

# Mobility of ringlet butterflies in high-elevation alpine grassland: effects of habitat barriers, resources and age

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**Abstract** Dispersal is a crucial feature for the long-term survival of metapopulations. Each individual that leaves the habitat and enters the matrix takes a risk. Consequently, even winged organisms, like butterflies, are often extremely sedentary and spend much of their lifetime in very restricted areas. For such species, large roads may be a serious obstacle for movement. Here, we aim to study if a large and highly frequented road in an alpine environment hinders the movement of relatively sedentary butterflies of the genus *Erebia*. We conducted a mark-release-recapture study on six alpine *Erebia* species (*E. eriphyle*, *E. epiphron*, *E. gorge*, *E. pharte*, *E. pandrose* and *E. nivalis*) in the Hohe Tauern National Park, Austria. We measured the following variables which we hypothesize to affect movement probability: (a) species identity, (b) nectar resource availability, (c) butterfly age or (d) patch isolation through the road. Population density estimates ranged from  $230 \pm 35$  individuals for *E. pharte* to  $1,316 \pm 205$  individuals for *E. epiphron* per hectare. More than 50 percent of recaptured butterflies were tracked within distances of <25 m. The maximum flight distance recorded was 332 m (*E. epiphron*). Our data indicate that species identity generally did not have a significant effect on mobility patterns in the studied *Erebia* butterflies. Only one species, *E. pharte*, was more likely to change the plot than the others. High resource availability decreased butterfly movement.

Age influenced mobility, with mid-aged butterflies being most likely to move between patches. The road hindered dispersal. Butterflies which had to cross the road to get to another suitable habitat patch were less likely to move than butterflies that did not have to cross the road.

**Keywords** Dispersal · Habitat fragmentation · *Erebia* · Alpine butterflies · Age · Mark-release-recapture

## Introduction

Dispersal—the movements of organisms away from a colonized habitat patch—is a key feature for the persistence of butterfly metapopulations (e.g. Ugelvig et al. 2012; Hanski et al. 2000). When suitable habitat is fragmented into smaller patches, dispersal patterns may change. In a highly fragmented landscape, entering the surrounding matrix to reach new suitable habitat patches becomes very risky. In the matrix, mortality is generally higher and reproductive success lower (Fahrig 2001, 2007). Hence, fragmentation may impose high costs during dispersal through the matrix (Andreassen and Ims 1998; Robinson et al. 1995). Therefore fragmentation may lead to lower dispersal rates between habitat patches (Schtickzelle et al. 2006), viz. individuals may stay sedentary once a suitable patch is found. Species that are naturally sedentary may thus be less affected by habitat fragmentation than more mobile species. Some satyrine grassland butterflies, e.g. *Maniola jurtina*—although capable of moving distances of more than 2 km—tend to stay within a distance of 100 m, even if their habitat does not seem to be fragmented (Grill et al. 2006).

Ringlet butterflies of the genus *Erebia*, which occupy alpine grasslands, are also relatively sedentary with most movements occurring within distances of 1 km (Kuras

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et al. 2003). Hence, it is possible that *Erebia* butterflies are particularly well adapted to persist in fragmented landscapes and will not be affected as strongly by anthropogenic barriers introduced into their habitats, e.g. roads cutting through high alpine habitat. On the other hand, habitat fragmentation might be particularly destructive to butterfly populations in alpine habitats. The overall harsh climatic conditions in combination with frequent and sudden episodes of bad weather in such an environment may increase mortality during dispersal events. This also renders the recolonization of patches where local populations have gone extinct due to stochastic processes less likely. Further, due to recent climate change, mountain butterfly species are presently shifting their distributions towards higher elevations (Settele et al. 2008; Hardy et al. 2014; Zografou et al. 2014). Hence, when distribution ranges shift upwards and high-altitude habitats become increasingly fragmented into smaller patches, organisms that are restricted to habitats above the tree line, like a number of species in the genus *Erebia*, might be those most threatened. Understanding dispersal patterns of such high alpine butterfly populations and what might be a barrier for dispersal is therefore fundamental for developing and adapting conservation plans.

Ringlets are univoltine species and their adults fly from May to September, depending on the respective species and altitude. They are relatively small butterflies with wingspans of about 3–5 cm. The larvae of all *Erebia* species feed on grasses and sedges (Sonderregger 2005).

In Austria, about 25 *Erebia* species occur, and most of them can be found within the Hohe Tauern National park, where we chose our study area (Huemer and Wieser 2008). In this genus, several species often occur sympatrically (Kudrna et al. 2011). The big advantage in working with different species within a single genus is that possible differences in mobility patterns are unlikely to result from phylogenetic origin or gross contrasts in morphological or physiological capacities. This makes *Erebia* a unique system for comparing mobility patterns among congeneric species in a high-elevation landscape.

Observed mobility patterns of butterflies might also depend on the individual's age. Karlsson (1994) suggested that flight characteristics in butterflies such as maneuverability and speed increase with age. Male butterflies might depend on increasing their mobility as they age in order to find mates and increase their fitness. Bergman et al. (2011) found that old virgin females of *Pararge aegeria* spent more time in flight and performed more individual flights than young virgin females and mated females. This behavior makes them more likely to encounter a male and thus increases their reproductive success. Kemp (2002) found that absolute body mass and abdomen mass in males of the tropical nymphalid butterfly *Hypolimnas bolina*

decreased with age. Absolute thoracic mass, however, which has been positively correlated to flight performance (Berwaerts et al. 2002), remained constant. This might indicate that relative mobility in males of *H. bolina* increases with age. Generally speaking, in female butterflies, abdomen mass is mainly made up of eggs. When they age and their abdomens lighten as a result of egg-laying, flight characteristics such as velocity and acceleration might well increase (Fischer and Kutsch 2000). Hence, butterflies might be more dispersive as they get older. However, to our knowledge, very few studies have thoroughly investigated the effect of the individuals' age on butterflies' mobility, especially in high alpine habitats.

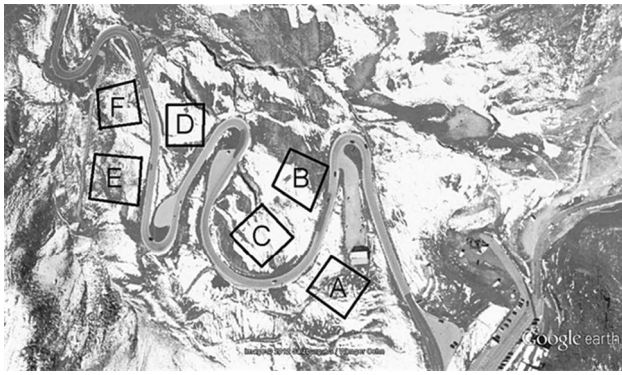
We analyzed dispersal patterns of six *Erebia* species in an anthropogenically fragmented alpine habitat in the Hohe Tauern National Park in Austria, where a large road cuts through the natural habitats of these butterflies, even far above the tree line. Large roads may constitute severe obstacles for butterflies. For example, in Poland at least 7 % of the butterflies on road verges died due to collisions with cars (Skórka et al. 2013). Since butterflies are model organisms for the study of dispersal, numerous studies on the mobility of butterflies already exist (e.g. Casula 2006; Hanski et al. 2006; Nève et al. 1996). However, while species of the genus *Erebia* make up an essential fraction of butterfly communities in alpine grassland habitats (Sonderregger 2005; Neumayer et al. 2005; Gutiérrez 1997) still little is known about their dispersal behavior.

The following questions were asked: (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? A higher dispersal rate was expected between habitat patches on the same side of the road than between patches on different sides. (2) Does the road have differential effects on the mobility patterns of the respective *Erebia* species? Species that are more restricted to particular habitats might be more affected by the road. (3) Do factors like nectar availability or age influence the mobility patterns? Butterflies might be rather drawn to leave a habitat patch when there is little nectar available. Age was expected to influence mobility, that is, dispersal likelihood was expected to increase with age. Finally the population density for the six analyzed *Erebia* species was estimated in the course of our study.

## Materials and methods

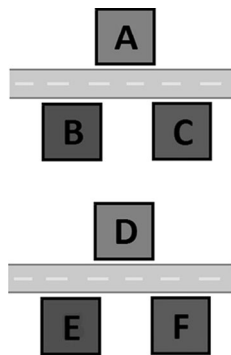
### Study area

Our field study was conducted in the Hohe Tauern National Park in Austria (for general information, see Stadel et al. 1996 and <http://www.hohetauern.at/en/>). For mark-release-



**Fig. 1** Map of the study area: Analyzed plots in the Hohe Tauern National Park. “upper triangle” with the plots ABC, “lower triangle” with the plots DE

**Fig. 2** Schematic overview of the “upper triangle” ABC and the “lower triangle”



recapture experiments, alpine meadows located distinctly above the natural tree line at an altitude of 2,300–2,400 m were chosen. These alpine meadows were relatively homogenous regarding slope and resources relevant to ringlet butterflies, with only small fractions of open soil and rocks. A large road of on average at least 8 m width, the “Großglockner Hochalpenstraße”, cuts through the national park. The road was built in 1935 and is highly frequented, with about 267,000 motor vehicles per year between May and November (Großglockner Hochalpenstraße 2013). To determine whether the road has a negative impact on dispersal of ringlet butterflies, two habitat plots were examined on one side of the road and one plot on the other. The plots were arranged within these relatively homogeneous meadows with no natural structures determining their borders. The three plots formed a triangle. This setting was replicated a second time, so that in total six plots were analyzed. Each plot had a size of  $40 \times 40 \text{ m}^2$  and the distance between plots was also 40 m. This is a distance even rather small-sized *Erebia* species can easily overcome (Kuras et al. 2003). The plots of the first (upper) triangle were named A, B and C, while plots of the second (lower) triangle were named D, E, and F (Figs. 1, 2). The plots A and D are referred to as “separated

plots” hereafter, since they were segregated from the other plots by the road.

#### Data collection

A mark-release-recapture study was conducted at these plots between 7 July and 14 August 2012. Study sites were visited daily (if weather permitted) in a random order, usually from 9:30 am to 6:00 pm. Sampling time at each plot per day was about 1 h. All representatives of six *Erebia* species, namely *E. eriphyle*, *E. epiphron*, *E. gorge*, *E. pharte*, *E. pandrose* and *E. nivalis* were captured with a hand-held net and individually marked with a consecutive number on the underside of one hind wing. For marking, a fine-point permanent marker (Staedtler Lumocolor) was used. Butterflies were released immediately after marking; handling time was  $<1$  min. According to Morton (1982) the impact of handling and marking can influence the outcome of mark-release-recapture studies. However, we did not have the impression that this was the case for the *Erebia* species under study, since they are rather robust butterflies. Sex, age, hour of capture and location was noted for every butterfly. Age was estimated by wing-wear on the following scale (1 = fresh, 2 = small pieces of wing missing, 3 = very damaged wings). The location was recorded with a GPS-device (Garmin Dakota 20). Once a week the available nectar sources (flower abundance, estimated on a rank scale from 1 to 4) were documented.

#### Data analysis

##### *Population density and structure*

The population size of each *Erebia* species was estimated in the program MARK 6.1 (White and Burnham 1999) using constraint linear models. The Jolly-Seber method as implemented in MARK: POPAN was used, because it is suitable for repeatedly sampled open populations (Schwarz and Arnason 1996). The method estimates daily and total population size. The four parameter index matrices (PIMs),  $\phi$  (apparent survival),  $p$  (capture probability),  $\text{pent}$  (probability of entering into the population) and  $N$  (super-population size) may be constant or dependent e.g. on time. The most appropriate model was selected for each data subset based on AIC-values corrected for small samples (White and Burnham 1999).

##### *Mobility, species identity, resources and age*

The distance covered by butterflies was scored as the shortest line distance between the site coordinates of the first and the subsequent capture using Google Earth. The impact of the road on the mobility was tested using

maximum likelihood estimation. This allows to control both for individual characteristics of the butterflies (e.g. age, sex) and characteristics of the plots (e.g. nectar availability).

To estimate the probability of changing the plot we made use of a logit model in the program STATA 11. In our model, the dependent variable “same plot” took the value 1 if the butterfly was recaptured on the same plot, and it took the value 0 if the butterfly came from a different plot. Further, a dummy variable was constructed 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 had come from any other plot. The same was done for the variable “plot D”. Butterflies captured on plot A or D, respectively, were expected to be more likely to stay on the same plots rather than crossing the road. It was further tested whether modelling results changed if just one dummy variable “plot A or D” was constructed, instead of using two dummy variables as described above. Again, it was expected that if a butterfly was recaptured on either of the separated plots A or D, it was more likely that this butterfly had initially been captured on these than on the other plots. This means, if a butterfly was captured on a separated plot, it was expected to be less likely that this butterfly had been on a different plot before, because otherwise it would have had to cross the road.

If we use a linear probability model instead of a logit model, we can predict probabilities which are negative or larger than one for certain values of the regressors. In general, the predictive probabilities of a linear model only lie between zero and one for observations whose regressors are close to the average of the sample. Moreover, for any unit change in the regressor, a linear model predicts a constant change in the probability of a butterfly changing the patch, while the logit model allows for diminishing effects (e.g. for nectar availability).

Nectar availability, species identity and age were included in the model. Nectar availability entered linearly into the regression equation. In contrast, age entered quadratically into the regression equation to account for possible unimodal effects. A dummy variable for species identity was constructed, e.g. the dummy variable “*Erebia pharte*” took the value 1 if the captured butterfly belonged to the species *E. pharte* and took the value 0 if it belonged to any other species. Information criteria (AIC) and likelihood ratio tests were used for model selection. First, a model containing the full set of variables was used. Then variables were successively eliminated and the model that explained our data best according to information criteria was selected. We also checked if species differed with respect to their representation among age classes using a  $\chi^2$  test.

**Table 1** Observed ringlet species (genus *Erebia*) and their respective mark and recapture rates

Species	Marked	Recaptured
<i>E. eriphyle</i>	88	35
<i>E. epiphron</i>	75	31
<i>E. pharte</i>	43	26
<i>E. gorge</i>	49	9
<i>E. pandrose</i>	34	6
<i>E. nivalis</i>	25	6

## Results

### Population density and structure

In the 6 weeks of mark-release-recapture a total of 429 individuals were marked and 113 of them recaptured (Table 1). 155 of the 429 captured butterflies were females, 211 were males, and for the remaining 63 the sex was not determined. The most frequently captured species were *Erebia eriphyle* and *E. epiphron* (Table 1). Except for *E. pandrose* all species occurred throughout the whole sampling time. The population of *E. pandrose* already collapsed at the end of July. 200 individuals were captured of age category 1, 157 of age category 2 and 72 of age category 3 (Table 2). There were significant differences in frequencies of captures among the species with respect to their age using a  $\chi^2$  test ( $p < 0.0001$ ). According to the POPAN model in the program MARK, total population densities were ranging from 230 individuals (*E. pharte*) to 1,316 individuals (*E. epiphron*) on roughly 1 ha (one plot = 1,600 m<sup>2</sup>, all six plots in total = 9,600 m<sup>2</sup>; Table 3). In the chosen best models phi and  $p$  were held constant. The only exception was the population size estimation for *Erebia gorge*, where according to the AIC-values our data could be best explained when phi was dependent on time and  $p$  was held constant.

### Mobility, species identity, resources and age

More than 50 % of the butterflies were recaptured within a distance of <25 m from the location of their initial capture (Fig. 3). The maximum flight distance recorded was 332 m for a female *E. epiphron*. Very few butterflies (~8 %) were recaptured at a distance of more than 100 m. Our data indicate that—regarding the disposition to change the plot—there was no difference between an alpine habitat generalist like *E. pandrose* and an alpine habitat specialist like *E. gorge*. *E. pharte* was overall more likely to change between plots than the other ringlet species (Table 4). The road, however, seemed to hinder movement. When pooling the triangles and comparing the “separated” plots A and D

**Table 2** Age distribution of six *Erebia* species in the MRR study

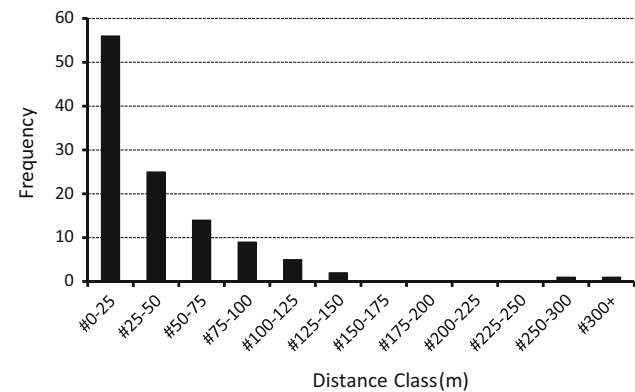
	<i>E. eriphyle</i>	<i>E. epiphron</i>	<i>E. pharte</i>	<i>E. gorge</i>	<i>E. pandrose</i>	<i>E. nivalis</i>
Age category I	64	71	21	21	9	14
Age category II	45	28	28	25	21	9
Age category III	14	7	20	12	10	8

Using a  $\chi^2$ -test for differences in frequencies of captures among the species with respect to their age the null hypothesis of homogeneity was rejected ( $p < 0.0001$ )

**Table 3** Total population sizes estimated in the program MARK

Species	Total population size	Standard error	95 % CI	
			Lower	Upper
<i>E. eriphyle</i>	1,260	207	853	1,666
<i>E. epiphron</i>	1,316	205	914	1,719
<i>E. pharte</i>	231	35	163	299
<i>E. gorge</i>	337	70	201	474
<i>E. pandrose</i>	797	258	290	1,303
<i>E. nivalis</i>	497	137	228	766

Jolly-Seber-method implemented in POPAN; phi (apparent survival) and  $p$  (capture probability) were held constant, except for *E. gorge*, where phi was dependent on time and  $p$  was held constant



**Fig. 3** Histogram of distances (m) moved by *Erebia* butterflies. The maximum flight distance recorded was 332 m (*Erebia epiphron*)

to the plots BCEF, we found that butterflies captured on the separated plots were less likely to change the plot across the road. If there was a high abundance of nectar flowers on a plot, butterflies were also significantly less likely to change the plot.

Other variables that we recorded but which turned out to be insignificant with respect to movement were vegetation height, wind and cloudiness. Our main findings remained valid if we included those variables in the statistical models.

According to the logit model (Table 4) butterflies captured on plot D were more likely to stay on the same plot

**Table 4** Maximum likelihood estimation (logit model) of the probability of ringlet butterflies changing between alpine grassland plots

Variables	Logit—Model 2 (Plot A or D)	
	Logit—Model 1 (Plot A, Plot D)	Logit—Model 2 (Plot A or D)
Plot A	0.669 (1.260)	
Plot D	2.801** (1.167)	
Plot A or D		2.135** (0.903)
Nectar	0.695** (0.289)	0.647** (0.286)
Age	−3.981** (1.839)	−3.977** (1.832)
Age squared	0.986** (0.467)	0.992** (0.465)
<i>Erebia pharte</i>	−0.748 (0.538)	−0.754 (0.536)
Constant	2.154 (1.751)	2.278 (1.737)
Observations	113	113
LR $\chi^2$	16.06	14.45
LR-test $p$ value	0.0135	0.0130

In model 1, two dummy variables (Plot A and Plot D) were used. In model 2, only one dummy variable (Plot A or D) was used. Regression coefficients; standard errors in parentheses

\*\*  $p < 0.05$

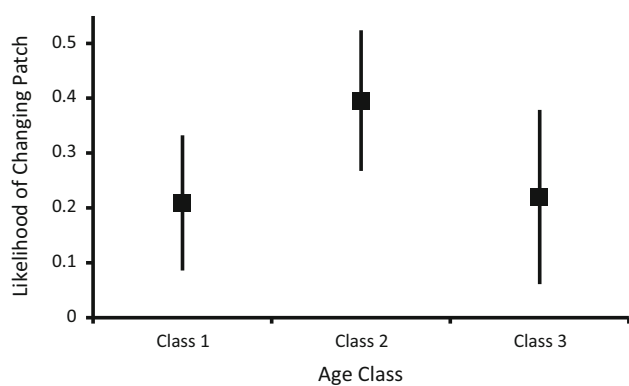
than butterflies captured on the other plots of the “lower triangle”. Analogous effects were not found for plot A relative to B and C, i.e. in the triangle of plots at higher elevation. This might be due to a lower sample size and thus reduced statistical power for data from the upper triangle.

Age entered quadratically into the regression equation. Very young butterflies were more likely to stay on the same plot. When they got older their probability to change the plot increased, whereas at the end of their flight period they became again more likely to stay on the same plot (Fig. 4).

**Discussion**

Population density and structure

The total population density estimates for the six *Erebia* species ranged from 240 individuals per hectare for *E. pharte* to 1,371 individuals per hectare for *E. epiphron* (Table 3). These densities are in a similar range as reported by Slamova et al. (2012) for congeneric *E. aethiops* in a



**Fig. 4** Likelihood of *Erebia* butterflies to change plot with respect to age. In order to display the effect of age on the likelihood of changing the plot, we used marginal effects based on the logit estimation shown in Table 4. For each age category, the graph depicts the average marginal effect ( $\pm 95\%$  confidence intervals) of an increase in age on the probability of changing the plot, holding all other variables of our regression model constant

montane nature reserve in the Czech Republic and by Brussard and Ehrlich (1970) for *E. epipsodea* in mountainous central Colorado. Estimated population densities of the studied *Erebia* species did not correlate with their absolute capture frequencies. According to the POPAN model *E. pharte* had the smallest population size of the six species under study, but it was the third-most frequently captured species during our fieldwork and recapture rates were high (Table 1). *E. pharte* was also the only species with a higher likelihood to change the plot than the other five species. Low recapture rates, in contrast, can lead to inflated population size estimations. This was the case for *E. pandrose*, with a moderate number of sightings, but few recaptures. Apparent sex ratios were biased towards males for four *Erebia* species, but not for *E. eriphyle* and *E. pandrose*. Biased sex ratios have also been found for *E. epiphron* and *E. sudetica* (Kuras et al. 2003). Male butterflies are often more active than females, patrolling in search for females (Slamova et al. 2011). This makes them more likely to be observed and can lead to a bias towards male individuals in the number of captures. *E. pandrose* butterflies disappeared from our study site at the end of July. According to Sonderegger (2005) *E. pandrose* is the earliest appearing *Erebia* species in the Alps with a flight period from early June to August. The rather early disappearance of adult *E. pandrose* butterflies in the summer of 2012 might be due to a period of inclement weather conditions including snowfall, after which they were not able to recover. Our field study started at the beginning of July. Therefore young individuals of *E. pandrose* might have been missed and predominantly mid-aged and old individuals were captured instead.

Does a large road act as a dispersal barrier for *Erebia* butterflies?

Our data indicate that the road constrained the movement of ringlet butterflies. Roads have previously been reported to restrain movements of sedentary butterfly species, while more mobile species were not affected (Munguira and Thomas 1992; Fjellstad 1998). This is in line with the results of the present study, as butterflies of the genus *Erebia* are generally thought to be rather sedentary (Kuras et al. 2003). A study on *Aphantopus hyperantus* in Finland showed that a highway significantly hindered butterfly movements (Valtonen and Saarinen 2005). Studies on the highly mobile *Anthocharis cardamines* by Dennis (1982, 1986) demonstrated that a large road reduced their mobility, while the matrix was no barrier to movement. Dennis' work showed that a road can be a real obstacle with many butterflies turning around when approaching the road and staying in the original patch.

The naturally low mobility of *Erebia* butterflies might be an advantage in this scenario, as they are generally unlikely to fly distances that would involve crossing the road. Of course, resources did play a role: *Erebia* butterflies were less likely to change a plot and take the risk of crossing the road as long as nectar availability on a site was high. Bhattacharya et al. (2003) found a similar behavior in bumblebees which were hindered in their movements by a railroad cutting through a conservation area. The bumblebees were reluctant to cross the barriers unless their resources were declining.

Does the road have differential effects on the mobility patterns of the respective *Erebia* species?

Contrary to expectation, it was not evident that the *Erebia* species under study differed much from each other with respect to their mobility. Although it has been suggested that relative habitat generalists—like *E. pandrose*—are more dispersive (Quinn et al. 1997), we did not find a significant difference to relative habitat specialists in their mobility. Only *E. pharte* had a higher probability to change the plot (Table 4). The analyzed species, however, are rather homogeneous regarding habitat requirements so that the gradient in specialization among the species might not be steep enough to reveal a variance in the mobility.

The small movement distances observed in our marked alpine ringlet butterflies correspond to what has been found in other studies, and underline that distances moved by grassland butterflies are on average short (>50% stayed within 25 m between two capture events, see Fig. 3). Kuras et al. (2003) also found that the alpine ringlet butterflies *Erebia sudetica* and *E. epiphron* in the Hrubý Jeseník Mountains (Czech Republic) were more likely to stay

within short distance with only rare movements of distances up to 1 km. A similarly constrained mobility was shown for an alpine population of *Euphydryas aurinia* by Junker et al. (2010). These authors suggested that low mobility might be an adaptation of alpine butterfly species to their high-elevation habitat. They argued that limited movement distances might prevent accidental drift events, e.g. by squalls, in these harsh environments. Low mobility, however, has also been shown to prevail for lowland *Satyrinae* species under far more favourable climatic conditions, such as *M. jurtina* (Grill et al. 2006). Although these latter butterflies are physiologically capable of moving more than 2 km, most individuals behave rather sedentarily and spend their whole lifetime in a small area. Different findings arose in a study by Dennis (2004), where butterflies of the same species frequently engaged in long direct flights, especially in unsuitable habitats.

An example for prevailing short distance movements in lycaenid butterflies comes from Nowicki et al. (2013), where the proportions of emigrants of *Maculinea* butterflies that reached other local populations through the matrix were low. Generally, in sedentary species, like *Erebia*, only a small fraction of the population acts as dispersers and take the risk of entering the matrix to reach new suitable habitat patches. Dennis et al. (2013) showed that the permeability of the border between patch and matrix also depends on the composition and structure of patch and matrix, as well as the connectivity of these elements.

Do factors like nectar availability or age influence the mobility patterns?

#### Resource availability

Nectar availability influenced the mobility of *Erebia* butterflies, i.e. butterflies captured on a plot with a high abundance of flowering plants were less likely to leave the plot than butterflies seen on a plot with a low nectar level. Loertscher et al. (1995) found that the micro distribution of the butterflies *Melanargia galathea*, *Polyommatus coridon*, *Ochlodes sylvanus* and the burnet moth *Zygaena loti* was strongly influenced by the distribution of their nectar plants. Later on, Kuussaari et al. (1996) observed that emigration rates in the butterfly *Melitaea cinxia* decreased with high flower abundance on a habitat patch. Not only butterflies are less mobile when they are on patches with abundant resources, but also other groups of organisms such as waders (Dias et al. 2009) or springtails (Westerberg et al. 2008). Accordingly, ringlet butterflies in alpine grassland tend to behave more sedentarily when residing on a suitable habitat patch and then avoid the risk of entering the surrounding matrix.

#### Age

The butterflies' age affected their mobility in a unimodal manner. Very young butterflies were more likely to stay on the same plot. With increasing age the butterflies were more prone to change the plot, but towards the end of their flight period the butterflies became more sedentary again. This is quite an interesting finding, since to our knowledge no in situ studies exist which show a similar mobility pattern with respect to the age of the individuals. Age was indirectly measured on wing-wear, which is not a perfect measure of age and may cause some noise in the results. On the other hand, wing-wear is a common measure for butterfly age (e.g. Walters et al. 2012), since wings cannot be repaired after eclosion from the pupa. Wing damage may also be a reason for very old butterflies moving less than mid-aged butterflies.

Karlsson (1994) suggested that male butterflies might be dependent on increasing their mobility as they age in order to find mates and increase their fitness. This author found that older individuals of *P. aegeria* and *Speyeria mormonia* had proportionally more flight muscles and more thorax mass than younger ones, which can indicate that an individual is more mobile (Hill et al. 1998). In contrast, Ahman and Karlsson (2009) observed reduced flight endurance in older *Pieris napi* butterflies. A possible explanation might be that adult butterflies are able to reallocate nitrogen resources from flight muscle mass and use it to increase their reproductive output (Stjernholm and Karlsson 2008). A decrease in flight muscle mass might lead to weaker flight performance towards the end of the flight period. The observed mobility patterns might also be explained by bad weather conditions including snow towards the end of our sampling time. After a few days of bad weather in mid-August a sharp decline in captures was notable. At this point the butterflies were probably no longer as dispersive as they had been at the peak of their flight period. The effect of age on mobility deserves consideration, and it would be worthwhile to explore differences between species within the genus *Erebia* with regard to the age-effect.

An aspect that has not been included into the present study is that the availability of larval host plants also plays a crucial role for the dispersal ability of a butterfly. This aspect should be taken up in future work. But most *Erebia* species in alpine grasslands feed on grasses, which are a less limiting factor than, for example, microclimate (Kleckova et al. 2014). Similarly, detailed studies on butterfly movement behavior right next to the road would reveal more information on what exactly prevents animals from crossing the road.

#### Conclusion

Our data show that besides resource availability, patch isolation is a limiting factor for the mobility of *Erebia*

butterflies. Dispersal of *Erebia* butterflies in alpine grassland above the treeline turned out to be limited. As expected, a large highly frequented road hindered the movement of *Erebia* butterflies.

To preserve a butterfly's metapopulation structure, the ability of dispersal is a key process (Hanski et al. 2000). If butterflies are restricted to habitat patches on one side of the road, genetic exchange between demes within a metapopulation on different sides of the road may ultimately become limited. This, in turn, can result in a decrease in heterozygosity and an increased extinction risk (Saccheri et al. 1998). Gene flow of the *Erebia* species under study might become even more restricted between demes on either side of the road, if traffic increases. During summertime, i.e. the flight time of butterflies, traffic on the Grossglockner Hochalpenstrasse is indeed heavy. Hence, over the years a population may ultimately become divided into two genetic pools. As already mentioned, the naturally low mobility of *Erebia* butterflies might be an advantage in the context of fragmentation, as their risk of dying in the matrix is lower than for species of intermediate mobility (Poniatowski and Fartmann 2010). Therefore, species with intermediate mobility might be more affected by the road. Studying the effect of this road on other species would therefore be interesting. Since many butterfly species are shifting their distribution areas upwards (Settele et al. 2008; Schmitt et al. 2014), high mountain habitats will probably harbor more and more species in the near future and should remain in the focus of ecological study.

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