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Dispersal patterns of endemic alpine butterflies with contrasting population structures: *Erebia epiphron* and *E. sudetica*

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Abstract We studied population sizes and mobility of *Erebia epiphron* and *Erebia sudetica*, two high mountain butterflies forming endemic subspecies in the Hrubý Jeseník Mountains, Czech Republic. *E. epiphron* formed two continuous populations containing $\approx 100,000$ and $\approx 4,500$ individuals on alpine grasslands. The butterflies moved freely within their habitats, but movements between the two populations were highly unlikely. *E. sudetica* formed a system of colonies at timberline sites on valley headwalls and in forest clearings. Two such colonies studied in detail contained $\approx 4,500$ and ≈ 450 adults and were interconnected by limited dispersal. The negative exponential function and the sigmoid function (this assumes flat decrease of movements over short distances) were superior to the inverse power function in fitting mobility data for both species. For *E. sudetica*, the functions describing movements within a habitat differed significantly from total movements, suggesting different behaviours of dispersing individuals. The habitats of *E. epiphron* are uniform and highly isolated, favouring free within-habitat mobility but prohibiting leaving their boundaries. The habitats of *E. sudetica* are diverse and disturbance-dependent; leaving such habitats is less

risky, and a source-sink model may explain the persistence of the species in the mountains.

Keywords Lepidoptera · Satyrinae · Dispersal · Metapopulation · Source-sink · Mountain environment

Introduction

The majority of recent studies of butterfly mobility has been conducted within the context of the metapopulation paradigm, which assumes that dynamics of colonisation and extinction within networks of habitat patches influence the long-term persistence of species (e.g. Kuussaari et al. 1998; Gutierrez et al. 1999; Hanski 1999; Petit et al. 2001). The appeal of the paradigm somehow limited the interests of researchers to situations when a species depends on well-defined habitat fragments scattered within an uninhabitable matrix (e.g. Thomas et al. 1992; Neve et al. 1996; Wahlberg et al. 1996, 2002). However, not all butterflies exhibit this specific population structure. For instance, widespread species may persist in their areas of distribution in single “densely packed” populations, whereas extremely restricted species may be limited to colonies that do not communicate with other such colonies. The spatial arrangements of animal populations are better viewed as continua (Sutcliffe et al. 1997; Brommer and Fred 1999); the observed patterns tend to be scale-dependent (Thomas and Kunin 1999; Menendez and Thomas 2000), and even populations of related species may exhibit diverse spatial structures.

Among butterflies that are of obvious conservation interest are taxa with highly restricted endemic distribution (Van Swaay and Warren 1999). In temperate Europe, several such taxa inhabit isolated “sky islands” on mountains. The population biology of these species is little studied, often due to technical difficulties with work in mountain areas (cf. Ravenscroft and Warren 1996). This may seriously hinder future conservation efforts: to

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highlight just one point, the organisms that are restricted to insular mountain habitats might be those most threatened by recent climate change (Hill et al. 2002).

We analysed dispersal patterns of two high mountain butterflies that occur as endemic subspecies in an insular mountain area, Hrubý Jeseník Mountains (Czech Republic), and whose populations differ in habitat use and spatial distribution. *Erebia epiphron silesiana* (Meyer et Dur, 1852) inhabits contiguous areas of alpine grasslands, whereas *Erebia sudetica sudetica* Staudinger, 1861 forms clearly defined colonies near the timberline (Kuras et al. 2001c). We provide background demography information on the two species, based on a mark-release-recapture study. Then, we assess their mobility patterns using three simple models recently applied in studies of butterfly dispersal: the negative exponential function, the inverse power function (Hill et al. 1996; Baguette et al. 2000) and a sigmoid function proposed by Heinz et al. (2003). We analyse the suitability of the three models with respect to differences in population structures of the two butterflies, asking how the mobility parameters reflect differences in population size and distribution. Finally, we synthesise the findings with available information on habitat selection and life history of the two butterflies, attempting to interpret the causes of their restricted distribution.

Materials and methods

Study sites

The Eastern Sudetens, part of the Hercynian system, is a middle-altitude mountain chain in the northeastern part of the Czech Republic. The Hrubý Jeseník Mountains (Mt. Praděd: 50°20'N, 17°12'E, 1,492 m alt.) is the only part of the chain that exceeds the timberline, which is at ca. 1,300 m there. The summit plateaux above the timberline are covered by species-poor alpine grasslands, whereas the most diverse habitats are the tall herb formations on slopes of glacial cirques and at valley headwalls.

Both of the studied butterflies are univoltine and their adult periods last from July to mid-August. Their solitary larvae feed on thin-bladed grasses that dominate the alpine grasslands. Several subspecies of *Erebia epiphron* inhabit most high European mountains (Warren 1936), whereas *E. sudetica* is restricted to a few widely isolated locations (Cupedo 1997).

There are two distinct populations of *E. epiphron* in the area (Fig. 1) separated by ca. 3 km of forested elevations and restricted to alpine grasslands (Kuras et al. 2000). We refer to them as the main ridge colony (MR, altitudinal range ca. 1,300–1,455 m, area ca. 16.5 km²), and the Mt. Mravenečník colony (MV, ca. 1,300–1,340 m, area 1.2 km²).

Erebia sudetica forms well-defined colonies either at tall herb sites near the timberline, or in clearings below it. Canopy closure at the localities is prevented by natural (avalanches) or human (logging) disturbances (Kuras et al. 2001c). We worked at five of the timberline sites (Fig. 1): the Malá Kotlina glacial cirque (two parts: MK1 and MK2) and the Volárka Springs (three parts: VS1, VS2 and VS3).

Since we studied different species/populations in different years, some of our results may have limited validity. However, we spent a total of five seasons in the area without observing any changes in distribution or relative abundances of the two species. Hence, the patterns presented should be sufficiently robust against variation among years.

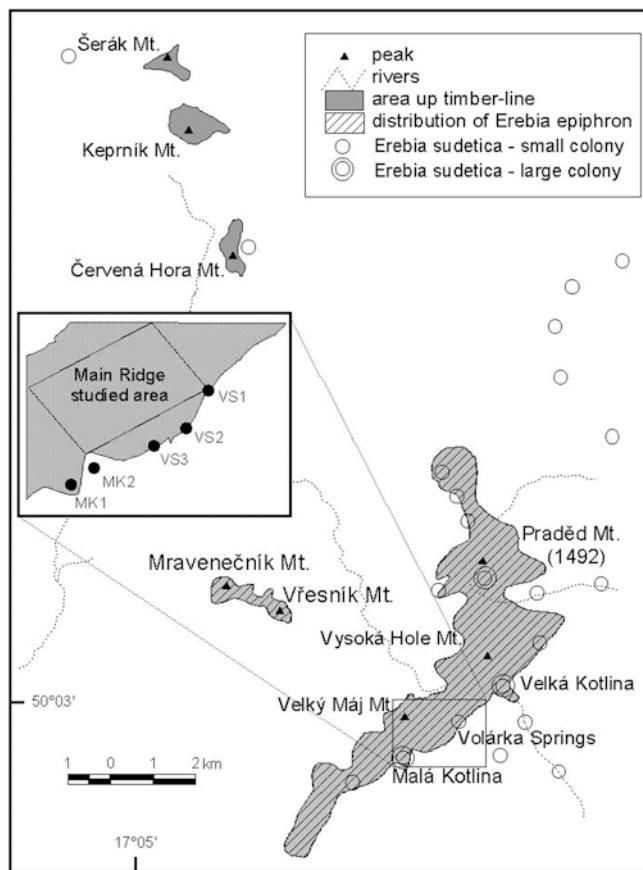


Fig. 1 Map of the central part of the Hrubý Jeseník Mountains, showing the areas above the timberline, the populations of *Erebia epiphron*, and all known colonies of *Erebia sudetica* in the area

Mark-recapture

We performed the mark-release-recapture study during the seasons 1996–1998, each season working on a different species/colony. We marked the butterflies with unique numbers and recorded their sex and the site of capture. The sampling proceeded as follows:

Erebia epiphron (MR): Sampled on each fine day from 16 July to 6 August 1996. It was not feasible to efficiently sample the entire extent of the colony, and we restricted the work to 21 contiguous quadrats of 200×200 m (0.84 km² in total) at the summit plateau and on adjoining slopes (ca. 1,280–1,384 m). We released marked butterflies en masse in the centres of the quadrats, which were the co-ordinates for analysing mobility.

Erebia epiphron (MV): The entire extent of the alpine grassland at Mt. Mravenečník was sampled from 23 July to 11 August 1997. The mobility co-ordinates were the centres of five plots, each 400 m long and spanning from timberline to timberline.

Erebia sudetica (MK and VS): Sampled in 1998 from 18 July to 16 August. All the sampled sites adjoined the timberline on the eastern slopes of the main ridge (Fig. 1).

The MK site is partly covered by impenetrable krumholz that separates two tall herb patches, MK1 (area ≈ 4 ha) and MK2 (≈ 1 ha). We divided the MK1 site into four quadrats, each approximately 1 ha. The three VS patches are islets of tall herb vegetation surrounded by *Nardus* grasslands uphill and spruce taiga downhill. They were much smaller than the MK sites: VS1 was 0.3 ha, VS2 and VS3 were 0.1 ha each. The co-ordinates for analysing *E. sudetica* mobility were the four sub-sites within the MK1 colony, the MK2 site, plus the three VS sites. The respective centre-to-centre distances were: MK1–MK2, 200 m; MK2–VS3, 1,000 m; VS3–VS2, 500 m; VS2–VS1, 200 m (Fig. 1).

Population size

We estimated the sizes of adult populations separately for the MR and MV colonies of *E. epiphron*, and for the MK1 and VS1 colonies of *E. sudetica*. The remaining colonies of *E. sudetica* were not sampled regularly enough to obtain reliable estimates.

The numbers of butterflies were estimated by the Jolly-Seber method (Jolly 1965), which is suitable for repeatedly sampled open populations, using model A in the program Jolly (Pollock et al. 1990). The model returns daily residence rates (ϕ_i s), i.e. per capita probabilities of staying alive at the site of capture, for each period between two successive marking occasions, and the numbers of individuals present in the population on each of the occasions. Total population sizes were estimated as in Matsumoto (1985):

$$N_i = \sum_{i=1}^n \frac{\hat{B}_i}{\sqrt{\hat{\phi}_i}} \quad (1)$$

where ϕ_i s are the daily residence rates, and B_i s the total numbers of new animals entering the population between i th and the $(i+1)$ th sample and still alive when the $(i+1)$ th sample is taken (returned by the program). We estimated population size individually for each sex.

Models of mobility

For the butterflies recaptured at least once, we fitted the distribution of dispersal distances, expressed as straight distances between the centres of the successive capture sites, using the following models.

The negative exponential function (NEF) (e.g. Southwood 1966; Hjermann and Ims 1996; Sutherland et al. 2000) expresses the probability density I of movements to distance D as

$$I_{\text{NEF}} = a \cdot e^{-k \cdot D}$$

or, using logs,

$$\ln I_{\text{NEF}} = \ln a - k \cdot D \quad (2)$$

The parameters a and k are estimated as the intercept and slope, respectively, of the regression of cumulative fractions of the individuals that moved certain or higher distances against the distances.

Since NEF reportedly underestimates rare long-distance movements, several authors (e. g. Hill et al. 1996; Bullock and Clarke 2000; Baguette 2003) have proposed using of wider-tailed inverse power function (IPF), which takes the form

$$I_{\text{IPF}} = C \cdot D^{-n}$$

i.e.

$$\ln I_{\text{IPF}} = \ln C - n(\ln D) \quad (3)$$

The parameters are estimated by regressing the natural logarithms of cumulative fractions of individuals that moved certain or higher distances against logarithms of the distances.

The sigmoid function (SIF) was proposed following the observation that, over short distances, the declines of movement probabilities tend to be flat rather than steeply decreasing. It combines initial flat declines with exponential decreases over long distances (Heinz et al. 2003). Using the same notations as for the NEF, we put it as

$$I_{\text{SIF}} = 1 - e^{-a \cdot e^{-b \cdot D}}$$

or

$$\ln[-\ln(1 - I)] = \ln(a) - b \cdot D \quad (4)$$

The cumulative fractions of individuals that moved certain or higher distance are linearised via the complementary log-log transformation and regressed against these distances.

The NEF and SIF assume that the probability of movements to zero distances equals unity. On the other hand, the IPF is fitted by expressing flight distances as logarithms, which causes problems with “zero” distances (i.e. with recaptured individuals that did not leave the sites of their original capture). Obviously, such individuals do not exhibit zero mobility: each of them may move any distance from zero to the middle distance between adjoining movement coordinates. Considering this, we fitted a minimum distance for each situation of the middle value from the interval between zero and the minimum movement co-ordinate, and we added this value to all longer distances.

We used Akaike’s information criterion (AIC) for comparing fits of the mobility models to the data. For each situation studied, we estimated movements according to each of the three models on their original scales (i.e. I s from Eqs. 2, 3 and 4 against distance in kilometres). Then we regressed the estimated numbers against actually measured cumulative proportions of movements. We selected as the best model the one that contributed to the highest decrease in AIC (Δ AIC) relative to the respective null model in which the proportions of movements were regressed against unity. We used the program S-plus 2000 (1999) for these computations.

Within the better-fitting models (NEF and SIF), we compared mobility between species, sexes and populations by testing for differences among slopes of the models’ linearised forms and by subsequent multiple comparisons among all the pairs of regression lines using Tukey’s HSD test (Zar 1996). Only nominally significant regressions were considered in these tests.

Besides assessing movements within populations of both *E. epiphron* (MR and MV) and *E. sudetica* (MK1), we compared the movements of *E. sudetica* within the MK1 colony with movements among the colonies. To do so, we constructed separate models for dispersal within the MK1 site (Within) and for all movements (Total, i.e. within MK1 + among sites + individuals not leaving the remaining four sites). We chose that approach despite frequent argument (e.g. Inoue 1978) that movements within and among populations should not be combined in the same model. We preferred to include the Within movements in the Total movements, and subsequently compare the two models, since this in fact tested a more conservative null hypothesis that movements among habitat were just an extension of movements within habitats.

Results

Population size, demography

Erebia epiphron

We captured and marked 4,034 individuals in the MR population and 2,542 individuals in the MV population (Table 1). The MR population (1996) was sampled from the beginning of its flight period, but we missed the beginning in the MV population (1997) (Fig. 2). Despite this difference in timing, both capture and recapture sex ratios remained biased towards males in both populations, and logit regressions of proportions of sexes captured in individual marking days pointed to the existence of protandry (MR: $\chi^2 = 126.8$, $P < 0.0001$; MV: $\chi^2 = 243.1$, $P < 0.0001$; tests significant at the 0.05 level after controlling for overdispersion).

The extremely low recapture rates in the MR population (Table 1) indicated its large size. Due to insufficient female recaptures, we estimated the total

Table 1 Summary of results of mark-release-recapture study of *Erebia epiphron* and *E. sudetica* in the Hrubý Jeseník Mountains (see text for details of site names), including basic estimates of population size per sampled areas and comparison of mobility of between the two species (split into different populations and sexes)

Site/sex	Marking days (duration)	Number captured	Number recaptured	Recapture events	Recapture probability	Estimated total	Staying in the same site ^a	Longest move (m)
<i>E. epiphron</i>								
MR 1996	11 (21)							
♂♂		3,444	222	236	0.064	≈ 19,000 ^b	71.9%	1,130
♀♀		590	14	14	0.024	N.A.	76.9%	630
MV 1997	8 (19)							
♂♂		1,884	374	489	0.196	≈ 1,900	58.4%	1,200
♀♀		658	66	79	0.100	≈ 2,400	57.1%	1,600
<i>E. sudetica</i>								
MK 1998	25 (29)							
♂♂		1,195	482	719	0.601	≈ 2,160	40.4%	1,100
♀♀		976	411	669	0.685	≈ 2,390	35.9%	600
VS 1998	24 (29)							
♂♂		180	60	97	0.544	306	40.3%	3,100
♀♀		73	20	23	0.185	150	45.7%	1,650

^aPercentage of recaptured individuals that were never recaptured outside the site of their original capture

^bThe estimate refers to sampling area only (i.e. 0.84 km²)

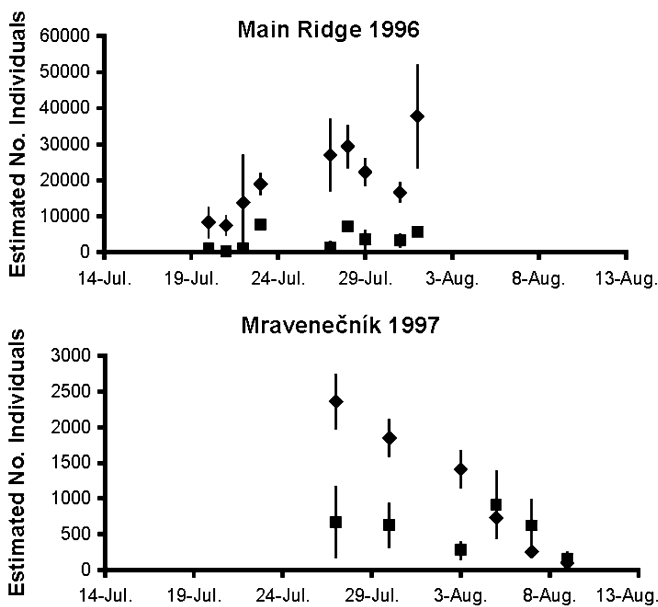


Fig. 2 The Jolly-Seber estimates of adult numbers of *E. epiphron* in the Hrubý Jeseník Mountains. Estimated daily numbers and their standard errors for the main ridge colony (MR) and the Mravenečník colony (MV). Note the different scales of the y-axes

number of individuals only for males. The result pointed to an enormous population size: the estimate of 19,000 males in 0.84 km² corresponded to 23,000 males per km², or to hundreds of thousands of individuals inhabiting the main ridge area. In the MV populations, the recapture rates were significantly higher (2x2 table of captures vs recaptures in MR vs MV: $\chi^2 = 222.0$, $df = 1$, $P < 0.0001$) and allowed us to estimate population sizes for both sexes. The MV population was one to two orders of magnitude smaller than the MR population and contained approximately equal numbers of each sex (Table 1, Fig. 2).

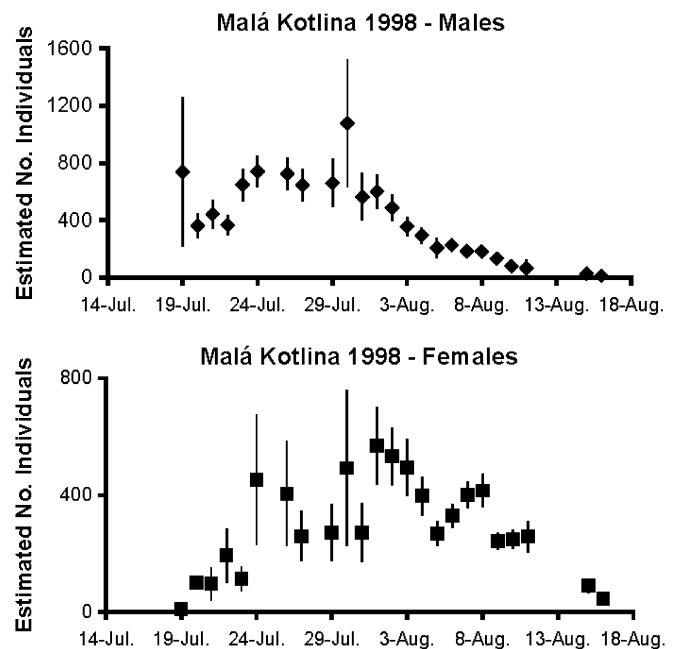


Fig. 3 The Jolly-Seber estimates of adult numbers of *E. sudetica* in the Malá Kotlina colony (MK1). Estimated daily numbers and their standard errors

Erebia sudetica

We marked 2,171 individuals in the Malá Kotlina cirque (MK1) and 253 individuals in the Volárka Springs (VS1) (Table 1). The capture sex ratios were male biased in both colonies, but the sex ratio of recaptured individuals was significantly male biased only in the VS1 colony (VS1: $\chi^2 = 10.7$, $df = 1$, $P < 0.01$; MK1: $\chi^2 = 2.9$, $df = 1$, $P = 0.08$) (Table 1). The adult emergence was protandrous in both colonies (logit regression: MK1: $\chi^2 = 152.4$, $P < 0.0001$; VS1: $\chi^2 = 50.8$, $P < 0.0001$; models significant after controlling for overdispersion) (Fig. 3).

Recapture rates were rather high, indicating relative closure of the colonies. Despite the fact that the marking effort was proportional to the areas of the colonies, the frequency of recaptures was higher in the MK1 colony (2x2 table, $\chi^2 = 7.76$, $df = 1$, $P < 0.01$), suggesting a higher turnover of individuals in the smaller colony. The estimate of population size for MK1 exceeded that for VS1 tenfold (Table 1).

Mobility: general observations

Within colonies, individuals of both species moved relatively freely, as indicated by the high proportion of movements among the mobility co-ordinates (Table 1).

We could not assess *E. epiphron* movements among colonies directly, since the two populations were studied in different years. However, the following results of parallel studies indicate mutual isolation of the two populations:

1. In 1997, we carried out a pan-trapping study within the MR population at sites directly facing the MV population and concurrent with the mark-release-recapture study in MV, and we observed that none of the 1,943 pan-trapped individuals had been marked (Kuras et al. 2000).
2. There were significantly more partial albinos in the MV population (1997) than the MR population (both in 1996 and 1997) (Kuras et al. 2001b).
3. *E. epiphron* is absent from the three smaller and more isolated patches of alpine grasslands in the Hrubý Jeseník Mts. (Fig. 1; Kuras et al. 2001c).
4. A population artificially transferred to the Krkonoše Mountains (Western Sudetens, Czech Republic) 60 years ago has colonised one of two alpine-elevation ridges in the new area, but failed to cross a 3-km-wide forested saddle to invade a ridge situated across a valley (Cizek et al. 2003).

Regarding *E. sudetica*, a total of 28 individuals (26 males and 2 females) moved between the colonies, crossing non-habitat in the process. Both sexes crossed distances above 1 km (Table 1). The distances separating individual Hrubý Jeseník colonies tend to be within the range of the longest individual movements (Fig. 1), suggesting that the colonies form an interconnected system.

Comparing the regression models

With the exception of *E. epiphron* females, for which we obtained too few recaptures for a reliable inference, all the three mobility models fitted the data significantly for the systems modelled. The NEF and SIF models achieved much better fits than the IPF model (Table 2). The SIF was superior for *E. epiphron* males, MR population, and Within-population movements of

Table 2 Comparison of fits of the negative exponential function (NEF), sigmoid function (SIF) and inverse power function (IPF) to data on movements of recaptured *E. epiphron* and *E. sudetica*. Differences in values of the Akaike information criteria (ΔAIC) between null models of dispersal data and models regress the data against values predicted from the three functions. Higher ΔAIC indicates better fit, best-fitting models are indicated by **bold**. Refer to Table 3 for parameters of the best-fitting functions

Species, sex and population	NEF $I_{NEF} = a \cdot e^{-k \cdot D}$	SIF $I_{SIF} = 1 - e^{-a \cdot e^{-b \cdot D}}$	IPF $I_{IPF} = C \cdot D^{-n}$
<i>E. epiphron</i>			
MR ♂♂	0.851	0.855	0.667
MR ♀♀	n.s.	n.s.	n.s.
MV ♂♂	0.686	0.678	0.582
MV ♀♀	n.s.	n.s.	n.s.
<i>E. sudetica</i>			
♂♂ Within	1.052	1.029	0.681
♀♀ Within	0.758	0.794	0.504
♂♂ Total	0.924	0.893	0.864
♀♀ Total	0.830	0.810	0.677

E. sudetica females. The NEFs achieved better fits for the remaining situations (Fig. 4).

The selected NEF and SIF models predicted high proportions of individuals of both species crossing short distances and steep decreases in numbers of longer distance dispersers (Table 3; Fig. 4). True long-distance movements (e.g. > 5 km) would be highly unlikely in all modelled systems (compare the predictions in Table 3 to the population sizes in Table 1).

Based on the poor fits of the IPF models, we limited further analysis to the NEF and SIF models. The slopes of respective regression lines differed among the modelled situations (NEF: $F = 19.3$, $df = 5, 44$, $P < 0.001$; SIF: $F = 16.2$, $df = 5, 44$, $P < 0.01$), suggesting mobility differences among species, populations and sexes. The subsequent multiple comparisons of the slopes (Table 3; results for SIF were congruent with those for NEF) showed that dispersal propensities of the two species overlapped. For instance, the slope for Within movements of *E. sudetica* was steeper (indicating lower mobility) than that for *E. epiphron*, MR, but did not differ from that for *E. epiphron*, MV.

In the case of *E. sudetica*, the slope for Total movements was gentler than the slope for the Within movements (Fig. 4), indicating that movements among habitats constituted an activity distinct from background within habitat movements.

Discussion

The population structures of *Erebia epiphron* and *E. sudetica* in the Hrubý Jeseník Mountains were in striking contrast. The former species lived in two large and contiguous populations of hundreds of thousands, and thousands, of individuals. The high population density and unrestricted within-population movements were similar to the situation reported for the related

Fig. 4a–c Three models fitted to data on mobility of *Erebia sudetica* butterflies from the Hrubý Jeseník Mountains, shown for *E. sudetica* males. *Left column* Linearised forms of the models as used for parameter estimation. *Right column* Models with original scales, illustrating different properties of the three functions. *Solid lines and open circles* Movements Within the MK1 colony. *Dashed lines and black diamonds* Total movements. **a** The negative exponential function. **b** The sigmoid function. **c** The inverse power function

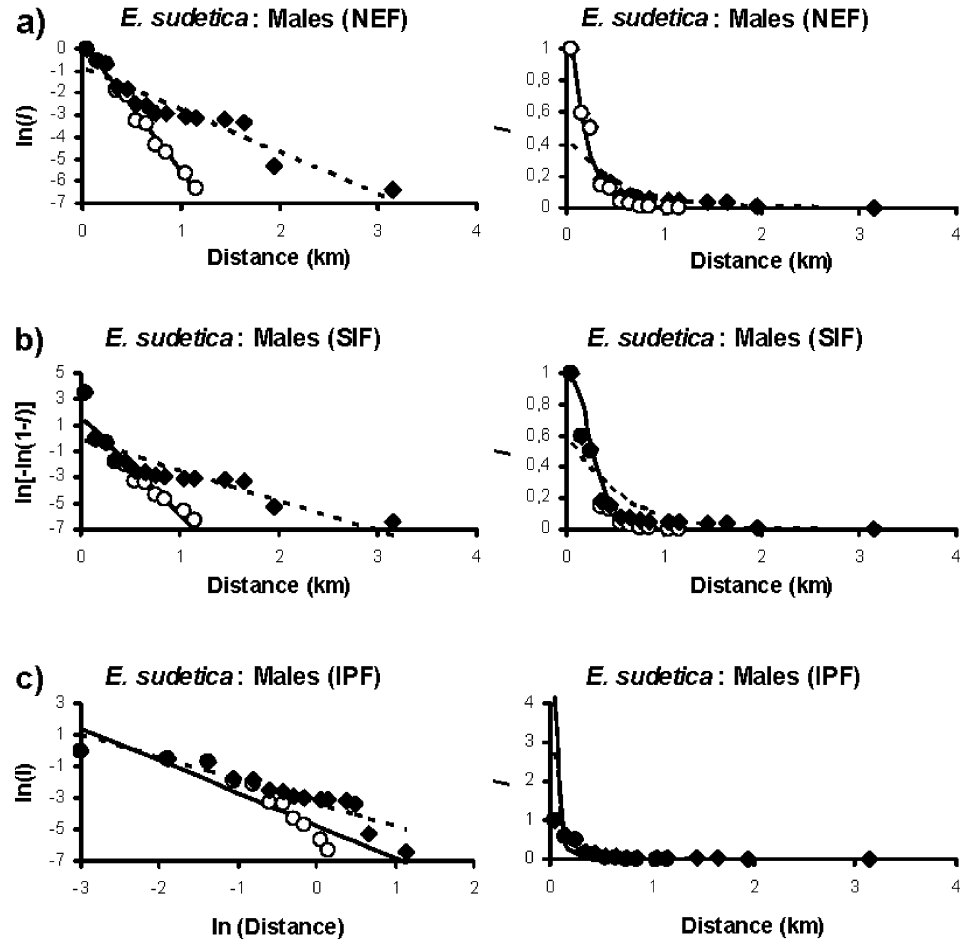


Table 3 Parameters (\pm standard errors), coefficients of determination, *F*-tests and predicted proportions of individuals that would move to the distances I_{dist} , for functions that achieved best fits in describing movements of adult *E. epiphron* and *E. sudetica*

Species/system ^a	Model	Regression equation (linearised form)	R^2	<i>F</i>	df	<i>P</i>	$I_{0.1}$ km	I_1 km	I_5 km	HSD ^b
<i>E. epiphron</i>										
MR ♂♂	SIF	$\ln[-\ln(1-I)] = 2.68(\pm 0.811) - 7.16(\pm 1.079)D$	0.86	44.1	1, 7	<0.001	0.999	0.011	4.2×10^{-15}	NA
¹ MR ♂♂ ^c	NEF	$\ln I = 0.873(\pm 0.385) - 5.18(\pm 0.512)D$	0.94	102.5	1, 7	<0.001	1.43	0.013	1.4×10^{-11}	4, 6
² MV ♂♂	NEF	$\ln I = 0.95(\pm 0.463) - 6.33(\pm 0.645)D$	0.97	96.2	1, 3	<0.01	1.37	0.005	4.6×10^{-14}	3, 6
<i>E. sudetica</i>										
³ ♂♂ Within	NEF	$\ln I = 0.354(\pm 0.147) - 5.88(\pm 0.222)D$	0.99	703.3	1, 9	<0.001	0.791	0.004	2.4×10^{-13}	2, 6
♀♀ Within	SIF	$\ln[-\ln(1-I)] = 2.87(\pm 0.632) - 12.02(\pm 1.568)D$	0.92	58.7	1, 5	<0.001	0.995	1.1×10^{-4}	≈ 0	NA
⁴ ♀♀ Within ^c	NEF	$\ln I = 0.75(\pm 0.270) - 7.80(\pm 0.670)D$	0.96	135.6	1, 5	<0.001	0.970	0.001	2.4×10^{-17}	1
⁵ ♂♂ Total	NEF	$\ln I = -0.83(\pm 0.238) - 1.92(\pm 0.191)D$	0.89	101.2	1, 13	<0.001	0.360	0.064	3.0×10^{-5}	all
⁶ ♀♀ Total	NEF	$\ln I = -0.89(\pm 0.472) - 2.95(\pm 0.500)D$	0.83	534.8	1, 7	<0.001	0.306	0.022	1.6×10^{-7}	1, 2, 3

^aThe superscripts (1, 2, 3, etc.) identify individual models and are referred to in the comparisons in the last column of the table

^bResults of Tukey’s HSD comparison among slopes of the NEF models. Numbers identify models that did not differ in their slopes from the model described in given line. The abbreviation “NA”

denotes situations for which the test was not applicable; “all” denotes a model that differed from all remaining models

^cThe NEF model for *E. epiphron* males, MR population and *E. sudetica* females, Within movements are shown for comparison, since their predictions are referred to in the text

North American *E. epipsodea* (Brussard and Ehrlich 1970) and agreed with the notion of “densely packed” populations occupying each piece of contiguous habitats (Hanski and Thomas 1994). *Erebia sudetica* lived in

discrete colonies interconnected by interchange of individuals, conforming to a traditional metapopulation pattern. Movements of both species were sufficiently described by the negative exponential model or, for the

larger population of *E. epiphron* and for Within movements of *E. sudetica* females, by the sigmoid model, both models predicting low probability of long distance movements. This even applied to movements of *E. sudetica* among habitats, although we originally expected that the wider-tailed IPF should be more appropriate for mobility of this patchily distributed species (cf. Hill et al. 1996).

Comparing the dispersal models

Since the NEF and SIF models returned similar predictions for long distance movements of both species, and since ecologists tend to be more interested in long-range dispersal than in details of short distance movements, it may be argued that SIF is of little practical value. However, as SIF deviates from NEF over short distances, its poor fit to empirical data may suggest that a sampling design missed the biologically justified (cf. Zollner and Lima 1997; Conradt et al. 2000) “short” movements. It cannot be decided in advance which distances are “short” and correspond to background within-site mobility, and which are “long” and constitute genuine dispersal. A comparison of fits between NEF and SIF may detect the distinction. As indicated by the different fits of the two models for *E. epiphron* males, MR population (movements recorded to closest 200 m) and MV population (movements recorded to closest 400 m), an inflection point between short “home range” movements and genuine dispersal was somewhere between the two distances.

Regression-based dispersal models should facilitate comparisons across species (Baguette et al. 2000). The k -parameters of the NEF models (Table 2) for *E. epiphron* and *E. sudetica* overlapped with each other and with k -values reported for the butterflies *Aporia crataegi*, *Melanargia galathea* (both in Baguette et al. 2000), *Boloria aquilonaris* (Baguette 2003) and *Parnassius apollo* (Brommer and Fred 1999). Absolute values of k depend on scaling of the x -axis and the latter authors used 100s of metres instead of kilometres. The mentioned species differ in habitat use: the *Erebia* satyrids inhabit alpine elevations, *P. apollo* is a specialist of open turf grassland, *B. aquilonaris* inhabits peat bogs, *M. galathea* prefers long bladed grasslands and *A. crataegi* prefers scrub. As we documented here, they may also differ in spatial patterns of their distributions (see also Baguette et al. 2000; Baguette 2003).

Since the striking differences in habitat use did not affect suitability of the NEF for modelling the dispersal of the above species, the extent to which the suitability of different dispersal models is influenced by other factors, such as behaviour, deserves to be explored. The above butterflies, for which NEF was a suitable model, share identical mate-locating behaviour: long-endurance patrolling flights (cf. Wickman 1992). In contrast, IPF was found to be a superior model for mobility of the skipper *Hesperia comma* (Hill et al. 1996), whose males

defend perching sites to attract females. It also suitably described dispersal of dung beetles, which alternate tenacity to their vital resources with relatively long-range dispersal (Roslin 2000). These considerations suggest that the NEF/SIF models might be more appropriate for species with relatively undirected mobility, whereas the IPF may perform well for organisms that alternate fidelity to limited resources with active effort to locate them.

In Baguette’s (2003) study of mobility of the fritillary *B. aquilonaris*, the NEFs attained better statistical fits than the IPFs, but the predictions of long-range movements derived from the IPFs were supported by empirical data. The author suggested using the IPF for modelling dispersal, claiming that long distance movements might be of a different nature than within-site mobility. Similarly, we found differences in k -parameters for Within and Total movements of *E. sudetica*. If the IPF was fitted to the Within movements of *E. sudetica*, it predicted that about one male per thousand individuals (i.e. 10^{-3}) should cross 3 km, which agreed with our observations (cf. Table 1). The respective prediction based on the NEF was 10^{-8} . However, if we fitted the NEF to collated Total movements, it matched the data well. This reminds us that performances of dispersal models critically depend on the scales considered (Schneider 2003). This was clearly visible from the significant between-population differences in mobility of *E. epiphron* males, for which the NEF model parameters (Table 3) indicated that the butterflies sampled from the larger area (MR population) were statistically more mobile. This shows the limits of dispersal models for understanding species’ ecology: in our study, two species with strikingly contrasting distributions overlapped in mobility parameters, but the parameters themselves depended on what was sampled, and how.

Dynamics of the two species

What, then, may explain the differences in distribution patterns between *E. epiphron* and *E. sudetica*? Understanding mobility is useful, but should be considered jointly with historical context, behaviour and life history of particular species.

Recent distribution of *E. epiphron* in European alpine regions (cf. Kudrna 2002) suggests that the butterfly had inhabited vast European tundras during the ice ages and became entrapped on high-altitude islands by postglacial forest invasion. The alpine grasslands of the Hrubý Jeseník do not pose barriers to within-habitat mobility, and the unconstrained movements within habitats should be beneficial, e.g. during fast changes of mountain vegetation during season. However, the grasslands are surrounded by contiguous timberline, a formidable dispersal barrier that has been there for millennia. The butterfly is strictly heliophilous (Konvicka et al. 2002) and its habitats form just small islands in a densely forested landscape. Hence, each individual that left the habitat would

probably perish before locating a new site. The ability to avoid non-habitat, which has been documented for several alpine butterflies (Roland et al. 2000; Ricketts 2001), should evolve rapidly in such circumstances.

All known populations of *E. sudetica* occur near timberlines (Cupedo 1997). Their habitats are more diverse than the uniform grasslands inhabited by *E. epiphron* and confront the butterfly with a higher variation in resources (Kuras et al. 2001a). It follows that occasional leaving of habitat should not be punished so severely and may even be beneficial, by allowing dispersing individuals to track temporarily suitable sites. Still, the dispersal must have an upper bound responsible for the restricted geographical distribution.

The largest Hrubý Jeseník colonies of *E. sudetica* are those located at the highest elevations of all the extant sites (Fig. 1; Kuras et al. 2001c), in glacial cirques near flat summits exposed to western winds. The sites are affected by frequent avalanches, had been devoid of forest for the entire Holocene and accumulate deep winter snow (Jeník 1998). They provide winter insulation for larvae and leeward conditions for adults. These considerations suggest that local distribution of *E. sudetica* is limited to proximity to its long-term Holocene refuges. The population dynamics of such a species arguably conforms to long-term source-sink dynamics (Harrison 1991), in which the large colonies near the timberline function as refuges/sources, and the small peripheral colonies as sinks. Recall that our smaller colony (VS1) experienced a higher turnover of individuals, which is often associated with sink populations. The difference between slopes of the NEF models for Within and Total movements suggested that, as soon as an individual leaves its habitat, it continues flying until reaching a new suitable place. The assumptions that the large populations produce more emigrants than the small ones, coupled with the limited long distance dispersion (Table 3), should suffice to set upper limits to local distribution of the butterfly. Also, *E. sudetica* males moved between colonies more often than females. The male sex spends most of time patrolling (Kuras et al. 2001a), and since it may not be easy to distinguish habitat boundaries in the rugged terrain of the colonies, the males incur a higher risk of leaving their natal patch.

Conclusion

Although the two *Erebia* butterflies contrasted in population structure, their mobility was better described by models based on the negative exponential function or the sigmoid function than by the inverse power function models. The mobility parameters were sensitive to the scale of sampling, which issues a warning against broad generalisation across species. On the other hand, the collected mobility information allowed firmly grounded inferences on patterns of local distribution of the two species, if it was considered together with information

on spatial structure and history of their habitats, and with life history and behavioural information.

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