



Research article

Habitat exploration in butterflies – an outdoor cage experiment

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Abstract. A large outdoor cage, measuring 7 × 30 m, was used to study the willingness of butterflies to move through unsuitable habitat in search of neighbouring patches. The area inside the cage was divided into two grassland parts by a 7 m long shady part of unsuitable habitat that the butterflies had to fly through to move between the grassland parts. In 1999 and 2000 we performed experiments on three Melitaeini species (*Melitaea cinxia* and *Mellicta athalia* were used both years and *Euphydryas aurinia* in 2000) and three additional species (*Brenthis ino* and *Aphantopus hyperantus* in 1999 and *Clossiana euphrosyne* in 2000). In both years the Melitaeini species moved at considerably lower rates through the shady part than the other species. Among the Melitaeini species *Mell. athalia* moved most frequently through the shady part while *E. aurinia* and *M. cinxia* moved at lower rates. The distribution of these butterflies differ from widespread to localized and the results are discussed in the context of their habitat preferences and distribution patterns.

Key words: butterfly distribution, dispersal behaviour, habitat use, Melitaeini, mobility

Introduction

The greatest part of a butterfly's flying time is typically spent on daily tasks such as foraging, egg laying or looking for mates. Relatively little is known about how the nature of these movements affects the distribution of butterflies at scales beyond that of a single habitat patch. It is likely that species differ in their way of exploring their surroundings. Some species may be more willing to cross the patch borders into unsuitable habitat and thereby have a greater chance of finding neighbouring patches and utilizing a larger habitat area. As a consequence those species may have a more extensive local distribution than species that are less explorative. We have investigated the tendency of different species to pass through unsuitable habitat, using a large outdoor cage. We believe that this method may be a good way to measure how efficient a butterfly is at exploring its habitat.

A large variation in mobility is found between adults of different butterfly species. Some migratory species, for example, can move several kilometres in one day (Baker, 1978) while other species seldom move more than a few 100 m (e.g., Thomas, 1985; Thomas and Harrison, 1992). Apart from true migratory behaviour there is still considerable variation in mobility between species, both in terms of distance moved and in frequency of inter-patch movements (e.g., Shreeve, 1995). The latter kind of mobility can be seen as a consequence of habitat exploration, by which we mean an individual's willingness to move through areas that are not part of its preferred habitat (also referred to as ranging, Dingle, 1996). A reluctance to cross unsuitable areas need not be because the terrain is hard to traverse; rather, a butterfly may 'choose' to stay within a certain area, an observation which led Ehrlich (1961) to use the term 'intrinsic barriers' to dispersal. There are also indications that such intrinsic barriers may differ between populations of the same species (Gilbert and Singer, 1973). The aim of this study is to compare the tendency towards habitat exploration between a number of species that differ in their distribution patterns.

Studies on mobility in butterflies are often based on mark–release–recapture methods. A possible drawback of this approach is that one does not know what happened to butterflies that were never recaptured, which is particularly troublesome when the recapture frequency is low. As an alternative we have used a large outdoor cage to study mobility. This method reduces some of the disadvantages associated with releasing butterflies in the wild. The cage consisted of two parts of open grassland. To move between the two parts individuals had to pass through a shady area. In 1999 and 2000 experiments were performed on a total of six species that are dependent on open land for foraging and egg-laying. Since densely vegetated areas are not included in the preferred habitat of these species, the tendency to move between cage parts may then reflect habitat exploration in nature. The distribution of these species in Sweden ranges from widespread and common to rare and localized. Provided that habitat exploration has an effect on distribution one might expect that the rarest of the six species would move at the lowest rate between cage parts and that the more common species would display greater mobility.

Materials and methods

Study species

The primary aim of the study was to compare the mobility of three checkerspot butterflies (Nymphalidae: tribe Melitaeini): *Melitaea cinxia* L. (Glanville fritillary), *Melitaea athalia* Rottemburg (heath fritillary) and *Euphydryas aurinia* Rottemburg (marsh fritillary). To put the results from these species into a

wider context, the following Nymphalidae species were used: *Clossiana euphrosyne* L. (pearl-bordered fritillary), *Brenthis ino* Rottemburg (lesser marbled fritillary) and *Aphantopus hyperantus* L. (ringlet).

Melitaea cinxia and *Mell. athalia* are rather closely related and, to a considerable extent, use the same hostplants. The habitat of *M. cinxia* is typically scrub/woodland clearings, dry slopes and hillsides (Nordström, 1955; Henriksen and Kreutzer, 1982). *Melitaea cinxia* has decreased its distribution in Sweden, as in most parts of western and northern Europe, during the past 30 years (Hanski and Kuussaari, 1995). It is most commonly found along the coast in southern Sweden and on the islands Öland and Gotland in the Baltic sea. *Mellicta athalia* is distributed all over Sweden (Henriksen and Kreutzer, 1982) but is most common in southern Sweden. It is sometimes found together with *M. cinxia* but may not be as restricted to dry and open areas (for a closer description of its habitat, see Nordström, 1955; Henriksen and Kreutzer, 1982, Warren, 1987a). *Melitaea cinxia* and *Mell. athalia* commonly use *Plantago lanceolata* and *Veronica spicata* as hostplants, and *Mell. athalia* also uses *Melampyrum* spp. (Henriksen and Kreutzer, 1982). *Euphydryas aurinia* is found in open and often damp grassland (Henriksen and Kreutzer, 1982; Warren, 1994). In Sweden, its major hostplant is *Succisa pratensis*, but possibly *Knautia pratensis* can also be used. *Euphydryas aurinia* is only found in few localities in south-eastern and central Sweden and, although it can occur at high densities, its local distribution range is often quite small (Porter, 1981; Henriksen and Kreutzer, 1982; Warren, 1994).

Clossiana euphrosyne, *B. ino* and *A. hyperantus* were chosen as comparisons to the checkerspot butterflies because they are widely distributed and common in southern Sweden (Henriksen and Kreutzer, 1982). Furthermore, these butterflies occurred abundantly in the experimental area. All of these species are found in several kinds of more or less open habitats, such as meadows, glades or scrub/woodland clearings (Nordström, 1955; Henriksen and Kreutzer, 1982). The hostplants used by *C. euphrosyne* are various *Viola* species (Henriksen and Kreutzer, 1982), *B. ino* uses mainly *Filipendula ulmaria* and *Rubus* spp. (Henriksen and Kreutzer, 1982) and *A. hyperantus* uses several species of grass as larval hostplant (Wiklund, 1984).

Collecting and rearing

In 1999, most of the *M. cinxia* individuals were collected as larvae from two sites on Öland (Hildeborg and Knisa alvar) and bred outdoors on *P. lanceolata*. Immediately prior to the experiment some adults were also caught at Stora alvaret on Öland and on the island Munkö in the Stockholm archipelago. *Mellicta athalia* adults were caught on Munkö and at Hildeborg. *Aphantopus hyperantus* and *B. ino* were collected as adults from areas around the cage (Tovetorp).

In 1999, several egg clutches were laid by *M. cinxia* and *Mell. athalia* on *P. lanceolata* plants inside the cage. Larvae of these eggs were raised indoors on *P. lanceolata* and used in the 2000 experiment. Some *Mell. athalia* individuals also originated from eggs taken from wild-caught Munkö females. *Euphydryas aurinia* were collected as third instar larvae from the site Hagge, located in the province Dalarna in central Sweden. *Euphydryas aurinia* larvae were raised on *S. pratensis* and were kept outdoors at first but later on indoors. *Clossiana euphrosyne* were wild-caught at Tovetorp.

Experimental setup

The experiments were performed in an oblong cage measuring 7×30 m and with a maximum height of 3.5 m. The construction is called a Richel tunnel (manufactured by Serres de France S.A) and is normally used as green house. The cage is supported by 16 arches, separated by a distance of 2 m, resulting in a half circle shaped tunnel. As cover we used a net that reduced the solar radiation by approximately 25%. The cage was set up in a pasture at Tovetorp field station, 100 km south-west of Stockholm, with its longitudinal axis pointing in a north-easterly direction. The ground inside the cage was mainly covered by herbage. In the middle of the cage a 7 m long part was covered by a non-transparent green tarpaulin placed on the roof of the cage (referred to as the 'shady part' in the following). This created two 11.5 m long grassland areas at opposite ends of the cage, separated by the shady part in the middle. To limit free sight through the shady part small trees of spruce were stuck into the ground. During the start of the experiment, in 1999, the scrub was rather dense, but it was later on thinned out to allow butterflies to pass through. After the scrub had been thinned out there was approximately 25% free sight through the shady part when standing on either side. In 2000 the scrub was replaced by several sheets of camouflage netting, hanging down from the roof, which created approximately the same amount of denseness as in 1999. The aim of the shady part was to create an area of unsuitable habitat between the two open grassland parts.

The cage location was selected to provide as suitable habitat as possible for all species. *Mellicta athalia* and the three comparison species were seen flying in immediate vicinity of the cage. *Plantago lanceolata*, the hostplant of *M. cinxia* and *Mell. athalia*, occurred naturally inside the cage. There were also several species of grass available as hostplants for *A. hyperantus*, but no hostplant for *B. ino* was present inside the cage in 1999. In 2000, hostplants were supplied for *E. aurinia* and *C. euphrosyne* as potted *S. pratensis* and *Viola tricolor*. Many species of nectar plants were abundant in the cage but to insure a constant supply of food, sugar solution was also provided.

Experimental procedure

The time between eclosion or capture of the butterflies until they were released in the cage was kept as short as possible and was at the longest 3 days. All butterflies were individually marked with dots on the wings using a permanent pen. The markings were possible to read without disturbing the butterflies, although we still refer to such an observation as a recapture. Once or twice each day, depending on the weather conditions, we inventoried the cage during 1 h, recording the cage part an individual was observed in. In 2000, we also recorded the location of the butterfly inside a cage part by dividing the cage into 15 sections (using the 16 cage arches as delimiters).

In 1999, *M. cinxia* and *Mell. athalia* were released in the cage on 1 July. No individuals moved through the shady section prior to the scrub had been thinned out on 3 July (as described above). Therefore, only the days from 3 July until 7 July (the end of the study) have been included in the analyses. *Brenthis ino* and *A. hyperantus* were released on 4 July. In the 1999 study, each species and sex was released at equal densities in the two open parts.

In 2000, the experiment ran from 4 June up to 16 June. We used the same cage as in 1999 and all species were released simultaneously. Two days were cloudy and since the butterflies did not fly during these days they were excluded. For *M. cinxia*, *E. aurinia* and *C. euphrosyne*, two densities were used in an alternating pattern; in one day, a species occurred in low density (four individuals) in one open part and in high density (16 individuals) in the other. In the evening we then reversed densities by moving individuals between the open parts. Due to lack of individuals, *Mell. athalia* was kept at low density in both open parts. For all species, new individuals were released as needed to maintain the numbers. The proportion males and females were also kept equal between the two open parts for each species.

Statistics

To calculate the number of movements through the shady part per hour of an individual, the total time potentially available for active flight was estimated. In order to do this, a day was given the length of 8 h (between 9:00 and 17:00). An individual was considered lost from the study at the time it was last observed. Individuals that were present less than 8 h (active flight time) were excluded from the analyses (see Table 1 for the numbers used). For the Wilcoxon tests, exact *p*-values were calculated with the computer program StatXact-4 for Windows (1999). Other statistical tests were performed with the computer program R (Ihaka and Gentleman, 1996).

Table 1. Total number of butterflies used in the analysis of the two experiments

| Species | 1999 | | 2000 | |
|----------------------|---------|-------|---------|-------|
| | Females | Males | Females | Males |
| <i>M. cinxia</i> | 30 | 29 | 9 | 20 |
| <i>Mell. athalia</i> | 5 | 10 | 6 | 9 |
| <i>E. aurinia</i> | – | – | 9 | 14 |
| <i>C. euphrosyne</i> | – | – | 10 | 18 |
| <i>B. ino</i> | 1 | 8 | – | – |
| <i>A. hyperantus</i> | 7 | 8 | – | – |

Results

Mobility between the open parts

The proportion of individuals that had moved between open parts, over the entire extent of each study are shown in Figure 1 for both sexes of the Melitaeini species. No Melitaeini individuals moved more than once through the shady part in 1999 and only a few in 2000, making it reasonable to use movement/no movement during the whole study period as a measure of mobility. Thus, a log-linear analysis was used to compare the movement rates between sexes and species for each study (Table 2). There were significant differences in movement rate between the species for both years but not between the sexes. In both years, *Mell. athalia* moved at the highest frequency (Fig. 1). In 2000, *E. aurinia* had a lower frequency of movement than *Mell. athalia* ($\chi^2_1 = 10.2$ and $p = 0.001$). *Melitaea cinxia* was intermediate between *Mell. athalia* and *E. aurinia* (Fig. 1). Using the Bonferroni method to adjust p -values required for significance in multiple comparisons, we could however not establish that *M. cinxia* differed from either of the two other species (*M. cinxia*–*Mell. athalia*: $\chi^2_1 = 2.24$, $p = 0.13$; *M. cinxia*–*E. aurinia*: $\chi^2_1 = 4.21$, $p = 0.040$).

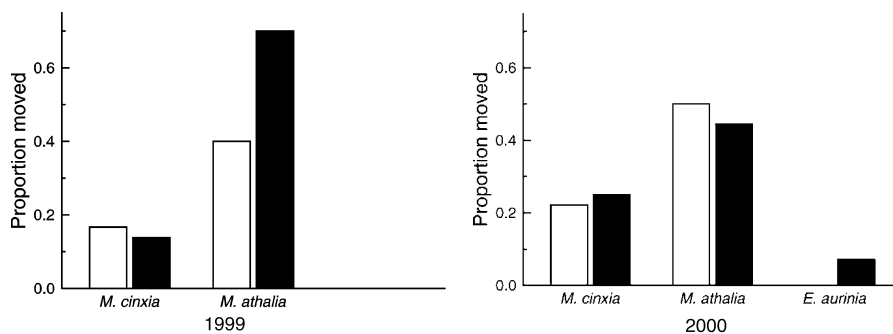


Figure 1. Proportion of individuals, of each sex (□ females, ■ males) and species, that moved through the shady part during the experiment in 1999 and 2000. The species differed significantly in both 1999 and 2000, but not the sexes (Table 2).

Table 2. Log-linear analysis with movement through the scrub section (yes/no) as response variable

| Effect | 1999 | | | 2000 | | |
|----------------------|-----------|----------|----------|-----------|----------|----------|
| | <i>df</i> | χ^2 | <i>p</i> | <i>df</i> | χ^2 | <i>p</i> |
| Species | 1 | 11.0 | <0.001 | 2 | 10.3 | 0.006 |
| Sex | 1 | 0.12 | 0.73 | 1 | 0.059 | 0.81 |
| Species \times sex | 1 | 1.2 | 0.27 | 2 | 1.0 | 0.60 |

The design variables were species (1999: *M. cinxia*/*Mell. athalia*; 2000: *E. aurinia*/*M. cinxia*/*M. athalia*) and sex (male/female).

The comparison species were not included in the log-linear analysis since most individuals of these species moved several times between the open parts. To compare the movement rates of all species, the number of movements per hour was calculated for each individual. The mean movement rates of each species, with sexes pooled, are given in Figure 2. The movement rate of each Melitaeini species was significantly lower than the movement rate of either of *B. ino* and *C. euphrosyne* (Table 3). The higher movement rate of *A. hyperantus* compared to the two Melitaeini species was only significant for *M. cinxia*. It should be stressed that the movement rates of the comparison species are likely to be heavily underestimated since the cage was only inventoried twice per day. It happened frequently that individuals of the comparison species flew through the shady part during inventory occasions, which was never observed for the checkerspot butterflies.

We found no significant differences in movement rate between females and males for any of the comparison species; *B. ino*: $U = 7$, $p = 0.44$; *A. hyperantus*: $U = 17$, $p = 0.22$; *C. euphrosyne*: $U = 55$, $p = 0.10$ (tested using a Mann–Whitney U -test; n -values are given in Table 1).

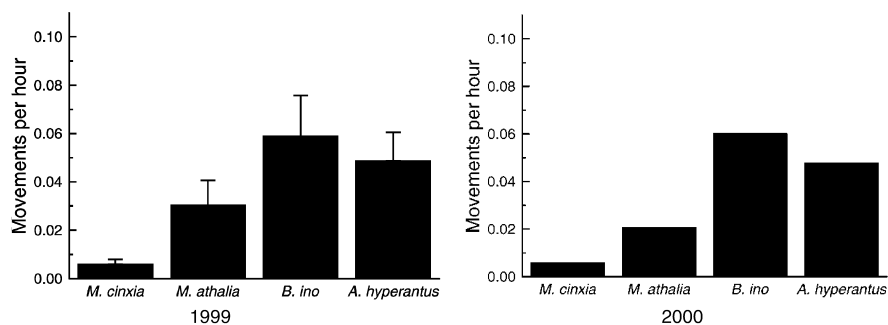


Figure 2. Mean number of movements through the shady part per hour (+SE). In 1999, there were significant differences between *B. ino* and the two Melitaeini species and also between *A. hyperantus* and *M. cinxia* (Table 3). In 2000 *C. euphrosyne* differed significantly from each of the checkerspot butterflies (Table 3).

Table 3. The number of movements per hour through the shady part (see Fig. 2) analysed using a Mann–Whitney U -test, with sexes pooled

| Comparison species | <i>E. aurinia</i> | | <i>M. cinxia</i> | | <i>Mell. athalia</i> | |
|----------------------|-------------------|--------|------------------|--------|----------------------|--------|
| | U | p | U | p | U | p |
| <i>B. ino</i> | | | 76 | <0.001 | 35 | 0.048 |
| <i>A. hyperantus</i> | | | 180 | <0.001 | 75 | 0.11 |
| <i>C. euphrosyne</i> | 70 | <0.001 | 100 | <0.001 | 55 | <0.001 |

See Table 1 for n -values.

Mobility within the open parts

Each section containing an observed individual was recorded in 2000, we could calculate a minimal distance an individual must have travelled inside the two open parts. Dividing this distance by an individual's total time in the cage gives an estimate of the mobility within the open parts (Fig. 3). Using the Bonferroni correction for multiple comparisons, there are significant differences between *C. euphrosyne* and each of the three Melitaeini species and between *E. aurinia* and *Mell. athalia* (Table 4). Although these figures may be used to compare the mobility between species, it should be stressed that the values are unlikely to be representative of their true movement speeds. Several movements between sections may well have taken place in between the observations, leading to an underestimate of the actual mobility.

Spatial distribution and the effect of the shady part

The distributions of the species in the cage were estimated from the recapture data. For each individual the relative proportions recaptures in each section were calculated. As seen in Figure 4 the individuals were not equally distrib-

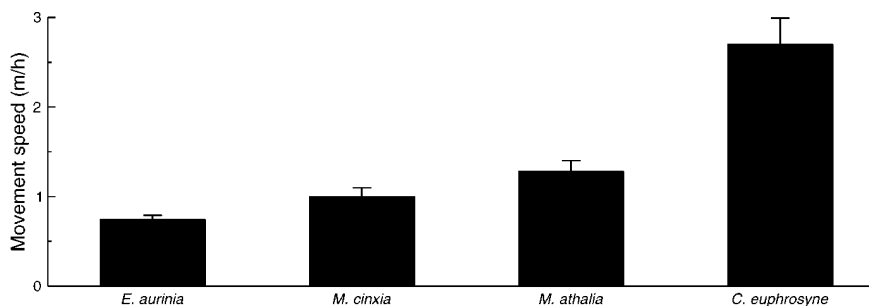


Figure 3. Average rates of movement (+SE) within cage parts along the longitudinal axis of the cage, in the year 2000. The values were calculated for each individual from the data on movements between the small, 2 m long, sections of the cage.

Table 4. Rates of movement within cage parts (see Fig. 3) analysed for each species pair using a Mann–Whitney U -test

| Comparison species | <i>E. aurinia</i> | | <i>M. cinxia</i> | | <i>Mell. athalia</i> | |
|----------------------|-------------------|---------|------------------|---------|----------------------|---------|
| | U | p | U | p | U | p |
| <i>C. euphrosyne</i> | 38 | < 0.001 | 89 | < 0.001 | 61 | < 0.001 |
| <i>Mell. athalia</i> | 35 | < 0.001 | 135 | 0.041 | | |
| <i>M. cinxia</i> | 240.5 | 0.088 | | | | |

See Table 1 for n -values.

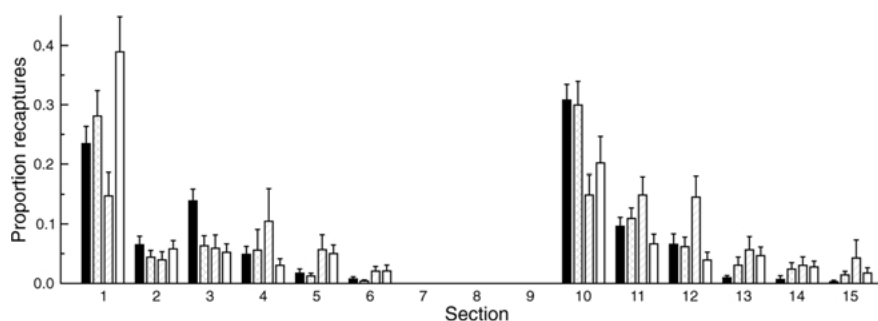


Figure 4. Proportions of recaptures in each section averaged over individuals (+SE) for the experiment in 2000; (■) *E. aurinia*, (⊠) *M. cinxia*, (□) *Mell. athalia*, (□) *C. euphrosyne*. Section 1 is at the south-western end of the cage and sections 7–9 make up the shady part. The means and standard errors were calculated for each species with sexes pooled.

uted over the cage. There were no recaptures in the shady part and the few observations made there were of individuals flying from one open part to the other. It also appears as though the butterflies were distributed toward the south-western ends of both open parts (Sections 1 and 10 had the highest proportions of recaptures). The reason for this distribution is probably that the butterflies preferred to move in a south-westerly direction. A similar effect was seen for movements through the shady part. For each species, there was a higher movement rate from the northern to the southern open part compared to the other direction. Using a Wilcoxon paired-sample test this effect was significant for *Mell. athalia* and *C. euphrosyne* ($T = 2$, $p = 0.047$ and $T = 55$, $p = 0.019$) but not for *M. cinxia* ($T = 11$, $p = 0.69$). *Euphydryas aurinia* was not analysed due to the low number of movements through the shady part.

Density effects on mobility

For the experiment in 2000, two different densities were used for *E. aurinia*, *M. cinxia* and *C. euphrosyne*. In the case of *M. cinxia*, each individual had

spent time in both high and low density. Thus, the movement rate through the shady part, from both high and low density could be calculated for each individual. On average, the rate of movement was 1.3 times higher from the high density open part. However, this difference was not statistically significant (Wilcoxon paired-sample test: $T = 13$, $p = 0.94$). There were only two movements through the shady part for *E. aurinia*, one from low and one from high density. *Clossiana euphrosyne* moved at such high rate through the shady part that the densities evened out during a day. Due to these reasons, *E. aurinia* and *C. euphrosyne* were not analysed statistically.

Potentially confounding effects

A difference in survival between *Mell. athalia* and *M. cinxia* in 1999 could potentially have influenced the results in Figure 1, since the species would not have had the same amount of time to move through the shady section. However, testing survival until the last day (yes/no) in a log-linear analysis with sex (male/female) and species (*M. cinxia*/*Mell. athalia*) as design variables produced no significant differences (sex: $\chi^2_1 = 0.11$, $p = 0.74$; species: $\chi^2_1 = 0.59$, $p = 0.44$, sex \times species: $\chi^2_1 = 1.26$, $p = 0.26$).

Data from previous studies suggest that mobility can change with age (Kuussaari *et al.*, 1996; Warren, 1987b). In 1999, *Mell. athalia* were collected as adults and could have been older than the *M. cinxia* individuals reared from larvae, so the difference between the species could have been influenced by a time dependent movement rate. However, this seems not to have been the case: between day 0 and day 2 (about halfway through the study) six out of a total of nine *M. cinxia* movements had taken place, compared to seven out of nine for *Mell. athalia*.

Discussion

The differences between species in the tendency towards habitat exploration suggested by this study seem rather consistent with the ranges of habitats over which these butterflies occur. For instance, the localities where *Mell. athalia* occurs are often described as being closer to woodland and more densely vegetated than the localities of *M. cinxia*, which agrees with the higher willingness of *Mell. athalia* to move through the shady part (Fig. 1). However, the habitat of *M. cinxia* and *Mell. athalia* often overlap and it might not be that *Mell. athalia* actually requires a more shady habitat. *Mellicta athalia* might rather be prepared to fly through small sections of denser vegetation on a daily basis and can thereby make use of smaller and more fragmented areas of suitable habitat than *M. cinxia*. A possible reason for this difference may be the

wider hostplant range of *Mell. athalia*. One of its hostplants, not used by *M. cinxia*, is *Melampyrum pratense*, which is common in glades and edges of wood where *P. lanceolata* and *V. spicata* are often absent, so *Mell. athalia* may have more to gain by visiting more densely vegetated and/or smaller patches than *M. cinxia*. *Euphydryas aurinia* occurs in rather different places than *M. cinxia* and *Mell. athalia*, but its low tendency to move through the shady part of the cage still seems to be in good agreement with the kind of habitat used. *Euphydryas aurinia* generally occurs in discrete areas of very open and unshaded habitat (Porter, 1981; Warren, 1994), which might suggest that *E. aurinia* seldom needs to pass shaded areas in its natural habitat.

Our finding that the Melitaeini species are relatively unwilling to move through unsuitable habitat is in good agreement with previous mark–recapture studies. Movements between habitat patches have been recorded in both *M. cinxia* (Hanski *et al.*, 1994; Kuussaari *et al.*, 1996) and *Mell. athalia* (Warren, 1987b), but during the extent of these studies the majority of individuals stayed in their natal patch. *Euphydryas aurinia* also seems to be rather unwilling to cross unsuitable habitat. In a study by Porter (1981), only a small number of adults moved in and out of a rather small habitat area and a 6 m high and 8 m wide hedge provided a substantial barrier to movements. Small belts of unsuitable vegetation were also found to act as movement barriers to *Mell. athalia* in the study by Warren (1987b). The Melitaeini species are generally sedentary and daily movements are often short, with a typical movement range from about 150 m for *Mell. athalia* (Warren, 1987b) to around 30 m per day for *E. aurinia* (Porter, 1981).

The much higher movement rates found for the comparison species, *A. hyperantus*, *B. ino* and *C. euphrosyne* (Fig. 2) also seem consistent with differences in habitat ranges and habitat use. For instance, *A. hyperantus* was often seen flying in the sparse woodland adjoining the pasture where the cage was located, which was never the case for *Mell. athalia*. None of the comparison species is typically seen in sheltered and densely vegetated areas that are similar to the shady part of the cage, but perhaps they fly through such areas daily in order to move between habitat fragments. Several *C. euphrosyne* and *B. ino* individuals were caught in an old clear-felled area consisting of small fragments of open areas surrounded by young forest stands that they either needed to fly over or through to move around in the area.

The species that were more mobile within open parts (Fig. 3) also seem to have had a higher tendency to move through the shady part (Fig. 2). This pattern would be expected if the shady part did not really function as a barrier to movements, since a more actively flying species would disperse at a higher rate from one open part to the other. However, Figure 4 clearly shows that the shady part was a substantial barrier to movements. Nevertheless, a consequence of a more active flight could be that the number of flights per unit time

near the shady part increases. Thus, if there is an increased probability of flying through the shady part when being close to it, the result in Figure 2 could be influenced by differences in flight activity between the species.

The mobility of butterflies is dependent on morphological characteristics. For long-distance movements the size of thorax muscles and the wing-shape may be of great importance, but for flying through small areas of unsuitable habitat, other traits may be more significant. For example, flying through shady areas, when the sun is shining, can result in a large drop in body temperature and maintaining flight at low temperature can be costly in terms of energy consumption (Shreeve, 1992). The checkerspots are sun-loving butterflies that, in Sweden, rarely fly when the sun is not shining. All of the comparison species, on the other hand, generally maintain flight for some time after the sun has passed into clouds. *Aphantopus hyperantus* is often seen flying in shady areas and sometimes maintains flight activity when it is warm but overcast. Thus, it seems likely that the costs of maintaining flight at low temperature differ considerably between the comparison species and the checkerspot butterflies used in this study.

A change in landscape structure is likely to alter several factors that could influence the evolution of dispersal tendency, e.g., the survival during dispersal or local extinction rate (Comins *et al.*, 1980; Southwood, 1981; Johnson and Gaines, 1990). In butterflies, a number of studies suggest that flight-related traits, such as thorax size, may adapt to differences in habitat structure (e.g., Dempster *et al.*, 1976; Dempster, 1991; Berwaerts *et al.*, 1998; Thomas *et al.*, 1998; Hill *et al.*, 1999). In addition to morphological traits, one ought to expect adaptation in behavioural traits, such as the willingness to pass through different types of habitat. However, there seems to be a lack of studies on the relationship between habitat structure and movement behaviour in this regard. It could nevertheless be the case that behavioural traits sometimes are more clearly related to inter-patch mobility than morphological traits. Since the flight capability of butterflies serves many purposes, it can be difficult to know whether a change in flight morphology is an adaptation to inter-patch mobility or to some other flight-related activity (van Dyck and Matthysen, 1999), such as different mate-locating strategies (Wickman, 1992).

Regardless of the selective background, it seems reasonable that a high degree of habitat exploration will contribute to a more extensive local distribution. Even though an individual may not move a long distance during its lifetime, a species less bound by its habitat borders could disperse a considerable distance within a few generations. Similarly, one might expect that habitat fragmentation, which is responsible for the decline of many butterflies, would affect the distribution of butterflies differently depending on the degree of habitat exploration, so that species having a higher tendency towards habitat exploration ought to be less sensitive to fragmentation.

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