials, there was no consistent effect of density on mobility, either for males or for females (Fig. 3). A statistical test at the individual level also failed to show any relationship between density and mobility (Table 3). However, the test indicated a significantly higher mobility within cage parts for males than for females (Table 3, Fig. 3).

As a check of consistency between the two experiments, the rate of traversal between cage parts were analysed also in the second experiment (Fig. 2b). There were 18 traversals in high density, but none in low density. Fitting a generalized linear model to individual level traversal showed a statistically significant effect of density on traversal ($\chi^2=5.7$, $df=1$, $p=0.03$), in agreement with the results from the first experiment. Although females seemed to move between the open cage parts somewhat more than males (Fig. 2b), the effect of sex was not statistically significant ($\chi^2=3.0$, $df=1$, $p=0.08$). Because there were no traversals in the low density treatments, it was not possible to test for the presence of a sex by density interaction.

Discussion

By studying mobility of *M. cinxia* in semi-natural field experiments, we found that the rate of leaving a habitat patch was density-dependent. More traversals per capita – measured as movements across a shady area of unsuitable habitat – occurred in high than in low conspecific density in the first experiment. This result was further supported by the second experiment, during which no traversal occurred in the low-density treatment, while several occurred in high density. The effect of density was present for both sexes, and males and females had roughly similar rates of traversal. There was a slightly higher traversal rate for females in both experiments (Fig. 2), although this was not statistically significant.

To perform inter-patch dispersal in our experiments, an individual had to first cross the border of the original patch, then move through the intervening non-habitat, and finally settle in a new patch. In a field situation,

Table 2. Classification of traversal events in the first experiment in high and low density as being from poor to rich habitat vs from rich to poor and towards the east vs towards the west*.

Sex	High density traversals				Low density traversals			
	from rich habitat	from poor habitat	to east	to west	from rich habitat	from poor habitat	to east	to west
Females	28	44	43	29	0	5	3	2
Males	35	50	52	33	2	1	2	1
Total	63	94	95	62	2	6	5	3

*The experiment was designed so that, over the trials, rich and poor habitat were equally often in the east and in the west.

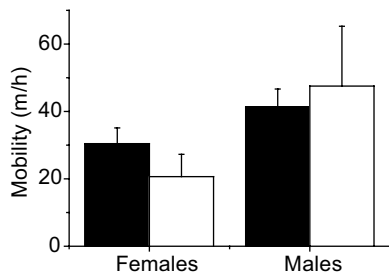


Fig. 3. The mobility within open cage parts on individual level in high (black bars) and low (white bars) conspecific density, given as $\bar{x} \pm se$ for $n = 10$ individuals of each sex in high density and $n = 6$ of each sex in low density.

where habitat patches can be much further apart, a butterfly crossing a patch boundary may continue moving away in search of new habitat, but it might also return to the original patch. A useful perspective on inter-patch dispersal in the field is to split the process into three stages (Ims and Yacoz 1997): emigration from the original patch, migration through non-habitat, and immigration into a new patch. Because of the relatively small spatial extent of the cages in our experiments, these three stages were perhaps not so clearly separated. It may be that the rates of traversal we have measured to a large extent reflect emigration and to a lesser extent the willingness of a butterfly to move through extended regions of non-habitat, and this needs to be taken into account when interpreting our results. If one assumes that a butterfly's tendency to emigrate is correlated with its tendency to migrate through non-habitat, which seems likely but which has not been empirically demonstrated, the rate of traversal in our experiments would be a reasonable measure of inter-patch dispersal in the field.

One aim of the design of the first experiment was to test for the effect of habitat quality on traversal at the trial level. We found no statistically significant effect in such a test, perhaps because of a confounding effect of compass direction. When simply summing up the numbers of traversals from each of the two habitat types and in the two compass directions, we found that there was a considerably larger number of traversals away from poor than from rich habitat, and also a larger number towards the east than towards the west (Table 2).

Table 3. Analysis of covariance for the total distance moved by an individual during the sessions of observations, with the corresponding total time as covariate. There is 1 df for each of time, sex, density and sex \times density, and 27 df for the residual.

Effect	F	p
Time	14.33	<0.001
Sex	4.25	0.049
Density	0.01	0.943
Sex \times density	0.321	0.58

It is possible that both habitat quality and the direction of sunlight affected movements, but these two would have counteracted each other in some trials of the experiment, which could be why we failed to prove an effect of either.

In their natural environments, butterflies perform many short-range movements that do not result in any inter-patch transport. Our results from the first experiment on positively density-dependent dispersal led us to the idea that there would in general be more movements per capita in high conspecific density. Such increased flight activity might then be the proximate factor driving a higher rate of emigration, since a butterfly ought to have a higher probability of crossing the shady barrier if it spends more time flying. However, the data on within-patch mobility from our second experiment revealed no relationship between conspecific density and mobility, so we cannot conclude that a higher overall mobility was an important factor driving positively density-dependent traversal in our experiments.

There could of course have been a rather weak effect of density on within-patch mobility, which we failed to detect in our second experiment. Nevertheless, we could establish that males were more mobile than females within open cage parts (Fig. 3, Table 3), illustrating that our sample sizes were sufficient to detect mobility differences. It thus seems that movements within and between the cage parts represent different categories of mobility, in the sense that they responded differently to density variation. Additional observations might however be needed to resolve the issue of relations between the two types of mobility. Although our data showed that the within-patch distance moved per unit time did not depend on density, other aspects of flight could be affected. For instance, it would be of interest to collect data on the effect of density on male–female and male–male flight interactions, as well as on the kind of flight behaviour that precedes emigration.

We found a substantially lower number of traversals in the second experiment compared to the first (Fig. 2). There are several factors that might have contributed to this difference, such as population differences between the Munkö and the Öland populations (population differences in mobility have been observed for some species of butterflies; Hanski et al. 2002, Mennechez et al. 2003, Merckx et al. 2003, Schtickzelle and Baguette 2003), the fact that there was no poor habitat treatment in the second experiment, and that the dispersal barrier had somewhat less free sight through it in the second experiment. Another factor that in principle could be important is a difference in weather conditions between the two field seasons, but since the temperatures were quite warm during the second experiment it is unlikely that the weather caused fewer traversals in the second season.

Comparing with previous work, our results on positively density-dependent dispersal are in agreement with data from several other butterfly species (Shapiro 1970, Odendaal et al. 1989, Baguette et al. 1996, 1998), but they seem to disagree with results from a field experiment on *M. cinxia* (Kuussaari et al. 1996). In a large mark–release–recapture study, using an artificial metapopulation where butterflies were released in habitat patches in an area containing suitable but unoccupied *M. cinxia* habitat, Kuussaari et al. (1996) investigated the effects of habitat attributes on mobility. They used two size classes of release patches and both high and low release densities for each size class, making it possible to study both effects of patch area and release density (butterflies m^{-2}). As measures of dispersal activity they used both the migration rate, defined as the proportion of recaptured butterflies that were last recaptured outside their release patch, and the stay time of recaptured butterflies, defined as the time from release to the last recapture in the release patch. For the migration rate, Kuussaari et al. (1996) found no effect of either release density or patch area, whereas stay times were positively correlated with both release density and release patch area (note that the data on stay times were subsequently reanalysed (Kuussaari et al. 1998) using a different measure of density – the number of released butterflies per square root of patch area – which combines the original measures of release density and patch area; here we use density to mean individuals per unit area). It is thus quite clear that Kuussaari et al. (1996) did not find positively density-dependent dispersal, but rather the opposite, with butterflies disappearing more rapidly from low density release patches.

Although we can only speculate about the reasons for these seemingly contradictory results, one plausible explanation is that the high density used by us was considerably higher than that used by Kuussaari et al. (1996). We kept the high density around $0.175 \text{ ind. m}^{-2}$, whereas they initially had around 0.07 ind. m^{-2} , with a possible rapid decline over time (the majority of the released butterflies disappeared without ever being recaptured). This would have produced considerably lower densities in their experiment compared to ours, also in their low density treatment, which in principle could explain the difference in results. Perhaps dispersal in relation to density in *M. cinxia* is best described by a u-shaped curve, with higher dispersal rates both at low and at high conspecific density, and with lower dispersal rates at intermediate densities. Further studies would be needed to investigate this matter. It is however likely that the whole range from very low to very high densities is relevant for *M. cinxia* in the field, because of the strongly fluctuating population dynamics of this species (Hanski 1999).

Concerning the effects of habitat quality, Baker (1984) suggested that positively density-dependent dispersal

might be explained by resource depletion and increased resource competition at higher conspecific density. Applying this hypothesis to our first experiment, one would predict particularly high dispersal rates for the combination of high density and low habitat quality. However, in that experiment we recorded more traversals away from poor than from rich habitat quality in both high and low conspecific densities (Table 2). Although we could not demonstrate conclusively an effect of habitat quality on dispersal, our results thus suggest that a poor habitat quality could promote dispersal also in sparse populations. Further, in our second experiment all butterflies encountered what should have been a surplus of both larval host plants and nectar resources, but still the number of traversals was higher in high than in low conspecific density. Thus, there seems to be some feature of a high conspecific density apart from per capita habitat quality that causes positively density-dependent dispersal.

One such factor could be social interactions, such as male harassment (Shapiro 1970, Odendaal et al. 1989). During our experiments, males were repeatedly seen pursuing females, and we did also observe a few intense chases that resulted in traversal across the shady part. Although we did not find an effect of density on within-patch mobility, we cannot really exclude that particularly intense chases, involving several males pursuing a female, could be more common at high density and play a role in inducing dispersal. Conversely, as suggested by Kuussaari et al. (1998) there might also be an effect of the lack of social interactions at very low conspecific density. At such low densities, individuals might face mate scarcity and therefore disperse to search for mates.

There have been a number of theoretical studies on the population dynamical consequences of density-dependent dispersal (Aars and Ims 2000, Heino and Hanski 2001, Okubo et al. 2001, Silva et al. 2001). Since dispersal plays a major role in maintaining and expanding the distributional range of a species (Hanski and Gilpin 1997), it is clear that an effect of local density on dispersal can be of importance for range fluctuations. For instance, positively density-dependent dispersal might cause population expansions during favourable years, since already occupied patches may accommodate dense local populations that produce a large number of dispersers, increasing the chance of successful recolonizations and new colonization. Positively density-dependent dispersal could thus be important for the distribution of a species, since it will improve the opportunity for range expansion during favourable years. Conversely, negatively density-dependent dispersal could slow down the rate of range expansion during good years, and possibly increase the rate of range loss during bad years, which ought to result in an overall more limited distributional range.

Acknowledgements – Many thanks to Carina Sjölin for field assistance and to Michel Baguette for helpful comments on the manuscript. This study was supported by grants from the Swedish Research Council (to OL).

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