

Habitat preference and habitat exploration in two species of satyrine butterflies

Olof Leimar, Ulf Norberg and Christer Wiklund

Leimar, O., Norberg, U. and Wiklund, C. 2003. Habitat preference and habitat exploration in two species of satyrine butterflies. – *Ecography* 26: 474–480.

We compared the habitat preference and the mobility of different populations of primarily forest living, satyrine butterflies by observing them in a manipulated environment, containing different habitat types inside a large outdoor cage. The cage was 30 m long and divided into three parts. Each end of the cage contained a shady habitat, made to be similar to the floor of a forest with sunlit spots. In between these shady parts, there was a 14 m long open part, like a glade or a meadow. We performed two studies in the cage. In the first study, we compared a population of a species with very restricted distribution in Sweden, *Lopinga achine*, and a population of a widely distributed and expanding species, *Pararge aegeria*. We found that the two species had similar habitat preferences in the cage, but that *L. achine* had a lower rate of dispersal from one shady part of the cage to the other. In the second study, we compared two populations of *P. aegeria*, a Swedish forest living population and a Madeiran population inhabiting a fairly open habitat. We found that, although individuals of the Swedish population avoided staying in the open, middle part of the cage, they dispersed between the shady parts of the cage at a higher rate than individuals of the Madeiran population. We argue that studies of the kind we performed can serve the purpose of testing hypotheses about habitat preference and mobility that derive from other field work or from information about distribution patterns.

O. Leimar (Olof.Leimar@zoologi.su.se), U. Norberg and C. Wiklund, Dept of Zoology, Stockholm Univ., SE-106 91 Stockholm, Sweden.

Individuals of migratory butterfly species regularly move over distances of hundreds of kilometres (Baker 1978, Dingle 1996), passing through various types of vegetation and landscapes on their journeys towards suitable habitat. At the other end of the scale, there are extremely sedentary species, whose members typically spend their entire lives in a local habitat patch (Thomas and Harrison 1992, Thomas 1995). There are also intermediates between these extremes, where at least a fair proportion of the individuals venture outside their patch of birth, perhaps in search of new habitat. Such dispersive movements could be the outcome of some special, migratory flight behaviour, designed for travelling through non-habitat (Baker 1984), but they could also be examples of so-called trivial movement (Southwood 1962), where individuals cover ground in more or

less direct search of resources. Movement through areas of seeming non-habitat, perhaps in search of resources, has been referred to as ranging (Dingle 1996) or habitat exploration (Norberg et al. 2002).

There is likely to be a relationship between habitat preference and mobility, in that populations or species whose habitat requirements are satisfied over a larger area will seem more explorative. Since butterflies use flight to perform activities such as mate location, foraging and egg laying, they will be mobile in their preferred habitat and will disperse through this habitat, although a tendency to establish smaller home ranges could of course constrain movement. This kind of relationship between habitat preference and mobility will be weakened if there is also variation between populations in the tendency to move through areas of

Accepted 12 November 2002

Copyright © ECOGRAPHY 2003
ISSN 0906-7590

non-habitat during everyday resource search. In this way, habitat exploration can contribute to overall mobility, as a component added to the mobility within the preferred habitat.

An important consequence of a greater capacity for habitat exploration could be a greater ability of such a population to expand its range when more habitat becomes available, in particular if the habitat is fragmented. Norberg et al. (2002) suggested that it may be typical for widely distributed butterfly species to have a greater tendency towards habitat exploration than localized and rare species and presented empirical evidence consistent with this idea. However, at present it is not known to what extent variation in habitat exploration, or similar kinds of mobility, can explain variation in distributional range. Recent investigations of butterfly range expansion indicate that insufficient mobility relative to the degree of habitat fragmentation could prevent the colonization of newly available habitat (Hill et al. 2001).

Apart from a possible relevance to range maintenance or expansion, a better understanding of habitat preference and habitat exploration could be of value in clarifying how populations have been adapted to the kind of landscapes they inhabit. If essential resources have a patchy distribution, it might not be the best resource search strategy to just move in directions of higher perceived habitat quality, but it could be more efficient in the long run to also pass through lower quality or non-habitat while searching. The importance of this kind of searching over a larger area is a likely ultimate explanation for the occurrence of habitat exploration.

Tracing the movements of individuals over their life times would be an ideal method of investigating habitat preference and habitat exploration. For practical reasons, this has so far proven infeasible when studying butterflies, and mark-release-recapture has instead become the method of choice. The method serves the purpose of providing data on mobility from natural situations, but it also suffers from notable limitations, such as low recapture rates and difficulties in manipulating environmental features with an effect on habitat preference and mobility. In this study we have used an alternative approach, where different kinds of habitat are created inside a large outdoor cage (Norberg et al. 2002). Compared to mark-release-recapture, there is a greater possibility to make controlled comparisons inside an outdoor cage, so that the approach can serve the purpose of experimentally testing hypotheses about butterfly mobility. There are of course also some drawbacks of the method. An important one may be the relatively small distances inside the cage, in comparison with the distances moved by butterflies in a natural situation, and this needs to be taken into account when interpreting data obtained with the method.

We report the results from two comparisons of different populations of primarily forest-living, satyrine butterflies. The first is between Swedish populations of *Pararge aegeria* and *Lopinga achine*. Since *P. aegeria* is widely distributed and has recently expanded its range (Ryrholm pers. comm.), whereas *L. achine* has a very restricted distribution in Sweden (Bergman and Landin 2001), our expectation was that *P. aegeria* would turn out to be the more explorative of the two. The second comparison is between Swedish and Madeiran populations of *P. aegeria* that are likely to differ in their habitat preferences, with the Madeiran population preferring a more open habitat than the Swedish population. Our aim was to investigate what consequences any differences in habitat preference might have for habitat exploration.

Materials and methods

A large outdoor cage ($W \times L \times H$: $8 \times 30 \times 4$ m) of oblong shape and with a half-circle shaped cross section was erected in an open pasture at Tovetorp field station, 100 km southwest of Stockholm. The cage roof and walls consisted of a fine-meshed net that reduced solar radiation by ca 25%. Each end of the cage was covered by camouflage nets (Fig. 1), extending a few meters beyond the ends of the cage and being made out of variously shaped, opaque patches (\varnothing 20–40 cm) placed in an irregular pattern, with the open areas between the patches varying in width from 5 cm up to ca 70 cm. This created a relatively shady habitat that also contained sunlit spots, not unlike the floor of a forest. Nine artificial Christmas trees were also placed in each shady part of the cage, and additional camouflage nets were hung inside the cage, from the arches bordering sections 4–5 and sections 11–12 (see Fig. 1), to add to the impression of a more closed and shady habitat. In this way, the cage was partitioned into two 8 m long relatively shady parts, separated by a 14 m long open part. The ground inside the cage was covered by various herbs and grasses, including for

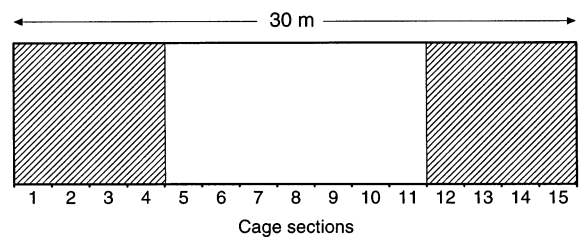


Fig. 1. Schematic of the outdoor cage used for the study. The cage was supported by 16 arches, dividing it into 15 sections, and was oriented in an east-westerly direction. The cage roof above sections 1–4 and 12–15 was covered with camouflage netting, making these sections shadier than the open, middle part.

instance *Dactylis glomerata* (which is one of the host plants of *P. aegeria*), but not including *Carex montana* (which is the favoured host plant of *L. achine*).

We performed two studies in the cage. For each study, individually marked butterflies of the different populations were released together and in equal amounts in sections 2 and 14 of the cage. We then recorded the positions of the butterflies by slowly walking through the cage, using binoculars to read individual markings at a distance, and noting the time and section number (Fig. 1) of individual positions. Such a session took about one hour, and there were sessions before noon, at midday, and in the afternoon. The first study started 31 May 2000 and the second 8 June 2000.

Two species of primarily forest-living (Henriksen and Kreutzer 1982), satyrine butterflies, from the sub-tribe Parargina, were used in the first study: *Lopinga achine* (woodland brown) from Gotland and *Pararge aegeria* (speckled wood) from Skåne. The habitat of both of these populations is forest: *L. achine* from Gotland occur in partly open pine forest with a well developed scrub layer (Bergman 2000) and *P. aegeria* from Skåne occur in partly open, mature deciduous forest (Wiklund unpubl.). For the second study, two populations of *P. aegeria* with different habitats were used. The habitat of the Riala population is mixed coniferous and deciduous forest, whereas the habitat of the Madeira population is fairly open land, with shrubs but with few trees (Wiklund unpubl.). There are other *P. aegeria* populations in Madeira with forest habitats (Owen et al. 1986, Jones and Lace 1992), and it is not known to what extent the population we used has diverged genetically from its forest-living ancestors. Nevertheless, it seems reasonable to hypothesize that members of this population might prefer a more open habitat. The latitude and longitude of the different populations are shown in Table 1.

Individuals of *L. achine* were reared in the laboratory, from eggs laid by females caught on Gotland during the summer of 1999. Similarly, individuals of the Skåne and Riala populations of *P. aegeria* were reared in the laboratory, from eggs laid by females that had been caught in 1999, whereas the individuals of the Madeira population derived from females caught in 1998. Individuals were released in the cage within three days of hatching (and were kept in the lab, at 10°C, between hatching and release).

For statistical testing, we used the individual butterfly as the unit of observation. We analysed the proportion of observations in the middle, open third of the cage (not including the bordering sections 5 and 11 that were shady during parts of the day) and the number of movements per h from one shady part of the cage to the other, assuming that a day lasted from 8:30 to 17:30. We also considered the overall mobility, measured as the number of cage sections traversed per h (Fig. 1), but since this only takes into account movement in the direction along the cage, and we most likely also failed to detect a number of movements, the measure will be an underestimate of the true mobility. To further look at mobility within the shady habitats at each end of the cage, we computed a similar measure where we did not include traversal of sections in the middle third of the cage. By suitably transforming the variables, we managed to achieve homogeneous variances, making it possible to employ analysis of variance. We used the statistical software R (Ihaka and Gentleman 1996) for the analysis.

Results

The behaviour shown by the butterflies in the cage was generally similar to what is seen in their natural habitats, including mating pairs, egg-laying females, and individuals basking in sunlit spots and perching on the branches of the artificial Christmas trees. A number of *P. aegeria* males also engaged in aerial combat over sunspot territories. We observed matings for members of the different populations, including *P. aegeria* from Madeira and *L. achine* from Gotland (for *L. achine*, matings were particularly apparent, perhaps because of a longer mating duration compared to *P. aegeria*). Females of *L. achine* were laying eggs, even though their preferred host plant (*C. montana*) was absent from the cage. A likely reason is that *L. achine* drop their eggs to the ground, without depositing them on any substratum (Wiklund 1984, Bergman 1999). Midday temperatures varied between 15 and 18°C during the first study, and between 18 and 20°C during the second, so that the second study was performed in warmer weather than the first. The number of observations and the time present in the cage for the individuals of the different populations are given in Table 1.

Table 1. Sample sizes, number of observations per individual, and total observation time per individual ($\bar{x} \pm \text{SE}$) for the different butterfly populations used in the studies. The estimated time an individual was present during a study is based on the assumption that a day starts at 8:30 and ends at 17:30, giving nine hours per day.

Species	Locality	Lat/Long	Males	Females	Obs/ind	Hours/ind
<i>L. achine</i>	Gotland	57°30'N/18°33'E	9	8	9.6 ± 0.9	44.3 ± 5.3
<i>P. aegeria</i>	Skåne	56°17'N/12°29'E	21	5	11.6 ± 1.4	36.5 ± 4.4
<i>P. aegeria</i>	Riala	59°38'N/18°37'E	9	8	7.8 ± 0.5	18.3 ± 1.2
<i>P. aegeria</i>	Madeira	32°40'N/16°45'W	8	10	7.5 ± 0.5	21.4 ± 0.7

Table 2. Analysis of variance of measures of habitat preference and mobility for individuals of the two butterfly populations in the first study: *L. achine* from Gotland and *P. aegeria* from Skåne. The degrees of freedom for sex, population, sex × population, and error are 1, 1, 1, and 39 in each analysis, and type II sums of squares have been used.

Variable and transformation	Effect	F	p
Proportion of obs. in sections 6–10 (arcsine square root transf.)	sex	11.164	0.002
	population	3.145	0.084
	sex × population	0.229	0.635
Dispersal rate (dispersals h ⁻¹) (square root transf.)	sex	0.001	0.986
	population	5.643	0.023
	sex × population	0.120	0.731
Mobility (sections h ⁻¹) (square root transf.)	sex	0.091	0.764
	population	8.794	0.005
	sex × population	1.493	0.229

Comparison between *L. achine* and *P. aegeria*

In the first study, where we used *L. achine* from Gotland and *P. aegeria* from Skåne, both species showed similar distributions in the cage, although there was a non-significant tendency for *L. achine* to be found less often than *P. aegeria* in the open part (Table 2, Fig. 2). Males of both species were less often in the open part of the cage than would be expected from random distribution (Fig. 2), whereas females were significantly more often in the open part than the males (Table 2). We could not establish statistically that females showed a preference for either the open or the shady parts, in the sense of a deviation from a random distribution (Fig. 2). Note, however, that females of both species were usually not found in the open part, in the sense that the observed proportions were clearly below 0.5 (Fig. 2).

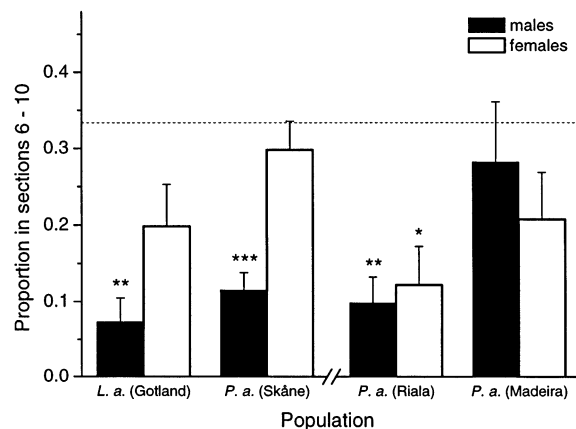


Fig. 2. The proportion of the observations of an individual that was recorded in the middle third of the cage ($\bar{x} \pm SE$, see Table 1 for sample sizes and Tables 2 and 3 for analyses of variance). The left half of the figure corresponds to the first study, comparing *L. achine* from Gotland and *P. aegeria* from Skåne, and the right half corresponds to the second study, comparing *P. aegeria* from Riala and *P. aegeria* from Madeira. The dashed line shows the expected proportion (1/3) given random distribution in the cage. The asterisks indicate significant differences from the random expectation (Bonferroni adjusted t-tests of arcsine square root transformed proportions: * – $p \leq 0.05/4 = 0.0125$; ** – $p \leq 0.01/4 = 0.0025$; *** – $p \leq 0.001/4 = 0.00025$).

For the rate of dispersal between the two shady parts, there were significant differences between the species, but not between the sexes (Table 2, Fig. 3a). A very similar pattern was found for the overall mobility in the cage (Table 2, Fig. 3b), with *L. achine* being less mobile than *P. aegeria*. For the measure of mobility that excluded the middle third cage part, the results (not shown) were qualitatively the same as for overall mobility, with a statistically significant difference between populations but no difference between the sexes.

Comparison between *P. aegeria* populations

In the second study, where we used two populations of *P. aegeria*, both males and females of the Riala population were found significantly less often in the open part than expected from random distribution (Fig. 2). The individuals of the Madeira population were observed more in the open part, but there was only a non-significant tendency towards a difference between the populations in their distribution in the cage (Table 3). We could not establish statistically that the distribution of the Madeira individuals in the cage deviated from random. Considering that this population occurs naturally in an open habitat, it is however striking that they were usually found away from the open part, in the sense that the proportions of observations in the open were < 0.5 (Fig. 2). In fact, for each of the Madeira individuals, with the exception of a single male, the majority of the observations were in the shady parts of the cage (i.e., sections 1–4 and sections 12–15).

We did find significant differences between populations in the rate of dispersal between shady parts (Table 3, Fig. 3a), with the Riala population being more dispersive than the Madeira population. For the overall mobility in the cage, the pattern was similar, although there was only a non-significant tendency towards a difference between populations (Table 3, Fig. 3b). We found no statistical significances from the analysis of the measure of mobility that excluded the middle third cage part, although the pattern was qualitatively similar to the one for overall mobility. It is also worth noting that the Madeira population – although somewhat less

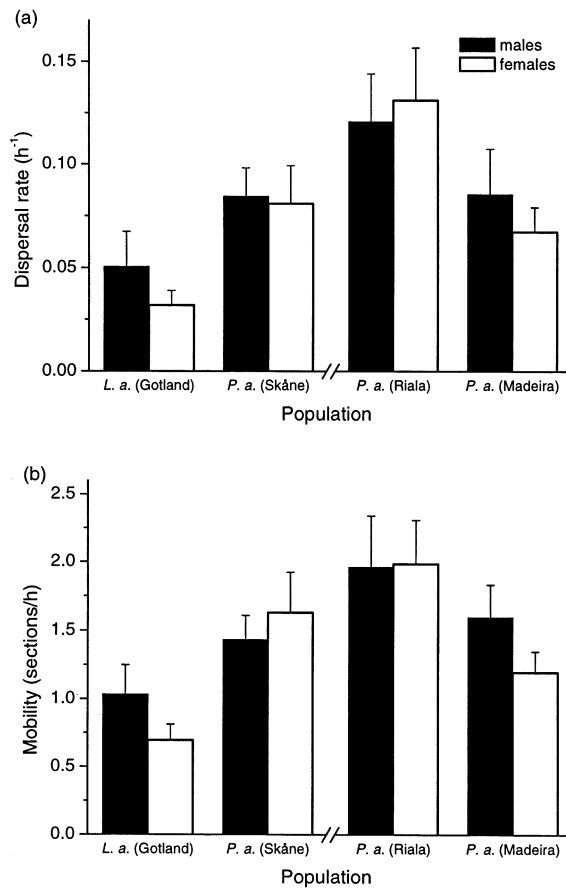


Fig. 3. (a) The dispersal rate, measured as the number of shifts between the two shady cage parts per h, and (b) the overall mobility, measured as the absolute number of cage sections traversed per h ($\bar{x} \pm \text{SE}$, see Table 1 for sample sizes and Tables 2 and 3 for analyses of variance). The left half of each panel corresponds to the first study, comparing *L. achine* from Gotland and *P. aegeria* from Skåne, and the right half corresponds to the second study, comparing *P. aegeria* from Riala and *P. aegeria* from Madeira.

mobile in the cage than the Riala population – was not at all sedentary, but displayed about the same mobility as the *P. aegeria* population from Skåne in the first study (see Fig. 3).

Table 3. Analysis of variance of measures of habitat preference and mobility for individuals of the two butterfly populations in the second study: *P. aegeria* from Riala and *P. aegeria* from Madeira. The degrees of freedom for sex, population, sex \times population, and error are 1, 1, 1, and 31 in each analysis, and type II sums of squares have been used.

Variable and transformation	Effect	F	p
Proportion of obs. in sections 6–10 (arcsine square root transf.)	sex	0.162	0.690
	population	3.007	0.093
	sex \times population	0.591	0.448
Dispersal rate (dispersals h ⁻¹) (square root transf.)	sex	0.001	0.972
	population	5.923	0.021
	sex \times population	0.142	0.709
Mobility (sections h ⁻¹) (square root transf.)	sex	0.451	0.507
	population	3.662	0.065
	sex \times population	0.735	0.398

Discussion

In the situation arranged in our cage, *L. achine* from Gotland and *P. aegeria* from Skåne displayed roughly similar habitat preferences. Males of both populations avoided staying in the open part of the cage, as might be expected for forest living species, but the females were found somewhat more often in the open. A possible explanation could be that temperatures were low during the first study, and that females preferred to spend more time than the males basking in the open part of the cage. For a British population of *P. aegeria*, Shreeve (1984) found that during periods of cooler weather females were located more often than males in open rides as compared to in woodland, and interpreted this as a greater allocation of time to basking by females. In addition to female basking, Shreeve (1986) found that egg-laying sites used by British *P. aegeria* females during cooler weather were usually in sunlit open areas, in contrast to the sites in woodland ground layer used during warmer summer months. However, Wickman and Wiklund (1983) observed egg laying primarily in shady places by Swedish *P. aegeria*. For the males of *P. aegeria*, it is likely that they were attracted to the spots of sunlight in the shady parts of the cage (Davies 1978, Wickman and Wiklund 1983, Shreeve 1984). Our observation suggests that there could be a similar sexual difference in habitat preference for *L. achine*, but there are no field data bearing on the issue. Bergman and Landin (2002) reported that *L. achine* from Östergötland (in southern Sweden) flew mostly in the glades of oak-dominated woodland, whereas *L. achine* from Gotland fly inside the pine forest (Wiklund unpubl.).

In accordance with our expectation, we found that *L. achine* from Gotland had a lower rate of dispersal between the two shady parts of the cage than *P. aegeria* from Skåne. This seems to have been a consequence of a lower overall mobility of *L. achine*, perhaps combined with a stronger reluctance to cross the open cage part. Since females of *L. achine* did not have access to their preferred host plant (*C. montana*) in the cage, one might have expected them to move about in search of

it. Assuming that such an effect was present, the mobility difference between the species would then be even greater without the effect.

The results of our second comparison, between *P. aegeria* from Riala and from Madeira, are at least suggestive of an interesting contrast between habitat preference and habitat exploration. The butterflies from Riala clearly avoided staying in the middle, open part of the cage, although they had a high rate of dispersal between the shady parts, indicating that they traversed the middle part fairly rapidly. The Madeira butterflies, on the other hand, seemed not to avoid the open part, and their rate of dispersal between the shady parts was lower. A somewhat speculative interpretation would be that the Riala butterflies moved into the open part with the intention of crossing over it, rather than spending time in it, whereas the Madeira butterflies may have regarded the open part as habitat.

The Riala and Madeira populations differ in wing colour, with Riala individuals being generally darker. This could mean that they also differ in thermoregulation, such that the Riala individuals might require less basking to maintain activity, or be more prone to overheating, whereas the Madeira individuals might tolerate quite warm and sunny conditions before they would seek shade. For *P. aegeria*, it is known that variation in wing colour within a population can be related to male behaviour (Van Dyck et al. 1997), such that pale males spend more time in sunlit spots. There can also be differences in wing colour between seasonal cohorts of *P. aegeria* (Van Dyck and Wiklund 2002), which could be adaptations to seasonal changes in solar radiation and ambient temperatures.

Since the natural habitat of the Madeira population is fairly open land, the observation that these individuals spent large fractions of their time in the shady parts of the cage was somewhat unexpected (see Fig. 2). Our study does not permit us to draw any definite conclusions as to the reasons for this, but one should keep in mind that there need not be a perfect correlation between the actual habitat of a population and the habitat preferences of its members. For a population to persist in a certain area, it is enough that its members do sufficiently well there. Thus, it is possible that forest-living and open-living *P. aegeria* on Madeira both have an inclination to be in forest, but the ones living in open land have less of an opportunity to satisfy this inclination. Studies in outdoor cages could be a good way of investigating such questions.

We found no difference in mobility between the sexes, in either the first or the second study, which is surprising, since there are field observations of greater female than male mobility for populations of both *P. aegeria* (Davies 1978) and *L. achine* (Bergman and Landin 2002). From our study, it is not clear what the reasons for the seeming discrepancy might be. One possibility is that males are more mobile over short

distances, but that females are more willing to pass through suboptimal habitats, allowing them to travel further, and that the two effects cancelled each other in the cage. If so, the set-up was too small to detect this kind of mobility difference between the sexes.

As illustrated by this possibility, a limited cage size can cause movements that otherwise would have extended over greater distances to be lumped together into a single category, corresponding to the maximum distance inside the cage. One way to avoid the problem would be to use a bigger cage, and it is perhaps feasible to use cages with lengths of 100 m or more. Nevertheless, we would argue that observations from the type of cage we used can contribute to the study of habitat preference and habitat exploration. In particular, such observations can be used to experimentally test hypotheses deriving from field studies or from information about distribution patterns. As with many other forms of experimentation, there is a trade-off between the advantage of a greater control over important circumstances in an experiment and the disadvantage of a certain artificiality. The basic idea of studying habitat exploration in a relatively large cage, as in the present work or that by Norberg et al. (2002), is that variation in individual characteristics, such as the willingness to stay in or pass through certain types of habitat, could be detected in a cage of moderate dimension, and that these characteristics might play a role also in the natural situation. Such an idea can only be valid for species of butterflies where a considerable fraction of an individual's natural movements are fairly short, corresponding to the scale of the cage, and it will not work for species that cover greater distances more or less every time they start flying. Concerning the butterflies used in the present study, they appear to be sufficiently sedentary to make it reasonable to study them in our cage (cf. Fig. 3b). At the same time, it is clear that our data cannot provide information on whether mobility involving sustained flight over greater distances is of importance for these populations.

Baker (1984) argued that a form of genuinely migratory behaviour, with straightened-out flight in a preferred compass direction, occurs in more butterfly species than is generally recognized. Concerning *P. aegeria*, he also reported having seen many single individuals crossing open fields in Britain, and that these transients invariably were female. From our own quite extensive experience of watching butterflies in Swedish meadows, we have no similar observations of *P. aegeria*, suggesting that there may be differences between populations in the tendency to move over large open areas. Such behaviour could also play a role for habitat shifts from forest to open land, as seems to have happened for *P. aegeria* in parts of Madeira (Owen et al. 1986, Jones and Lacey 1992).

At the present time, there is a lack of detailed observation of butterfly movements through non-habitat.

Straightened-out flight in some given direction is one possibility, and this would be an efficient behaviour for covering large distances, but there are of course alternative ways of searching for suitable habitat. An interesting possibility would be a form of systematic area search, for instance using a sequence of loops to cover an area. This has been observed in homing flights after experimental displacement of individuals out of their habitat (Conradt et al. 2000, 2001), although this kind of behaviour has so far not been observed in butterflies that spontaneously emigrate from the home patch.

The ability of a population to maintain or expand its distributional range will depend on both the availability of colonisable habitat and on sufficient dispersal or exploration by members of the population to actually locate this habitat. Over the last century, *P. aegeria* has gradually expanded its range in Sweden (Nordström 1955) and this expansion has continued into recent years (Ryrholm pers. comm.). The situation is quite different for *L. achine*, for which there has been a decrease of the range (Bergman and Landin 2001). It is possible that a relatively low mobility of adult *L. achine* has played a role in keeping the distribution restricted, but the fairly special habitat requirements of the juvenile stages might be equally or more important (Bergman 1999, 2000, 2001). Since there will be risks involved in leaving the home patch in search of new or better habitat, such explorative behaviour will only be selected for if the chances of success are large enough.

Acknowledgements – We thank Bertil Borg for helpful comments. This study was supported by grants from the Swedish Research Council (to O. L. and C. W.).

References

- Baker, R. R. 1978. The evolutionary ecology of animal migration. – Hodder and Stoughton, London.
- Baker, R. R. 1984. The dilemma: when and how to go or stay. – In: Vane-Wright, R. I. and Ackery, P. R. (eds), *The biology of butterflies*. Academic Press, pp. 279–296.
- Bergman, K.-O. 1999. Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. – *Biol. Conserv.* 88: 69–74.
- Bergman, K.-O. 2000. Oviposition, host plant choice and survival of a grass feeding butterfly, the woodland brown (*Lopinga achine*) (Nymphalidae, Satyrinae). – *J. Res. Lepidop.* 35: 9–21.
- Bergman, K.-O. 2001. Population dynamics and the importance of habitat management for conservation of the butterfly *Lopinga achine*. – *J. Appl. Ecol.* 38: 1303–1313.
- Bergman, K.-O. and Landin, J. 2001. Distribution of occupied and vacant sites and migration of *Lopinga achine* (Nymphalidae: Satyrinae) in a fragmented landscape. – *Biol. Conserv.* 102: 183–190.
- Bergman, K.-O. and Landin, J. 2002. Population structure and movements of a threatened butterfly (*Lopinga achine*) in a heterogeneous landscape in Sweden. – *Biol. Conserv.* 108: 361–369.
- Conradt, L. et al. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implication for metapopulation models. – *Proc. R. Soc. Lond. B* 267: 1505–1570.
- Conradt, L., Roper, T. J. and Thomas, C. D. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. – *Oikos* 95: 416–424.
- Davies, N. B. 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. – *Anim. Behav.* 26: 138–148.
- Dingle, H. 1996. *Migration: the biology of life on the move*. – Oxford Univ. Press.
- Hill, J. K. et al. 2001. Impacts of landscape structure on butterfly range expansion. – *Ecol. Lett.* 4: 313–321.
- Henriksen, H. J. and Kreutzer, I. 1982. *The butterflies of Scandinavia in nature*. – Skandinavisk Bogforlag, Odense.
- Ihaka, R. and Gentleman, R. 1996. R: a language for data analysis and graphics. – *J. Comp. Graph. Stat.* 5: 299–314.
- Jones, M. J. and Lacey, L. A. 1992. The speckled wood butterflies *Pararge xiphia* and *P. aegeria* on Madeira: distribution, territorial behaviour and possible competition. – *Biol. J. Linn. Soc.* 46: 77–89.
- Norberg, U., Enfjäll, K. and Leimar, O. 2002. Habitat exploration in butterflies: an outdoor cage experiment. – *Evol. Ecol.* 16: 1–14.
- Nordström, F. 1955. De fennoskandiska dagfjärilarnas utbredning. – *Lunds Univ. årsskrift*, N. F. Avd. 2, Bd 51. No 1.
- Owen, D. F., Shreeve, T. G. and Smith, A. G. 1986. Colonization of Madeira by the speckled wood butterfly, *Pararge aegeria* (Lepidoptera: Satyridae), and its impact on the endemic *Pararge xiphia*. – *Ecol. Entomol.* 11: 349–352.
- Shreeve, T. G. 1984. Habitat selection, mate location, and microclimate constraints on the activity of the speckled wood butterfly *Pararge aegeria*. – *Oikos* 42: 371–377.
- Shreeve, T. G. 1986. Egg-laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behaviour, host plant abundance and temperature. – *Ecol. Entomol.* 11: 229–236.
- Southwood, T. R. E. 1962. Migration of terrestrial arthropods in relation to habitat. – *Biol. Rev.* 37: 171–214.
- Thomas, C. D. 1995. Ecology and conservation of butterfly metapopulations in the fragmented British landscape. – In: Pullin, A. S. (ed.), *Ecology and conservation of butterflies*. Chapman and Hall, pp. 46–63.
- Thomas, C. D. and Harrison, S. 1992. Spatial dynamics of a patchily distributed butterfly species. – *J. Anim. Ecol.* 61: 437–446.
- Van Dyck, H. and Wiklund, C. 2002. Seasonal butterfly design: morphological plasticity among three developmental pathways relative to sex, flight and thermoregulation. – *J. Evol. Biol.* 15: 216–225.
- Van Dyck, H., Matthysen, E. and Dhondt, A. A. 1997. The effect of wing colour on male behavioural strategies in the speckled wood butterfly. – *Anim. Behav.* 53: 39–51.
- Wickman, P. O. and Wiklund, C. 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). – *Anim. Behav.* 31: 1206–1216.
- Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. – *Oecologia* 63: 23–29.