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Mobility patterns of alpine *Erebia* populations: Does a large road act as a dispersal barrier?

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Abstract

Dispersal is a crucial feature for the preservation of butterfly metapopulations, which can be affected by habitat fragmentation. Each individual that enters the matrix takes a risk. Therefore, even winged organisms, like butterflies, are often extremely sedentary and spend their whole lifetime in a relatively small area. For such species, large roads may constitute a real obstacle for movement. We conducted a mark-release-recapture study on six alpine *Erebia* species in the Hohe Tauern National Park in order to investigate if theGroßglocknerHochalpenstraße – a large and highly frequented road in an alpine environment – acts as a barrier to movement for these relatively sedentary butterflies. We aimed at analysing which of the following variables predicts movement probability: (a) species membership, (b) ecological specialization, (c) nectar availability, (d) age or (e) patch isolation.

We marked a total of 429 individuals, of which 113 were recaptured. Our data indicates that neither body-size nor ecological specialization significantly influenced mobility patterns in these *Erebia* butterflies.Butterflies that were on a patch with a high nectar level were less likely to leave the patch. Age influenced mobility with mid-aged butterflies being most likely to change between patches. The road, however, seemed to be a barrier for dispersal. We found that butterflies that had to cross the road to get to another suitable habitat patch were less likely to leave the patch than butterflies that did not have to cross the road.

Keywords

habitat fragmentation, *Erebia*, mobility, dispersal, alpine butterflies, mark-release-recapture, metapopulation

Introduction

Numerous studies show that dispersal is a key feature for the preservation of butterfly metapopulations (e.g., HANSKI et al. 2000, HILL et al. 1996). In a fragmented landscape individuals have to take the risk of entering the matrix to reach new suitable habitat patches with costs during dispersal through the matrix, for example due to an increased predation risk (ANDREASSEN & IMS 1998, ROBINSON et al. 1995). This might cause individuals to stay sedentary. When species are forced to live in isolated populations, the genetic exchange is limited which may increase homozygosity and thus, in the long run, the risk of extinction (SACCHERI et al. 1998). Once a population on an isolated patch is extinct, recolonization is unlikely (HEINO & HANSKI 2001).

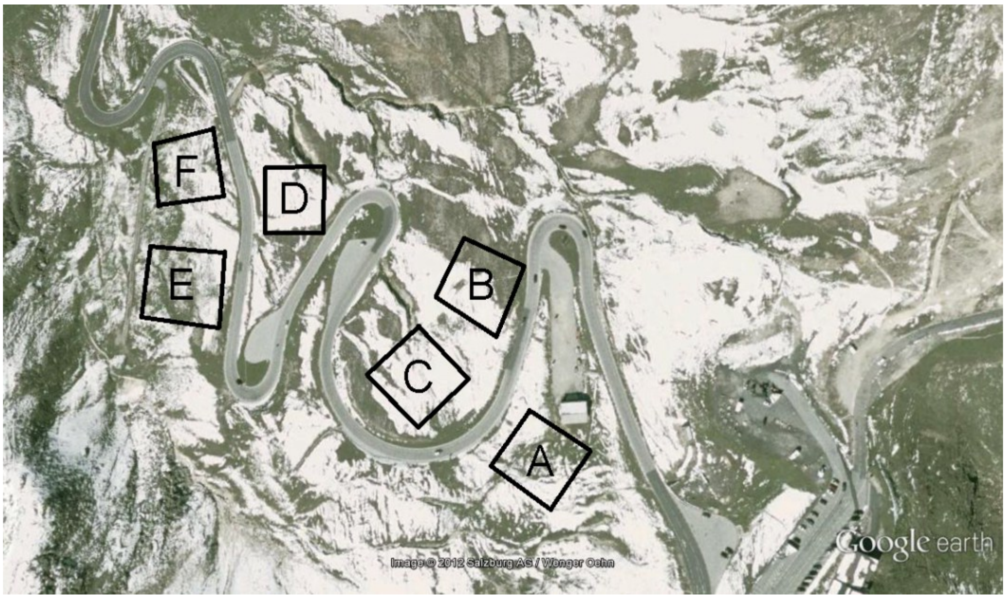

Figure 1: Map of the study area: Analysed plots in the Hohe Tauern National Park. "Upper triangle" with the plots ABC, "lower triangle" with the plots DEF. Source: Google Earth.

Habitat fragmentation might be more destructive to alpine butterfly populations as opposed to lowland conditions. The harsh climatic conditions and sudden onsets of bad weather in such environments may increase the mortality during dispersal events. Due to recent climate change, mountain butterfly species have shifted their distributions towards higher elevations (PARMESAN 1996). Hence, when distribution ranges are shifted upwards and high-altitude habitats become fragmented into smaller patches, organisms that are restricted to alpine habitats might be those most threatened. Understanding the dispersal patterns of alpine butterfly populations and what might be a barrier for dispersal is therefore fundamental for developing and adapting conservation plans. In Austria, the butterfly genus *Erebia* contains about 25 species adapted to alpine habitats, several of them occurring sympatrically (STETTMER et al. 2007).

We analysed the dispersal patterns of *Erebia* butterflies in an anthropogenically fragmented habitat in the Hohe Tauern National Park in Austria, where a large road cuts through the natural habitats of the butterflies. The genus *Erebia* (Nymphalidae: Subfamily Satyrinae) contains species adapted to alpine habitats (NEUMAYER et al. 2005), occurring on altitudes of 500 m to more than 2500 m (STETTMER et al. 2007). According to KOMONEN et al. (2004) habitat generalists are more mobile than habitat specialists. Hence, we compared a habitat generalist, like *E. pandrose* to a habitat specialist, like *E. gorge*. *E. pandrose* is relatively widespread in European mountain habitats, colonizing rocky and dry habitats as well as moist grassland, in contrast to *Erebia gorge*, which is restricted to rocky habitats such as moraines (TOLMAN & LEWINGTON 2012). BERWAERTS et al. (2002) found that the flight performance of *Parargeaegeria* butterflies was positively correlated with total body mass, forewing area and forewing length. Therefore, we compared larger butterflies to smaller butterflies.

We analysed six alpine *Erebia* species, namely *E. eriphyle, E. epiphron, E. gorge, E. pharte, E. pandrose* and *E. nivalis*. We aimed at analysing which of the following variables predicts movement probability: (a) species membership, (b) ecological specialization, (c) nectar availability, (d) age or (e) patch isolation. We asked the following questions: (1) Does a large road act as a dispersal barrier for *Erebia* butterflies in the sense that butterflies do not (or less often) fly across the road? We expected higher dispersal rates between habitat patches on the same side of the road than between patches on different sides. (2) Is there a difference in the mobility patterns between a habitat generalist like *E.pandrose* and a habitat specialist like *E. gorge*? The specialist was expected to be more affected by habitat fragmentation and to be more likely to stay on the same habitat patch. (3) Is there a difference in the mobility patterns between larger species like *E. eriphyle* with wingspans of about 4 cm and smaller species like *E. epiphron* and *E. pharte* with wingspans of less than 3 cm? We expected larger species to be more mobile and smaller species to be more likely to stay on the same patch. (4) Do nectar availability or age influence the mobility patterns? We expected nectar availability to influence mobility in the sense that if butterflies are on a patch with sufficient resource availability, they might be less likely to leave that patch. We expected the migration rate to increase with age as this has been found e.g. by KARLSSON (1994).

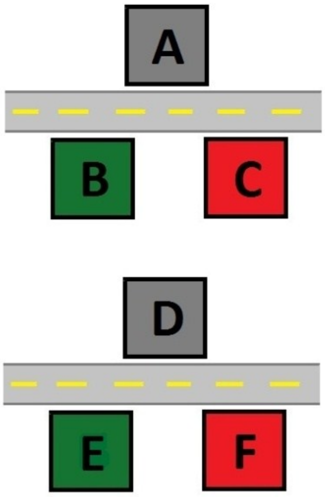

Figure 2: Schematic overview of the "upper triangle" ABC and the "lower triangle" DEF.

Material and Methods

Study area

We conducted our field study in the Hohe Tauern National Park in Austria, which comprises suitable alpine habitats for these butterflies like meadows or dwarf shrub heaths, hence 21species of *Erebia* occur there (HUEMER & WIESER 2008). We chose alpine meadows located at an altitude of 2300-2400 m,relatively homogenous regarding slope and resources. A large road, the "Großglockner Hochalpenstraße", leads through the national park and cuts through these meadows. The Großglockner Hochalpenstraße is a highly frequented alpine road with about 267.000 motor vehicles per year between May and the beginning of November, according to the Großglockner Hochalpenstraßen AG. To determine whether the road has an impact on dispersal of ringlet butterflies, we examined two habitat plots on one side of the road and one plot on the other. The plots were arranged in a triangle within these meadows with no natural elements determining the borders of the plots. This setting was replicated a second time, so that we analysed six plots in total. Each plot had a size of 40 x 40 m² and the distance between plots was 40 m. The plots of the first (and upper) triangle were named A, B and C, while the plots of the second (and lower) triangle were named D, E, and F (Figure 1, Figure 2). The plots A and D will be referred to as the "separated plots" hereafter, since they were segregated from the other plots by the road.

Data collection

We conducted a mark-release-recapture study on six different *Erebia* species in the Hohe Tauern National Park between 7 July and 14 August 2012. Study sites were visited daily (if weather permitted) in a random order, usually from 9:30 a.m. to 6:00 p.m. Butterflies were captured with a hand-held net and individually marked with a consecutive number on the underside of one hind wing with a fine-point permanent marker. Sex, age, hour of capture and location was noted for every butterfly. Age was estimated by wing-wear on a scale from 1-3. The location was recorded with a GPS-device. Once a week the available nectar sources were estimated on a scale from 1-4.

Table 1: Analysed species and recapture rates for the categories "sedentary", "same side" and "cross road". Using the Fisher test for differences among these species with respect to their mobility we could not reject the null hypothesis (p = 0.11).

	E. eriphyle	*E. epiphron*	*E. pharte*
sedentary	25	24	16
same side	8	3	9
cross road	1	4	1

Data analysis

We analysed the distance covered by butterflies by measuring the distance between the site coordinates of the first and the subsequent capture using Google Earth. We classified recaptures into three categories: (1) "sedentary", if the butterfly was recaptured on the same plot; (2) "same side", if the butterfly was recaptured on a different plot but on the same side of the road; and (3) "cross road", if the butterfly was recaptured on a plot on the other side of the road. To find out if the species differ from each other with respect to their mobility patterns, we compared recapture frequencies of *E. eriphyle, E. epiphron*and *E. pharte*, and the three categories using the Fisher test (Table 1). A rejection of the null hypothesis of no difference among the species meant that the species differ from each other with respect to their mobility. The same was done for *E. pandrose* and *E. gorge*.

The impact of the road on the mobility was tested using a logit model. First, we excluded the butterflies that had only been captured once. Second, we checked if the modelling results changed if we also included the butterflies that had only been captured once. In our model, the dependent variable "same plot" took the value 1 if the butterfly was recaptured on the same plot (or was only captured once in the second case), and it took the value 0 if the butterfly came from a different plot. We constructed a dummy variable that indicated on which side of the road the butterfly had been captured. For instance, the dummy variable "plot A" took the value 1 if the butterfly had initially been captured on plot A and took the value 0 if it came from any other plot. We did the same for the variable "plot D". We expected that butterflies captured on plot A or Dwere more likely to stay on the same plots rather than to cross the road. We tested if modelling results changed if weused just one dummy variable "plot A or D". We controlled for the effect of nectar availability, age and species identity. Age enteredquadratically into the regression equation to account for possible unimodal effects. We constructed a dummy variable for each species. Information criteria (AIC, BIC) were used for model selection.

Table 2: Summary-Table. Analysed species and their respective mark and recapture rates.

Species	Marked	Recaptured
E. eriphyle	88	35
E. epiphron	75	31
E. pharte	43	26
E. gorge	49	9
E. pandrose	34	6
E. nivalis	25	6
E. euryale	1	0
E. manto	1	0

Results

We marked a total of 316 individuals, of which 113 were recaptured (Table 2). Roughly 62 % of the butterflies were recaptured within a distance of less than 30 m(Figure 3). 155 of the 429 captured butterflies were females, 211 were males and for the remaining 63 the sex could not be determined. Our data indicates that neither body-size nor ecological specialization significantly influenced the mobility in *Erebia* butterflies. The road seemed to be a barrier against dispersal.

Using the Fisher test we could not reject the null hypothesis of no difference in mobility neither between *E. eriphyle, E. epiphron* and *E. pharte* (p = 0.11) nor between *E. gorge* and *E. pandrose* (p = 0.60). According to the logit model (Table 3) butterflies captured on plot D were significantly more likely to stay on the same plot than butterflies captured on the other plots. We did not find analogous effects for plot A. If we used just one dummy variable for plots A or D, we found that butterflies captured on these plots were significantly less likely to change the plot across the road. If there was a high abundance of nectar flowers, butterflies were less likely to change the plot. We did not get this result if we included butterflies that were captured only once. We found significant evidence that very young butterflies were more likely to stay on the same plot. When they got older they were more mobile and thus, more likely to change the plot, and at the end of their flight period they were more likely to stay on the same plot (Figure 4). We found that *E. pharte* was more likely to change between plots than the other species.

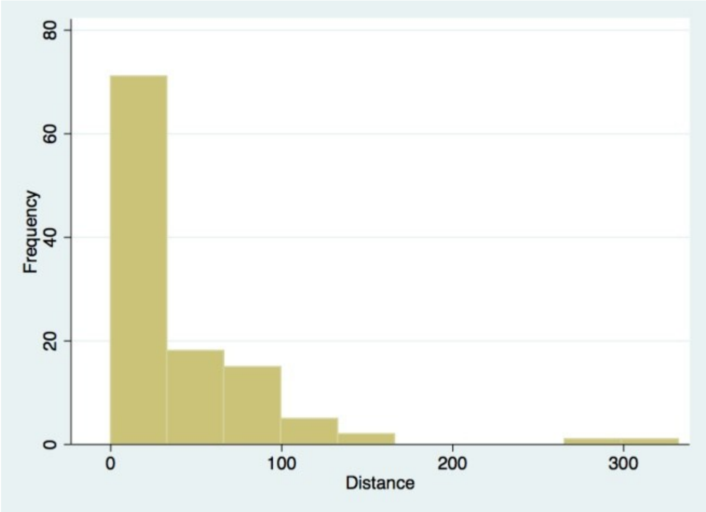

Figure 3: Histogramm of distances [m] moved by Erebia butterflies. The maximum flight distance recorded was 331,93 m (Erebia epiphron).

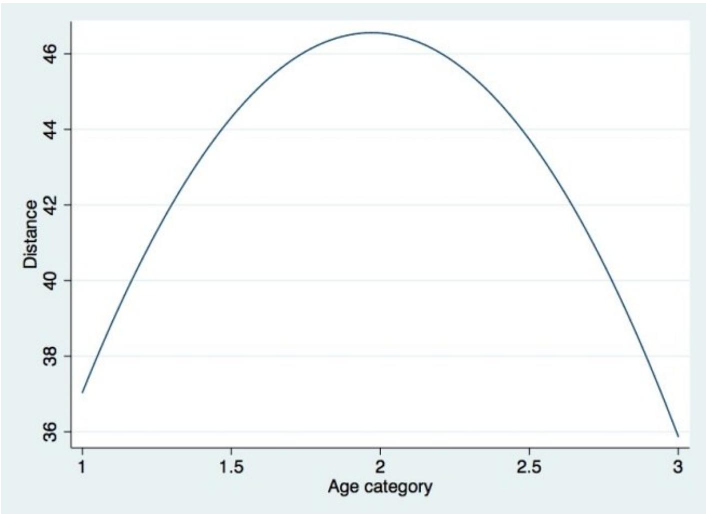

Figure 4: Graph of the prediction for Distance [m] from a linear regression of Distance on Age [categories 1-3] and Age squared.

Discussion

Most of the butterflies did not move more than 40 meters (≈ 69 %) between two capture events (Figure 3). JUNKER et al. (2010) suggested that a low mobility might be an adaptation of alpine butterfly species to a high elevation habitat, as limited movement distances might prevent accidental drift events, e.g. by squalls, in these high-altitude environments.Apparent sex ratios were biased towards males for all *Erebia* species except for *E. eriphyle* and *E.pandrose*. Male butterflies are more active most of the time, spending more time patrolling, presumably searching for females (SLAMOVA et al. 2011). This makes them more likely to be observed, which can lead to a bias towards males in the number of captures.

Patch isolation. The logit model suggested that butterflies captured on plot D were less likely to change the plot than butterflies captured on the other plots. Butterflies captured on plot D had to cross the road to change the plot, which leads us to assume that the Großglockner Hochalpenstraße is a decisive factor for the lower mobility of the butterflies captured on plot D. We did not find this pattern for the upper triangle ABC, which might be due to a lower sample size. These results confirm our prediction, that a large road can hinder butterflies from dispersing from a suitable habitat patch on one side of the road to another suitable habitat patch on the other side of the road.

Table 3: Maximum Likelihood Estimation, logit model. The dependent variable is "same plot", which takes the value 1 if the butterfly was recaptured on the same plot (or was only captured once in the model that also included the butterflies that were only captured once) and takes the value 0 if the butterfly came from a different plot. The independent variable "plot A" takes the value 1 if the butterfly was captured on plot A and takes the value 0 if the butterfly was captured on another plot. The same goes for the dummy variables "plot D" and "plot A or D", respectively.

VARIABLES	(1) Logit - recaptured	(2) Logit - recaptured	(3) Logit - all	(4) Logit - all
Plot A		0.669		1.233
		(1.260)		(1.054)
Plot D		2.801**		2.301**
		(1.167)		(1.094)
Plot A or Plot D	2.135**		1.871**	
	(0.903)		(0.808)	
Nectar	0.647**	0.695**	0.262	0.284
	(0.286)	(0.289)	(0.219)	(0.221)
Age	-3.977**	-3.981**	-3.761**	-3.837**
	(1.832)	(1.839)	(1.509)	(1.513)
Age squared	0.992**	0.986**	0.861**	0.880**
	(0.465)	(0.467)	(0.380)	(0.381)
Erebia pharte	-0.754	-0.748	-0.803*	-0.804*
	(0.536)	(0.538)	(0.418)	(0.418)
Constant	2.278	2.154	5.184***	5.185***
	(1.737)	(1.751)	(1.497)	(1.500)
Observations	113	113	427	427
LR chi-squared	14.45	16.06	20.97	21.49
LR-test p-value	0.0130	0.0135	0.000820	0.00150

Standard errors in parentheses

*** p<0.01, ** p<0.05, * p<0.1

Species membership. In contrast to our expectations, we did not find evidence that the *Erebia* species under study differed much from each other with respect to their mobility, neither regarding body-size – when we compared larger species like *E. eriphyle* to smaller species like *E. pharte* – nor ecological specialization – when we compared a habitat generalist like *E. pandrose* to a habitat specialist like *E. gorge*. The analysed species are rather homogeneous so that the gradient in body-size and ecological specialization among the species might not be steep enough to show a variance in the mobility. We found that *E. pharte* was more likely to change the plot than the other species. However, this weakly significant effect only emerged if we also included butterflies that were captured only once (Table 3). Hence, evidence for higher mobility in *E. pharte* remains mixed, which could be due to the small sample size.

Nectar availability. Butterflies captured on a plot with a high abundance of nectar flowers were less likely to change the plot than butterflies seen on a plot with a low nectar level. However, we only got this result when we excluded butterflies that were captured only once. We suggest that ringlet butterflies in alpine grassland tend to be sedentary when a suitable habitat patch is found and do not take the risk of entering the surrounding matrix.

Age. We found that age influenced mobility in a unimodal manner. Very young butterflies were more likely to stay on the same plot. With increasing age the butterflies were more likely to change the plot, but towards the end of their flight period the butterflies became more likely to stay on the same plot. We did not find any studies which show a similar mobility pattern with respect to age of butterflies. The decrease in the mobility at the end of the flight period found in the present study could be explained by bad weather conditions, including snow towards the end of our sampling time. After a few days of bad weather we noticed a sharp decline in captures and a few days later the *Erebia* butterflies at our study sites disappeared. At this point the butterflies were probably no longer as dispersive as they had been at the peak of their flight period.

Conclusion

As expected, the Großglockner Hochalpenstraße constrained the mobility of *Erebia* butterflies in the Hohe Tauern national park, i.e. individuals were significantly less likely to change a patch if they had to cross the road. Contrary to expectation, we found but slight differences between *Erebia* species with respect to their mobility. Only *E.pharte* seemed to be more mobile than the other five species. When butterflies were on a plot with high nectar availability, they were significantly less likely to change the plot. Age influenced mobility in a unimodal manner, i.e. mid-aged butterflies were most likely to change the plot. It would be worthwhile to further explore the genus *Erebia* with respect to mobility using data from a wider range of sites over a longer period of time and under more variable conditions.

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