The role of niche breadth, resource availability and range position on the life history of butterflies

Atte Komonen, Alessandro Grapputo, Veijo Kaitala, Janne S. Kotiaho and Jussi Päivinen

Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J. S. and Päivinen, J. 2004. The role of niche breadth, resource availability and range position on the life history of butterflies. – Oikos 105: 41–54.

We analysed the relationship between three life history characteristics (mobility, length of flight period and body size) and niche breadth (larval host plant specificity and adult habitat breadth), resource availability (distribution and abundance of host plants) and range position (distance between the northernmost distribution record and southernmost point of Finland) of the butterfly fauna of Finland. The data is based on literature and questionnaires. Often in across species studies phylogeny may create spurious relationships between life-history and ecological variables. We took the phylogenetic relatedness of butterfly species into account by analysing the data with phylogenetically independent contrasts (CAIC method). Butterfly mobility was positively related to the niche breadth, resource availability and range position. The length of the flight period was negatively related to the range position, indicating that the species at the northern edge of their distribution range have shorter flight period than species which are further way from the range edge. After controlling for the phylogenetic relatedness we found no significant correlations between body size and niche breadth, resource availability or range position. We suggest that the relationship between the length of the flight period and range position may arise as a consequence of lower hatching asynchrony in edge species as a result of lower environmental variance in larval growth conditions. Our results on the mobility suggest that there is selection pressure towards lower migration rate in species that have restricted niche breadth, low resource availability and in species that are on the northern edge of their geographical distribution range. In such species, selection against mobile individuals is likely to result from the decreased probability of finding another habitat patch suitable for egg laying.

A. Komonen, Faculty of Forest Sciences, Univ. of Joensuu, P.O. Box 111, FIN-80101, Joensuu, Finland (atte.komonen@joensuu.fi). – A. Grapputo, V. Kaitala, J. S. Kotiaho and J. Päivinen, Dept of Biological and Environmental Science, Univ. of Jyväskylä, P.O. Box 35, FIN-40014, Jyväskylä, Finland.

A positive interspecific relationship between local abundance and regional distribution has been documented in a variety of species assemblages over a spectrum of spatial scales, and it has been considered an almost universal pattern in ecology (Hanski 1982, Brown 1984, Hanski et al. 1993, Lawton 1993, Gaston et al. 1997, Johnson 1998, Gaston and Blackburn 2000). Of the several variables that may influence this relationship (Cowley et al. 2001a, b), niche breadth and resource availability are among the most important ecological factors (Brown 1984, Hanski et al. 1993, Gaston et al. 1997). In addition, range position, i.e. species in any given area being at different positions relative to the centre of their geographical distribution range, can have a substantial influence on the distribution and abundance of species (Hengeveld and Haeck 1982, Bock and Ricklefs 1983, Brown 1984, Hanski 1999, Brändle et al. 2002). Although evidence for the role of niche breadth,

resource availability and range position on the distribution-abundance relationship is accumulating, the effect that these three ecological factors have on life history traits of the species is not well known (Pollard 1991, Shreeve 1992, Warren 1992, Loder et al. 1998, García-Barros 2000). Here we analyse the relationship between niche breadth, resource availability and range position and three life history traits: mobility, length of the flight period and body size of butterflies.

Many butterfly species are regarded as relatively sedentary (Dempster 1989, Thomas 1993, Thomas et al. 1999; but see Baker 1969, Dennis and Shreeve 1996). This may be related to immediate reproductive gains and potential risks associated with moving from occupied sites to new areas (Dennis 1982, Shreeve 1992). For a dispersing butterfly female, successful location of suitable larval host plant is vital for its reproductive success. Thus, butterfly species with wide niche breadth, i.e. species where the larvae are polyphagous foraging on several host plant species, or butterfly species with high resource availability, i.e. species whose larval food plants are widespread and abundant, may be expected to be more mobile than the more specialised species (Shreeve 1992). There are also some indications that resource availability determine butterfly mobility (White and Levin 1981, Murphy and White 1984, Kuussaari et al. 1996).

The length of the flight period of a butterfly species can reflect at least two things: the average longevity or life span of an individual, or variance in the timing of hatching and consequently appearance on wing. The length of the flight period can vary between species as well as between years for a given species (Warren 1992). Interspecific variation in flight period length is particularly profound between butterfly species that overwinter as adults because they appear on wings both in the autumn and in the spring, and species which overwinter as larvae or pupae. Intraspecific variance in the length of the flight period between years suggests that flight period is at least partially dependent on environmental factors. Indeed, there is evidence that geographical range, temperature, aridity and the openness of the habitat can affect the length of the flight period of butterflies (Pollard and Greatorex-Davies 1997, Dennis et al. 2000, García-Barros 2000). Perhaps ecologically more interesting, however, are the findings that the flight period tends to be longer among polyphagous butterfly species which are able to exploit several host plant species than among monophagous species (García-Barros 2000), and that the flight period tends to be shorter closer to the edge of the species geographical distribution range (Pollard 1991). To our knowledge, there are no previous studies investigating the relationship between the length of the flight period and resource availability on butterflies.

Body size is considered to be one of the most important life history characteristics of a species (Roff 1992, 2002, Stearns 1992). Generally in Lepidoptera there seems to be a positive association between the niche breadth and body size such that polyphagous species tend to be larger than monophagous (Niemelä et al. 1981, Inkinen 1994, Lindström et al. 1994, Loder et al. 1998). However, according to García-Barros (2000), such pattern does not hold for butterflies as a whole. Both Loder et al. (1998) and García-Barros (2000) point out that there is no single explanation for the relationship between niche breadth and body size which would enjoy solid support from the data, and that most of the evidence for such relationships come from a few families of Lepidoptera in cool temperate areas. However, there is one study on a nymphalid butterfly (Kelly and Debinski 1998) which suggests that host plant abundance may correlate positively with the body size of the species. Also, a latitudinal gradient in the body size of butterflies has been observed across Europe (Nylin and Svard 1991, Nylin et al. 1996). This suggests that there might be an effect of the range position on the body size of the butterflies.

Methods

The data on Finnish butterflies and larval host plants are based on literature (Marttila et al. 1990, Lahti et al. 1995, Hämet-Ahti et al. 1998, Huldén et al. 2000). A total of 116 species of butterflies has been recorded from Finland (Kullberg et al. 2002). In the present paper, we included 95 butterfly species, classified as resident or fluctuating, excluding the species which are classified as migratory, irruptive or extinct (Huldén et al. 2000). Appendix 1 gives the species-specific values of life-history and ecological variables.

Niche breadth

We estimated the niche breadth of each butterfly species using two different measures: larval host plant specificity and adult habitat breadth, i.e. the number of habitat types adults occupy. From the analyses involving niche breadth we excluded the species which only occur in northern Finland (n = 14, Marttila et al. 1990). This was done because their larval host plants are unknown or are not confirmed, but also because the habitat types in northern Finland do not fit the division of habitat types in the rest of Finland. The data on larval host plant specificity in Finland are based on Huldén et al. (2000) and Wahlberg (2000). We classified the larval host plant specificity into three classes: (1) monophagous species (feed on a single plant species), (2) oligophagous species (restricted to one genus of food plants) and (3) poly-

phagous species (feed on at least one family of food plants). The habitats occupied by adult butterflies have been categorised into four main types (Marttila et al. 1990): (1) uncultivable lands (e.g. edge zones beside industrial area, harbour and storage areas, loading places, uncropped fields and other unbuilt areas, which have been exposed to heavy human impact, (2) meadows (many kinds of open fields under natural state), (3) forest edges, and (4) bogs. We estimated the adult habitat breadth as the number of habitat types occupied, value one representing specialist species (one habitat type), value two representing intermediate species (two habitat types) and value three representing generalist species (three or four habitat types). As there were only two species (*Pieris napi* L. and *Gonepteryx rhamni* L.) that occupied all four habitat types, classes three and four were combined.

Resource availability

We estimated the resource availability for the butterflies with two measures: the distribution and the abundance of host plants. Only the monophagous butterfly species (n = 23) were included. The plant distribution data are based on the national floristic database (Lahti et al. 1995), which illustrates the plant distribution as the occupied 10-km grid squares on the Finnish national coordinate system; the authors of the atlas kindly provided us with the numerical data. Data on the abundance of plants is taken from Hämet-Ahti et al. (1998), in which the plant abundance is given as rare or common separately for each biogeographical province of Finland (n = 20). Each plant species was given a value of zero or one, indicating rare or common respectively, in each province. We then calculated the mean abundance for each plant species in Finland.

Range position

To determine the range position of the butterflies in Finland, we measured the distance between the northernmost distribution record and the southernmost point of Finland using maps included in Huldén et al. (2000). In our analysis, we included only the butterfly species, the distribution range of which overlap southern Finland. We excluded the species, which only occur in northern Finland (n = 14, Marttila et al. 1990), and *Lycaena helle*, the distribution of which is limited to central Finland, and *Clossiana thore thore*, which only occurs in eastern Finland. In our measure of range position, a small distance from the northernmost distribution record to the southernmost point of Finland indicates that the species is closer to the northern edge of its geographical distribution range.

Mobility

To estimate the mobility of butterfly species, we adopted the method described in Cowley et al. (2001a). We sent a questionnaire to experienced lepidopterists in Finland and asked them to give a "mobility index" (0–10) for each butterfly species. In the questionnaire, value zero indicated that a given butterfly species is extremely sedentary, while value ten means that a given butterfly species is extremely mobile. To obtain relative mobility value for each butterfly species, we calculated the average mobility index from the returned questionnaires (n = 13).

To be sure our measure of mobility is reliable we tested how our measure corresponds with the mobility indices estimated previously by Bink (1992, nine mobility classes), Pollard and Yates (1993, three mobility classes based on mark-release-recapture studies), Cowley et al. (2001a, continuous variable based on questionnaires) and Cook et al. (2001, continuous variable based on vagrancy in grids). The correlations between our measure and Bink's (1992), Pollard and Yates's (1993), Cowley et al.'s (2001a) and Cook et al.'s (2001) indices were strongly positive and significant ($r_p = 0.672$, n = 73, $P < 0.001$; $F_{3,27} = 8.74$, $r_p = 0.567$, $P < 0.001$; $r_p = 0.703$, n = 31, $P < 0.001$; and $r_p = 0.602$, n = 11, $P = 0.050$, respectively) indicating that our mobility index is in line with other independent estimates.

Length of flight period

The average length of the flight period (i.e. appearance on wing; d) for each butterfly species is based on Marttila et al. (1990). When the flight period of a given species was different in northern and southern Finland, we used the flight period in southern Finland. For butterfly species with two generations per year, we used the length of the flight period of the first generation because in many cases the second generation is facultative and also smaller in size. To get the length of the flight period for species with overwintering adults, we summed the flight periods of autumn and spring.

Body size

We used a wing span (mm) as a measure of butterfly body size (Niemelä et al. 1981, García-Barros 2000). Only female wing spans were used as there is a very strong positive correlation between female and male wing spans ($r_p = 0.98$, n = 95, $P < 0.001$). Wing span measurements for both sexes are based on Marttila et al. (1990), in which the mean of 20 individuals was given, with an exception of some rare species with fewer individuals measured.

Phylogenetic relatedness

Lack of statistical independence among species for the traits of interest was controlled for by using the method of phylogenetically independent contrasts (Harvey and Pagel 1991) as implemented in the CAIC program (Purvis and Rambaut 1995). Statistical control of phylogenetic non-independence requires knowledge of the phylogeny (Harvey and Pagel 1991, Freckleton et al. 2002). Knowledge of the general phylogenetic relationships among butterfly species is still in a state of flux (De Jong et al. 1996), and there are no studies available that look explicitly at the relationships of species in Finland. However, the recent surge of published studies on various groups of butterflies (De Jong et al. 1996, Martin et al. 2000, Wahlberg and Zimmermann 2000, Caterino et al. 2001, Wahlberg and Nylin 2003, Wahlberg et al. 2003) allowed Päivinen et al. unpubl. to compile a likely phylogeny for Finnish butterflies, which is also used in this study. In the analyses, all branch lengths were assumed equal because no estimate of evolutionary distance exist for the entire data-set. However, this option is justified under the assumption of punctuated evolution. In case of continuous variables, regression analysis was used to investigate the standardised linear contrasts calculated by CAIC (Harvey and Pagel 1991). Note that the regression lines must pass though the origin (Garland et al. 1992, Pagel 1992). See Table 1 for results after controlling for phylogenetic relatedness.

Statistical analysis

We used correlation, simple and multiple linear regressions and analysis of variance in analysing the data. Prior to analyses, natural logarithm transformation was applied on resource distribution, flight period and body

size. Analyses were conducted with the SPSS-programme (version 11.0).

Results

The effect of niche breadth, resource availability and range position on mobility

Niche breadth was estimated with two variables: larval specificity and adult habitat breadth. There was no interaction effect between larval specificity and habitat breadth on mobility (ANOVA, $F_{4,72} = 1.69$, $P = 0.162$), and the interaction term was removed from the analysis. Larval specificity had a significant effect on the mobility of butterflies ($F_{2,76} = 5.51$, $P = 0.006$, Fig. 1a). Monophagous butterfly species were less mobile than oligo- or polyphagous species (tukey multiple comparison test, mean difference (MD)$\pm$SE $= -1.62 \pm 0.62$, $P = 0.029$ and MD $= -1.40 \pm 0.49$, $P = 0.014$, respectively). However, there was no significant difference in the mobility between the oligo- and polyphagous species (MD $= -0.23 \pm 0.45$, $P = 0.872$). Adult habitat breadth had a significant effect on mobility ($F_{2,76} = 22.47$, $P < 0.001$, Fig. 1b) in that specialist butterfly species were less mobile than intermediate or generalist species (MD $= -1.55 \pm 0.41$, $P < 0.001$ and MD $= -3.04 \pm 0.48$, $P < 0.001$, respectively). Intermediate species were also less mobile than generalist species (MD $= -1.49 \pm 0.53$, $P = 0.017$).

Resource availability was estimated with two variables: resource distribution and resource abundance. We only included monophagous butterfly species, i.e. species where the larvae are feeding on a single food plant species. Resource distribution and resource abundance both had a positive effect on butterfly mobility when tested with simple linear regressions (Table 2). The

Table 1. Linear regression results between all variables after controlling for the phylogenetic non-independence. N is the number of independent contrasts. Resource availability is the first principal component of resource distribution and resource abundance.

| Dependent variable	Independent variable	n	Slope	r^2	P
Mobility	Larval specificity	14	0.126	0.542	0.002
Mobility	Habitat breadth	17	0.128	0.500	0.001
Mobility	Resource distribution	14	0.290	0.355	0.019
Mobility	Resource abundance	14	0.955	0.400	0.011
Mobility	Resource availability	14	0.277	0.383	0.014
Mobility	Range position	42	0.000	0.203	0.002
Flight period	Larval specificity	14	0.055	0.186	0.109
Flight period	Habitat breadth	17	0.070	0.307	0.017
Flight period	Resource distribution	14	0.045	0.019	0.622
Flight period	Resource abundance	14	0.110	0.012	0.697
Flight period	Resource availability	14	0.037	0.016	0.655
Flight period	Range position	42	0.000	0.206	0.002
Body size	Larval specificity	14	−0.019	0.110	0.225
Body size	Habitat breadth	17	−0.032	0.181	0.079
Body size	Resource distribution	14	0.015	0.005	0.799
Body size	Resource abundance	14	−0.020	0.001	0.917
Body size	Resource availability	14	0.005	0.001	0.935
Body size	Range position	42	0.000	0.048	0.160
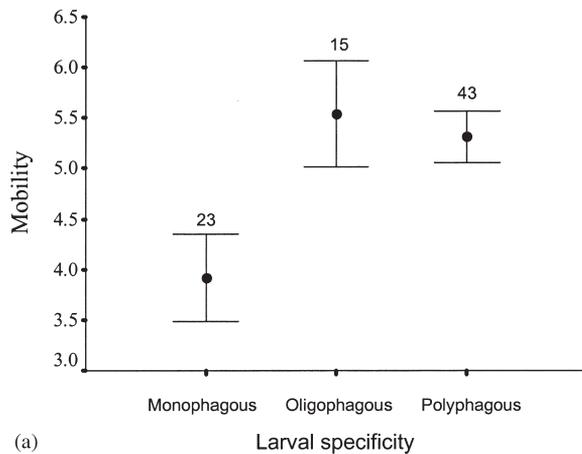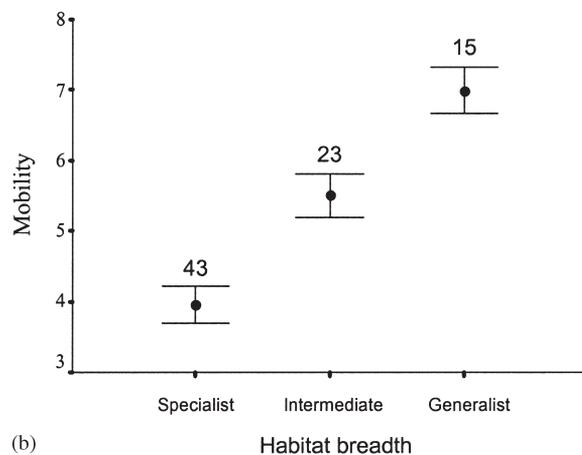
Fig. 1. (a) Mean mobility score $(0-10) \pm 1$ SE for the butterfly species with mono- (one plant species), oligo- (one genus) or polyphagous (one family) larvae. (b) Mean mobility score ± 1 SE in relation to the adult habitat breadth, i.e. the number of habitat types $(1-3)$ in which they occur. N gives the number of species in each category.

relationship between mobility, resource distribution and resource abundance is depicted in Fig. 2a. To partial out correlated effects of resource distribution and resource abundance, we analysed the multicollinearity between the two variables before proceeding with multiple regression. The multicollinearity statistics revealed a very strong collinearity between the resource distribution and resource abundance and over 93% of both variables were associated with the same condition index of 72.7. Because of multicollinearity the standard errors of

Table 2. Simple linear regressions. The dependent variable is the mobility index of the butterflies and independent variables are resource distribution and resource abundance.

	Slope ± 1 SE	df	t	P
Resource distribution	1.22 ± 0.48	21	2.76	0.012
Resource abundance	3.60 ± 1.27	21	2.82	0.010
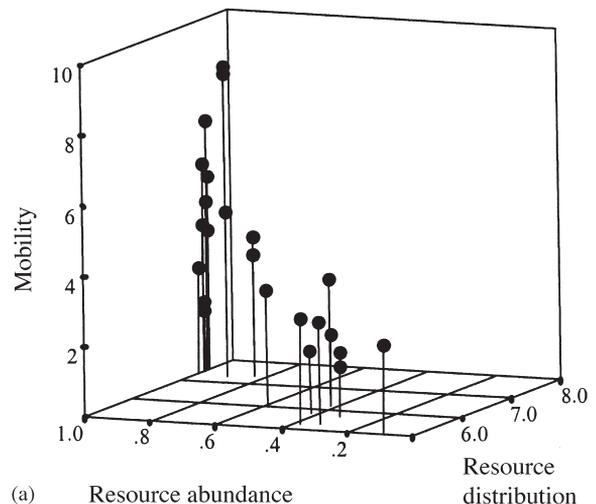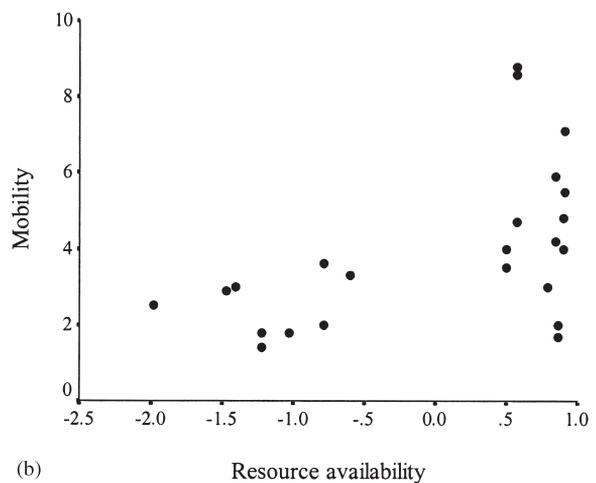
Fig. 2. (a) Mobility score for the monophagous butterfly species (n = 23) in relation to host plant abundance index (0 or 1; averaged over the twenty biogeographical provinces in Finland), and host plant distribution (number of occupied 10-km grid squares in Finland). Resource distribution is ln-transformed. Note that the axis of resource abundance increases from right to left. (b) Mobility score for the monophagous butterfly species in relation to resource availability. Resource availability is the first principal component of resource distribution and resource abundance.

multiple regression coefficients are inflated and the slopes drawn out of multiple regression are likely to be spurious. However, in order to include both independent variables in the same analysis and to obtain a single measure of resource availability, we extracted a principal component from resource distribution and resource abundance and then ran a simple linear regression between mobility and the first principal component. The first principal component explained 98.6% of the total variance, and both resource distribution and resource abundance were strongly, positively correlated with it (r = 0.993 for both). Linear regression between
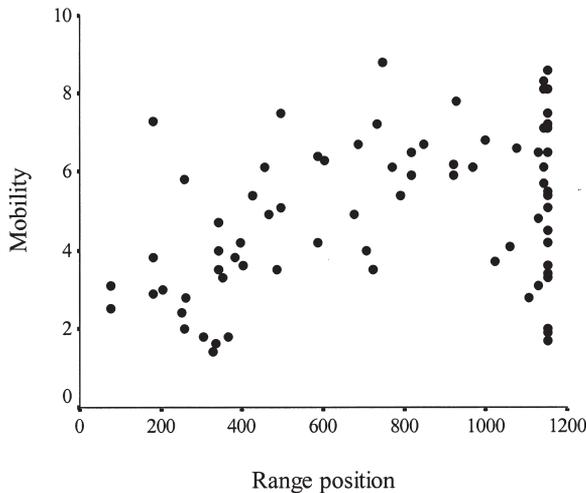
Fig. 3. Mobility score (0–10) for the butterfly species (n = 79) in relation to the range position, measured as a distance between the northernmost distribution record and southernmost point of Finland.
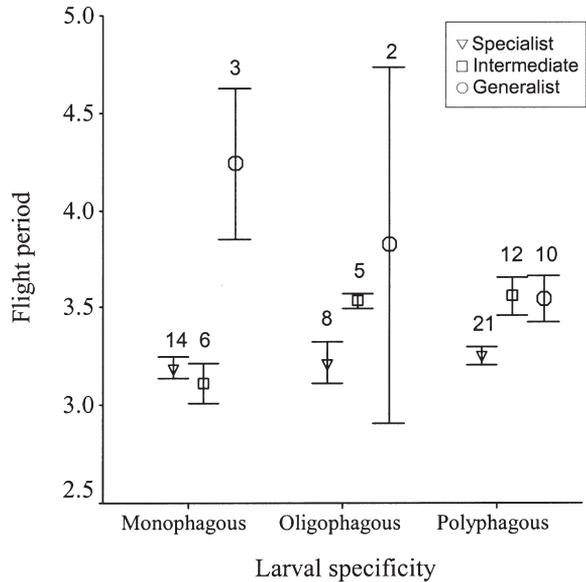

Fig. 4. The relationship between the length of the flight period, larval specificity and adult habitat breadth. See Fig. 1 for variable definitions.

the mobility of butterflies and the first principal component revealed that there was a positive relationship between mobility and resource availability (slope $\pm$ SE = 1.10 $\pm$ 0.39, t = 2.82, df = 21, P = 0.010, Fig. 2b).

There was a significant, positive relationship between range position and mobility, such that species closer to the northern edge of their geographical range were less mobile than species further away from the northern range edge (r_p = 0.42, n = 79, P < 0.001, Fig. 3). Controlling for phylogenetic relatedness did not change these results (Table 1).

The effect of niche breadth, resource availability and range position on the length of the flight period

There was a significant interaction effect between larval specificity and adult habitat breadth on the length of the flight period ($F_{4,72}$ = 4.68, P = 0.002). However, the sample size was small for habitat generalists that have mono- or oligophagous larvae, i.e. for the groups that seemed to cause the observed interaction (Fig. 4). For this reason, in order to determine whether larval specificity and adult habitat breadth have main effects on the length of the flight period, we analysed them separately. There was no effect of larval specificity on the flight period length ($F_{2,78}$ = 0.51, P = 0.600, Fig. 5a), whereas adult habitat breadth had an effect on the length of the flight period ($F_{2,78}$ = 11.41, P < 0.001, Fig. 5b). Specialist and intermediate butterfly species had shorter flight period than generalist species (MD = −0.49 $\pm$ 0.11, P < 0.001 and MD = −0.28 $\pm$ 0.12, P = 0.048, respectively), but there was no significant difference between specialist and intermediate species (MD = −0.21 $\pm$ 0.09, P = 0.057).

Resource distribution and resource abundance had no effect on the length of the flight period when tested with simple linear regressions (Table 3). Due to the multicollinearity between the two independent variables, we analysed the common effect of resource availability with a principal component extracted from the relationship between resource distribution and resource abundance (see above). Still, resource availability had no effect on the flight period length of the butterflies (slope $\pm$ SE = 0.107 $\pm$ 0.10, t = 1.07, df = 21, P = 0.295).

Range position was positively related to the length of the flight period (r_p = 0.35, n = 79, P < 0.002). Species closer to the northern edge of their geographical range had shorter flight period than species further away from the edge (Fig. 6). Controlling for phylogenetic relatedness did not change these results (Table 1).

The effect of niche breadth, resource availability and range position on body size

In general, we found very little evidence that body size of the butterflies would be influenced by any of the factors studied. There was no interaction between larval specificity and habitat breadth on the body size of butterflies ($F_{4,72}$ = 1.00, P = 0.412), and we removed the interaction term from the final test. Initially, larval specificity seemed to be related to the body size ($F_{2,76}$ = 5.72, P = 0.005), but this effect was removed after controlling for the phylogeny (Table 1). Habitat breadth had no effect on the body size of the butterflies ($F_{2,76}$ = 1.76, P = 0.179).

46
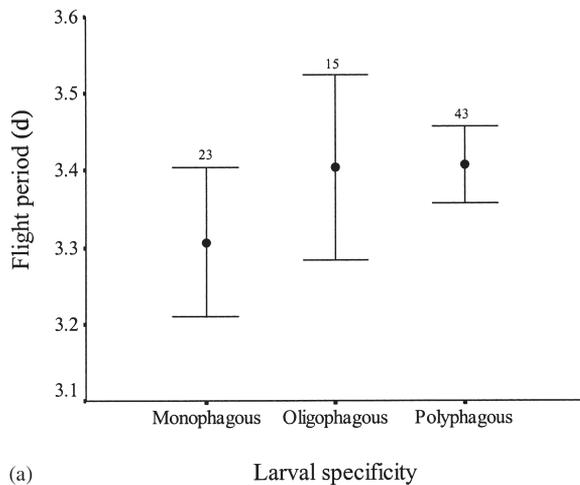
(a)

Larval specificity
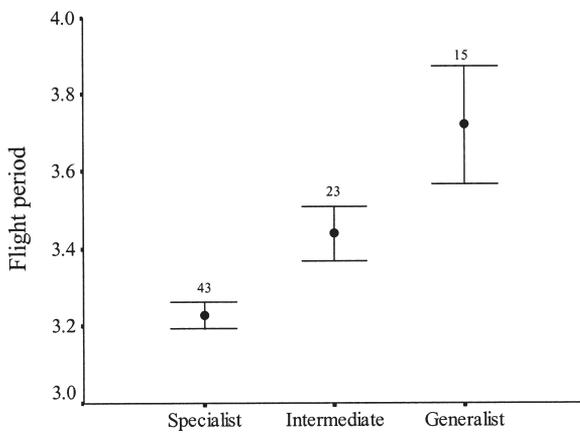
(b)

Habitat breadth

Fig. 5. (a) The mean length of the flight period d ± 1 SE for the butterfly species with mono- (one plant species), oligo- (one genus) or polyphagous (one family) larvae. (b) The mean flight period length ± 1 SE in relation to adult habitat breadth, i.e. the number of habitat types (1–3) in which they occur. The length of the flight period is ln-transformed and n gives the number of species in each category.

In simple linear regressions, we found no effect of resource availability on the size of the butterflies: neither resource distribution nor resource abundance affected body size (Table 4). Similarly, there was no effect of the principal component of resource availability on the body size ($r_p = -0.16$, $n = 23$, $P = 0.481$). There was no relationship between body size and range position ($r_p = -0.10$, $n = 79$, $P = 0.383$).

Table 3. Simple linear regressions. The dependent variable is the length of the flight period and independent variables are resource distribution and resource abundance.

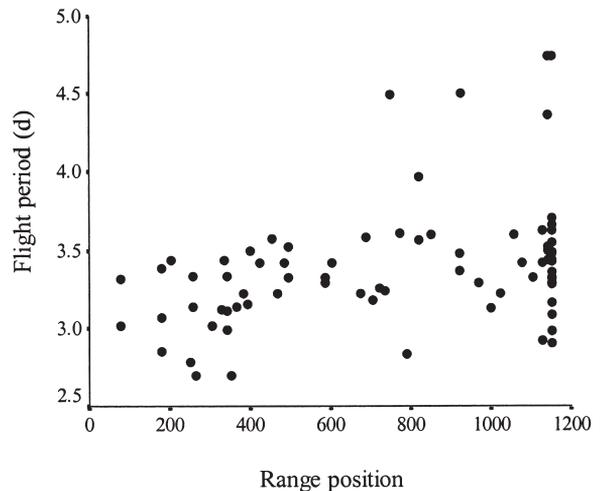|	Slope ± 1 SE	df	t	P
Resource distribution	0.125 ± 0.11	21	1.12	0.277
Resource abundance	0.33 ± 0.33	21	1.02	0.321

Range position

Fig. 6. The length of the flight period (d; ln-transformed) for the butterfly species (n = 79) in relation to the range position, measured as a distance between the northernmost distribution record and southernmost point of Finland.

Table 4. Simple linear regressions. The dependent variable is the body size and independent variables are resource distribution and resource abundance.

	Slope ± 1 SE	df	t	P
Resource distribution	− 5.51 ± 0.76	21	− 0.72	0.479
Resource abundance	− 0.16 ± 0.22	21	− 0.71	0.488

Discussion

Our main result is that niche breadth, resource availability and range position all are related to the mobility of butterflies. This indicates that species with narrow niche breadth in terms of larval feeding specificity or adult habitat breadth, are less mobile than species with wider niche breadth. Resource availability had a similar effect: species with low resource availability, measured as resource distribution or resource abundance, were less mobile than species with high resource availability. Finally, range position was related to the mobility such that the species that were closer to the northern edge of their geographical range were less mobile than species further away from the edge. These results lend support to Shreeve's (1992) hypothesis that specialist butterfly species should rarely move outside the habitat patch in which their larval food resources are located, while species with less specialised requirements may be more mobile (Hanski and Kuussaari 1995).

We suggest that there may be a common denominative behind the results: restricted niche breadth, low resource availability and being on the edge of the geographical distribution range are all likely to increase the dispersing individuals' hazard of failing to find a new suitable habitat patch. If mobility is at least partially determined by additive genetic variance, and dispersing individuals

do not enjoy reproductive success due to their unsuccessful location of a new habitat patch, there will be strong selection against high mobility (Hamilton and May 1977). Such negative selection on mobility could be responsible for the observed pattern of low mobility among specialist and edge species.

We found out that the length of the flight period was related to the niche breadth and range position, while there seemed to be no relationship between the length of the flight period and resource availability. However, our analysis on the effect of resource availability was restricted to monophagous butterfly species, which may well have underscored the link with flight period. From our two measures of niche breadth, larval specificity had no main effect, while adult habitat breadth had a positive effect on the length of the flight period. Interestingly, however, the length of the flight period was influenced by an interaction between larval specificity and adult habitat breadth: some of the most specialised species in terms of their larval feeding specificity, which at the same time were habitat generalists as adults, had the longest flight period. Even though very interesting, this finding must be interpreted with caution, because the sample size in the groups causing the interaction was very small and thus the true effect size is likely to be overestimated (Kotiaho and Tomkins 2002, Tomkins and Kotiaho 2004). Range position was related to the length of the flight period such that the species closest to the northern edge of their geographical range had the shortest flight period.

Length of the flight period of a butterfly species can reflect the average longevity or life span of an individual, or variance in the timing of hatching and consequently appearance on wing. Accurate information on adult longevity in wild populations of butterflies is extremely difficult to obtain. However, based on mark-release-recapture studies, the average residence time for many butterfly species has been estimated to be less than 10 days (Warren 1992). Because of dispersal, however, residence time based on mark-release-recapture studies must generally be an underestimate of the adult life span. However, as there seems to be no relationship between residence time (data from Warren 1992) and our estimate of butterfly mobility ($r_p = -0.104$, $n = 12$, $P = 0.748$), residence time may be used as an unbiased, albeit, underestimate of adult life span. In our data, the average length of the adult flight period was about four weeks. Thus, it is likely that the length of the flight period is more determined by hatching asynchrony than adult life span.

The species with narrow niche breadth and particularly the species close to the northern edge of their geographical distribution range both had a shorter flight period than the species with wider niche breadth and species further away from the range edge. This may be explained by lower environmental variance in growth conditions, resulting in lower variance in hatching synchrony (Pollard et al. 1986, Pollard 1991, García-Barros 2000). Metapopulation theory suggests that if patches are more isolated towards range edges, only the largest or best quality patches will be occupied (Hanski 1999). Thus, environmental variation (e.g. microclimate, food-plant availability) could be smaller in such high quality patches at the edge of the distribution range resulting in greater hatching synchrony in comparison with the species that are further away from the edge that also inhabit poor quality patches.

We found no evidence that body size of butterflies would be related to niche breadth, resource availability or range position. In Lepidoptera there are some reports of a positive association between the niche breadth and body size such that polyphagous species tend to be larger (Niemelä et al. 1981, Inkinen 1994, Lindström et al. 1994, Loder et al. 1998), but it seems that such pattern is not general for butterflies (García-Barros 2000).

Our results demonstrate that niche breadth, resource availability and range position play a role in determining the mobility, but have no effect on the body size of the butterflies. Shorter flight period in the species with narrow niche breadth and in the species at the northern edge of their distribution range is likely to represent differences in hatching synchrony due to lower environmental variance in their growth conditions. We conclude that studies on the relationships between species-specific ecological variables and life-history characteristics in a distribution-abundance relationship framework are needed to enable us to understand the ultimate factors driving any particular distribution-abundance relationship. In Finnish butterflies, there is an unusual negative distribution-abundance relationship, which is likely to be partially driven by the differences in butterfly mobility (Päivinen et al. unpubl.). Thus, explaining the variance in butterfly mobility may aid in explaining the variance in distribution-abundance relationships.

References

Baker, R. R. 1969. The evolution of the migratory habit in butterflies. – J. Anim. Ecol. 38: 703–746.

Bink, F. A. 1992. Ecologische atlas van de dagvlinders van Nordwest-Europa. – Haarlem, Schuyt.

Bock, C. E. and Ricklefs, R. E. 1983. Range size and local abundance of some North American songbirds: a positive correlation. – Am. Nat. 122: 295–299.

Brändle, M., Öhlschläger, S. and Brandl, R. 2002. Range sizes in butterflies: correlation across scales. – Evol. Ecol. Res. 4: 993–1004.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Caterino, M. S., Reed, R. D., Kuo, M. M. et al. 2001. A partitioned likelihood analysis of swallowtail butterfly phylogeny (Lepidoptera: Papilionidae). – Syst. Biol. 50: 106–127.

Cook, L. M., Dennis, R. L. H. and Hardy, P. B. 2001. Butterfly-hostplant fidelity, vagrancy and measuring mobility from distribution maps. – Ecography 24: 497–504.

Cowley, M. J. R., Thomas, C. D., Roy, D. B. et al. 2001a. Density-distribution relationships in British butterflies. I. The effect of mobility and spatial scale. – J. Anim. Ecol. 70: 410–425.

Cowley, M. J. R., Thomas, C. D., Wilson, R. J. et al. 2001b. Density-distribution relationships in British butterflies. II. An assessment of mechanisms. – J. Anim. Ecol. 70: 426–441.

De Jong, R., Vane-Wright, R. I. and Ackery, P. R. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. – Entomol. Scand. 27: 65–101.

Dempster, J. P. 1989. Insect introductions: natural dispersal and population persistence in insects. – Entomologist 108: 5–13.

Dennis, R. L. H. 1982. Observations on habitats and dispersion made from oviposition markers in north Cheshire Anthocharis cardamines (Lepidoptera: Pieridae). – Entomol. Gaz. 33: 151–159.

Dennis, R. L. H. and Shreeve, T. G. 1996. Butterflies on British and Irish offshore islands: ecology and biogeography. – Gem Publishing Comp.

Dennis, R. L. H, Donato, R., Sparks, T. H. et al. 2000. Ecological correlates of island incidence and geographical range among British butterflies. – Biodiv. Conserv. 9: 343–359.

Freckleton, R. P., Harvey, P. H. and Pagel, M. P. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

García-Barros, E. 2000. Body size, egg size, and their Interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). – Biol. J. Linn. Soc. 70: 251–284.

Garland, T. Jr., Harvey, P. H. and Ives, A. R. 1992. Procedures for the analysis of comparative data using independent contrasts. – Syst. Biol. 41: 18–32.

Gaston, K. J. and Blackburn, T. M. 2000. Pattern and process in macroecology. – Blackwell Science.

Gaston, K. J., Blackburn, T. M. and Lawton, J. H. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. – J. Anim. Ecol. 66: 579–601.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. et al. (eds) 1998. Retkeilykasvio (Field flora of Finland), Finn. Mus. Nat. Hist., Bot. Mus. Helsinki, Finland.

Hamilton, W. D. and May, R. M. 1977. Dispersal in stable habitats. – Nature 269: 578–581.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. – Oikos 38: 210–221.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hanski, I. and Kuussaari, M. 1995. Butterfly metapopulation dynamics. – In: Cappuccino, N. and Price, P. (eds), Population dynamics: new approaches and synthesis. Academic Press, pp. 149–171.

Hanski, I., Kouki, J. and Halkka, A. 1993. Three explanations of the positive relationship between distribution and abundance of species. – In: Ricklefs, R. E. and Schluter, D. (eds), Community diversity: historical and geographical perspectives. Chicago Univ. Press, pp. 108–116.

Harvey, P. H. and Pagel, M. D. 1991. The comparative method in evolutionary biology. – Oxford Univ. Press.

Hengeveld, R. and Haeck, J. 1982. The distribution of abundance. I. Measurements. – J. Biogeogr. 9: 303–316.

Huldén, L., Albrecht, A., Itämies, J. et al. 2000. Atlas of Finnish Macrolepidoptera. – Lepidopterol. Soc. Finland, Finn. Mus. Nat. Hist., Helsinki, Finland.

Inkinen, P. 1994. Distribution and abundance in British noctuid moths revisited. – Ann. Zool. Fenn. 31: 235–243.

Johnson, C. N. 1998. Species extinction and the relationship between distribution and abundance. – Nature 394: 272–274.

Kelly, L. and Debinski, D. M. 1998. Relationship of host plant density to size and abundance of the regal fritillary Speyeria idalia drury (Nymphalidae). – J. Lepidopt. Soc. 52: 262–276.

Kotiaho, J. S. and Tomkins, J. L. 2002. Meta-analysis, can it ever fail? – Oikos 96: 551–553.

Kullberg, J., Albrecht, A., Kaila, L. et al. 2002. Checklist of Finnish Lepidoptera. – Sahlbergia 6: 45–190.

Kuussaari, M., Nieminen, M. and Hanski, I. 1996. An experimental study of migration in the Glanville fritillary butterfly Melitaea cinxia. – J. Anim. Ecol. 65: 791–801.

Lahti, T., Lampinen, R. and Kurtto, A. 1995. Atlas of the distribution of vascular plants in Finland. Computer Version 2.0. – Univ. of Helsinki, Finn. Mus. Nat. Hist., Bot. Mus., Helsinki, Finland.

Lawton, J. H. 1993. Range, population abundance and conservation. – Trends Ecol. Evol. 8: 409–413.

Loder, N., Gaston, K. J., Warren, P. H. et al. 1998. Body size and feeding specificity: macrolepidoptera in Britain. – Biol. J. Linn. Soc. 63: 121–139.

Lindström, J., Kaila, L. and Niemelä, P. 1994. Polyphagy and adult body size in geometrid moths. – Oecologia 98: 130–132.

Martin, J.-F., Gilles, A. and Descimon, H. 2000. Molecular phylogeny and evolutionary patterns of the European satyrids (Lepidoptera: Satyridae) as revealed by mitochondrial gene sequences. – Mol. Phylogenet. Evol. 15: 70–82.

Marttila, O., Haahtela, T., Aarnio, H. et al. 1990. Suomen päiväperhoset (The Finnish butterflies), Kirjayhtymä, Helsinki, Finland.

Murphy, D. D. and White, R. R. 1984. Rainfall, resources, and dispersal in southern populations of Euphydryas editha (Lepidoptera: Nymphalidae). – Pan-Pacific Entomol. 60: 350–354.

Niemelä, P., Hanhimäki, S. and Mannila, R. 1981. The relationship of adult size in noctuid moths (Lepidoptera: Noctuidae) to breadth of diet and growth form of host plants. – Ann. Entomol. Fenn. 47: 17–20.

Nylin, S. and Svard, L. 1991. Latitudinal patterns in the size of European butterflies. – Holarct. Ecol. 14: 192–202.

Nylin, S., Gotthard, K. and Wiklund, C. 1996. Reaction norms for age and size at maturity in Lasiommata butterflies: predictions and tests. – Evolution 50: 1351–1358.

Pagel, M. D. 1992. A method for the analysis of comparative data. – J. Theor. Biol. 156: 431–442.

Pollard, E. 1991. Changes in the flight period of the hedge brown butterfly Pyronia tithonus during range expansion. – J. Anim. Ecol. 60: 737–748.

Pollard, E. and Yates, T. J. 1993. Monitoring butterflies for ecology and conservation. – Chapman & Hall.

Pollard, E. and Greatorex-Davies, J. N. 1997. Flight-periods of the small heath butterfly, Coenonympha pamphilus (Linnaeus) (Lepidoptera: Nymphalidae, Satyrinae) on chalk downs and in woodland in southern England. – Entomol. Gaz. 48: 3–7.

Pollard, E., Hall., M. L. and Bibby, T. J. 1986. Monitoring the abundance of butterflies 1976–1985. – Research and survey in nature conservation series. No. 2. Nature Conservancy Council, Peterborough.

Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. – Computer Appl. Biosci. 11: 247–251.

Roff, D. A. 1992. The evolution of life histories: theory and analyses. – Chapman & Hall.

Roff, D. A. 2002. Life history evolution. – Sinauer.

Shreeve, T. G. 1992. Monitoring butterfly movements. – In: Dennis, R. L. H. (ed.), The ecology of butterflies in Britain. Oxford Univ. Press, pp. 120–138.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Thomas, J. A. 1993. Holocene climate change and warm man-made refugia may explain why a sixth of British butterflies inhabit unnatural early successional habitats. – Ecography 16: 278–284.

Thomas, J. A., Rose, R. J., Clarke, R. T. et al. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. – Funct. Ecol. 13 (Suppl. 1): 55–64.

Tomkins, J. L. and Kotiaho, J. S. 2004. Publication bias in meta-analysis: seeing the wood for the trees, Oikos 104: 194–196.

Wahlberg, N. 2000. Comparative descriptions of the immature stages and ecology of five Finnish melitaeine butterfly species (Lepidoptera: Nymphalidae). – Entomol. Fenn. 11: 167–174.

Wahlberg, N. and Zimmermann, M. 2000. Pattern of phylogenetic relationships among members of the tribe Melitaeini (Lepidoptera: Nymphalidae) inferred from mtDNA sequences. – Cladistics 16: 347–363.

Wahlberg, N. and Nylin, S. 2003. Morphology versus molecules: resolution of the positions of *Nymphalis*, *Polygonia* and related genera (Lepidoptera: Nymphalidae). – Cladistics 19: 213–223.

Wahlberg, N., Weingartner, E. and Nylin, S. 2003. Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). – Mol. Phylogenet. Evol. 28: 473–484.

Warren, M. S. 1992. Butterfly populations. – In: Dennis, R. L. H. (ed.), The ecology of butterflies in Britain. Oxford Univ. Press, pp. 73–92.

White, R. R. and Levin, M. P. 1981. Temporal variation in vagility: implications for evolutionary studies. – Am. Nat. 105: 348–357.

Appendix 1. Range position, larval specificity, habitat breadth, larval host plant, host plant distribution, host plant abundance, mobility, body size and flight period. See the main text for variable descriptions.

FAMILY/species name (*species occurs only in northern Finland)	Range position (km)	Larval specificity	Habitat breadth	Larval host plant	Distribution of host plant	Abundance of host plant	Mobility score	Body size (mm)	Flight period (d)
HESPERIIDAE									
Pyrgus malvae	586	3	2				4.2	22.7	27.8
Pyrgus alveus	383	3	2				3.8	28.2	25.1
Pyrgus andromedae*							2.3	29.2	17.0
Pyrgus centaureae	1154	1	1	Rubus chamaemorus	1732	1.00	1.7	29.2	26.9
Carterocephalus palaemon	1023	3	1				3.7	27.2	25.1
Carterocephalus silvicola	789	3	1				5.4	25.1	17.0
Thymelicus lineola	604	3	3				6.3	25.5	30.5
Hesperia comma comma	466	3	1				4.9	30.6	25.1
Ochlodes sylvanus	688	3	3				6.7	29.9	35.9
PAPILIONIDAE									
Parnassius apollo	401	1	1	Sedum telephium	494	0.43	3.6	81.4	33.0
Parnassius mnemosyne	203	1	1	Corydalis solida	192	0.38	3.0	59.3	31.1
Papilio machaon	1154	3	3				8.1	80.5	26.7
PIERIDAE									
Leptidea sinapis	1142	3	1				5.7	38.3	33.0
Aporia crataegi	999	3	1				6.8	62.7	22.9
Pieris napi	1154	3	4				7.5	40.2	40.7
Anthocharis cardamines	1142	3	3				7.1	39.5	31.1
Colias palaeno	1154	1	1	Vaccinium uliginosum	1866	1.00	7.1	47.8	31.1
Colias hecla*							3.3	42.8	10.8
Colias tyche*							3.3	42.3	14.0

Appendix (*Continued*)

FAMILY/species name (*species occurs only in northern Finland)	Range position (km)	Larval specificity	Habitat breadth	Larval host plant	Distribution of host plant	Abundance of host plant	Mobility score	Body size (mm)	Flight period (d)
Gonepteryx rhamni	1142	2	4				8.3	49.8	114.4
LYCAENIDAE									
Thecla betulae	341	1	2	*Prunus padus*	1511	0.83	4.0	35.5	19.8
Favonius quercus	179	1	2	*Quercus robur*	200	0.33	2.9	30.6	17.3
Satyrium w-album	78	1	1	*Ulmus glabra*	159	0.10	2.5	30.0	27.5
Satyrium pruni	341	1	2	*Prunus padus*	1511	0.83	3.5	32.3	22.4
Callophrys rubi	1154	3	2				6.5	23.9	40.7
Lycaena phlaeas	1154	2	3				5.1	27.7	18.3
Lycaena helle		1	1	*Bistorta vivipara*	1528	1.00	3.0	24.6	20.3
Lycaena virgaureae	921	1	3	*Rumex acetosella*	1673	1.00	5.9	25.9	32.5
Lycaena hippothoe	1154	1	1	*Rumex acetosella*	1673	1.00	4.2	31.3	27.5
Cupido minimus	335	3	1				1.6	23.0	31.0
Celastrina argiolus	1130	3	2				6.5	26.3	37.4
Scolitantides vicrama	329	1	1	*Thymus serpyllum*	308	0.33	1.4	23.7	22.6
Scolitantides orion	257	1	1	*Sedum telephium*	494	0.43	2.0	27.1	23.1
Glaucopsyche alexis	724	3	2				3.5	28.8	25.9
Glaucopsyche arion	365	1	1	*Thymus serpyllum*	308	0.33	1.8	35.9	23.1
Plebeius argus	819	3	2				6.5	23.0	53.1
Plebeius idas	1154	3	2				6.5	24.6	38.8
Aricia artaxerxes	1059	2	1				4.1	28.1	36.5
Aricia nicias	706	1	1	*Geranium sylvaticum*	1839	1.00	4.0	25.4	24.0
Aricia eumedon	1130	1	2	*Geranium sylvaticum*	1839	1.00	4.8	28.1	18.5
Albulina optilete	1154	1	2	*Vaccinium uliginosum*	1866	1.00	5.5	25.9	32.3
*Agriades glandon**							2.0	23.2	10.6
Polyommatus semiargus	921	3	2				6.2	28.8	29.1
Polyommatus amandus	771	3	3				6.1	31.4	37.0
Polyommatus icarus	1142	3	1				6.1	28.5	33.7
NYMPHALIDAE									
Apatura iris	257	2	1				5.8	72.7	28.0
Limenitis populi	736	2	1				7.2	78.8	25.4
Nymphalis antiopa	1142	3	2				8.1	66.5	78.8
Nymphalis io	748	1	3	*Urtica dioica*	1402	0.90	8.8	54.0	89.6

FAMILY/species name (*species occurs only in northern Finland)	Range position (km)	Larval specificity	Habitat breadth	Larval host plant	Distribution of host plant	Abundance of host plant	Mobility score	Body size (mm)	Flight period (d)
Nymphalis urticae	1154	1	3	*Urtica dioica*	1402	0.90	8.6	47.3	114.4
Nymphalis c-album	927	3	3				7.8	45.8	90.2
Araschnia levana	341	1	2	*Urtica dioica*	1402	0.90	4.7	35.1	28.0
Argynnis paphia	455	2	2				6.1	61.8	35.7
Argynnis laodice	179	2	2				7.3	56.4	29.6
Argynnis aglaja	1154	2	1				7.2	53.1	30.9
Argynnis niobe	425	2	1				5.4	50.6	30.5
Argynnis adippe	496	2	2				7.5	53.6	34.0
Issoria lathonia	819	2	2				5.9	44.7	35.3
Brenthis ino	849	3	2				6.7	37.7	36.6
*Boloria napaea**							2.9	38.9	13.1
Boloria aquilonaris	1154	3	1				3.6	34.7	34.8
Boloria eunomia	1154	3	2				3.3	37.2	28.7
Boloria selene	1154	2	2				6.5	36.6	37.5
Boloria freija	1154	2	1				1.9	37.1	18.3
*Boloria polaris**							2.9	41.1	12.2
Boloria thore thore		2	1				2.0	44.3	22.6
Boloria frigga	1154	1	1	*Rubus chamaemorus*	1732	1.00	2.0	42.0	21.8
*Boloria improba**							1.8	34.0	14.8
Boloria titania	263	2	1				2.8	41.0	14.8
Boloria euphrosyne	1154	3	3				7.5	37.3	23.5
*Boloria chariclea**							3.7	38.4	10.5
Melitaea cinxia	78	3	1				3.1	48.5	20.3
Melitaea diamina	305	1	1	*Valeriana sambucifolia*	325	0.43	1.8	36.9	20.3
Melitaea athalia	1154	3	1				5.4	35.3	30.9
Euphydryas maturna	496	3	1				5.1	41.8	27.8
*Euphydryas iduna**							3.3	41.2	9.4
Euphydryas aurinia	353	1	1	*Succisa pratensis*	418	0.6	3.3	38.0	14.9
Hipparchia semele	179	3	1				3.8	49.5	21.5
Erebia ligea	1154	3	1				6.5	41.4	32.7
*Erebia medusa**							3.9	38.6	8.1
*Erebia disa**							3.3	44.7	9.9
Erebia embla	1154	3	1				3.4	46.9	19.7

Appendix (*Continued*)

FAMILY/species name (*species occurs only in northern Finland)	Range position (km)	Larval specificity	Habitat breadth	Larval host plant	Distribution of host plant	Abundance of host plant	Mobility score	Body size (mm)	Flight period (d)
*Erebia pandrose**							4.2	39.6	17.9
*Oeneis norna**							3.2	47.2	16.1
*Oeneis bore**							2.9	44.4	17.9
Oeneis jutta	1130	3	1				3.1	53.2	30.5
Maniola jurtina	484	3	1				3.5	43.9	30.5
Aphantopus hyperantus	1076	3	3				6.6	38.9	30.5
Coenonympha pamphilus	1154	3	3				4.5	28.5	27.8
Coenonympha tullia	1106	3	1				2.8	31.6	27.8
Coenonympha glycerion	676	3	1				4.9	30.2	25.1
Pararge aegeria	395	3	1				4.2	40.7	23.3
Lasiommata maera	586	3	1				6.4	46.5	26.9
Lasiommata petropolitana	969	3	2				6.1	37.5	26.9
Lopinga achine	251	3	1				2.4	44.9	16.1