MASTERARBEIT

Titel der Masterarbeit

„Mobility of ringlet butterflies in high-elevation alpine grassland: Effects of habitat barriers, resources and age"

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Contents

1   Introduction

Numerous studies show that dispersal – the movements of organisms away from an existing population – is a key feature for the preservation of butterfly metapopulations (e.g., Hanski et al. 2000, Hill et al. 1996, Nève et al. 1996). When suitable habitat is fragmented into smaller patches, dispersal patterns may change. An increase in fragmentation causes an increasing amount of edge conditions to occur in the suitable habitat and frequent encounters with patch edges may increase the probability of individuals to leave the habitat and enter the matrix. In the matrix, the mortality rate is generally higher and the reproductive rate is lower (Fahrig 2001). On the other hand, fragmentation may also lead to lower dispersal rates between habitat patches and higher mortality rates during dispersal for butterflies (Schtickzelle et al. 2006). In a highly fragmented landscape, if habitat patches become too small to undergo the entire life-cycle, the majority of individuals have to take the risk of entering the matrix to reach new suitable habitat patches. Hence, fragmentation may cause high 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 once another suitable habitat patch is found. Schtickzelle and Baguette (2003) found in a behavioral study that butterflies engaged in U-turns when they reached the boundary of a habitat patch. Some nymphalid butterflies, e.g. *Maniola jurtina* – even though capable of moving distances of more than 2 kilometers – tend to stay in the same area within a distance of 100 meters, even if habitat fragmentation is not a limiting factor for movement (Grill et al. 2006). Butterflies of the genus *Erebia* are relatively sedentary and often form dense populations. For instance, Kuras et al. (2003) have shown for *E. epiphron* that about 4300 individuals occurred on just 1.2 km^2 of habitat in alpine grassland in the Hrubý Jeseník Mountains in the Czech Republic. Species that are relatively sedentary and thus, rather restricted in their mobility might be even more affected by habitat fragmentation. Fragmentation causes species to live in restricted areas of suitable habitat, which can affect the genetic variability and the extinction risk of populations (e.g., Lande 1988). When species are forced to live in restricted 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). Further, a reduced habitat area may constrain local abundance so that ultimately species go lost from patches. This process likely affects habitat specialists more than habitat generalists. Habitat generalists might also use other landscape elements in the surrounding landscape matrix, whereas habitat specialists depend on their respective type of habitat (Krauss et al. 2003). Besides reducing habitat patch sizes, fragmentation is also known to increase isolation (Andrén 1994). When suitable habitat is fragmented into relatively isolated patches, the individuals' interpatch migration rate may become low. If a local population on an isolated patch additionally experiences random extinction, the persistence of the whole metapopulation can be at risk (Leimar & Norberg 1997). Once a population on an isolated patch is extinct, recolonization is very unlikely (Heino & Hanski 2001).

Habitat fragmentation might be more destructive to butterfly populations in an alpine habitat as opposed to lowland conditions. The harsh climatic conditions and frequent and sudden onsets of bad weather in such an environment may increase the mortality during dispersal events. This also makes the recolonization of patches where local populations went extinct due to stochasticity processes less likely. Due to recent climate change, mountain butterfly species have shifted their distributions towards higher elevations (Parmesan 1996). Hence, when distribution ranges are shifted upwards due to global warming and high-altitude habitats become fragmented into smaller patches, organisms that are restricted to habitats above the tree line 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 often occurring sympatrically (Stettmer et al. 2007). This makes *Erebia* unique for comparing mobility patterns among congeneric species in a high elevation landscape.

I analysed the dispersal patterns of alpine *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, even far above the tree line. Since butterflies are model organisms for the study of dispersal, numerous studies on this subject already exist

(e.g., Casula 2006, Hanski et al. 2006, Nève et al. 1996). However, little is known about the dispersal patterns of the butterfly genus *Erebia* (Nymphalidae: Subfamily Satyrinae) with numerous species adapted to alpine habitats, such as *E. gorge, E. pandrose, E. nivalis, E. epiphron, E. eriphyle, E. manto* and *E. cassioides* (Neumayer et al. 2005, Gutiérrez 1997). They are univoltine species and their adults fly from May to September, depending on the respective species and altitude. The butterflies occur on altitudes of 500 m to more than 2500 m. They are relatively small butterflies with wingspans of about 3–5 cm. The larvae of all *Erebia* species feed on different types of grass (Stettmer et al. 2007). While some species are habitat generalists like *E. medusa*, others are habitat specialists like *E. aethiops* (Polus et al. 2007). I was able to compare habitat specialists to habitat generalists as well as larger butterflies to smaller butterflies that are phylogenetically close. That is, possible differences in mobility patterns do not necessarily result from a different phylogenetic origin. According to Komonen et al. (2004) and Quinn et al. (1997) habitat generalists are more mobile than habitat specialists. Hence, I compared a habitat generalist, like *Erebia pandrose* to a habitat specialist, like *Erebia gorge*. *Erebia 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 (Verovnik 2000, Stettmer et al. 2007, Tolman & Lewington 2012). Hill et al. (1998) suggested that butterflies with a relative high investment in thorax mass – which is principally associated with flight muscle mass – are more dispersive than butterflies with a relative low investment into the thorax. The adults of the summer-generation of the polyphenic map butterfly *Araschnia levana*, for example, have a heavier thorax and a larger wing area than the spring-generation in order to achieve a greater mobility in summer (Zdenek & Konvicka 2002). Berwaerts et al. (2002) found that the flight performance of *Pararge aegeria* butterflies was positively correlated with total body mass, thorax mass, forewing area, forewing length and wing loading. It has also been shown for the Sand Cricket that the propensity and duration of flight is positively correlated to wing length (Fairbairn & Roff 1990). Therefore, I wanted to compare larger butterflies to smaller butterflies.

In this study, I analysed the movement of six alpine *Erebia* species, namely *E. eriphyle,*

E. epiphron, E. gorge, E. pharte, E. pandrose and *E. nivalis.* I aimed at analysing which of the following variables predicts movement probability: (a) species membership, (b) ecological specialization, (c) nectar resource availability, (d) age or (e) patch isolation. I 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? I expected a higher dispersal rate between inhabited 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 an alpine habitat generalist like *Erebia pandrose* and an alpine habitat specialist like *Erebia gorge*? Note that all analysed *Erebia* species are relatively specialized since they are all adapted to alpine habitats. However – as already mentioned above – some species are more specialized than others. I expected the habitat generalist to be more mobile than the habitat specialist, i.e. the habitat specialist to be more affected by habitat fragmentation and hence 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? I expected larger species to be more mobile and smaller species to be more likely to stay on the same habitat patch. (4) Do factors like nectar availability, vegetation height or age influence the mobility patterns? I expected nectar availability and vegetation height to influence the butterfly mobility in the sense that if butterflies are on a habitat patch with sufficient resource availability, they might be less likely to leave that patch. Such a behavior has been found by Kuussaari et al. (1996) for the butterfly *Melitaea cinxia*. Resource availability has also been shown to influence the distribution of *Polyommatus coridon* (Krauss et al. 2005) and it may influence butterfly migration rates as well (Dennis et al. 2003). High vegetation may be important for butterflies when weather conditions change abruptly and get harsh which is quite common in an high-elevation environment. Higher vegetation features may then serve as a shelter for butterflies. Dover et al. (1997) found that butterflies spent more time in sheltered areas as wind speed increased. I expected age to influence the mobility, that is the migration rate was expected to increase with age. Karlsson (1994) suggested that flight characteristics of butterflies such as maneuverability and speed increased with age.

2   Material and Methods

2.1   Study area

Since numerous *Erebia* butterflies are adapted to alpine habitats, I conducted my field study in the Hohe Tauern National Park in Austria (for general information see Stadel et al. 1996 and http://www.hohetauern.at/en/). This national park comprises many suitable alpine habitats for these butterflies like meadows or dwarf shrub heaths and 22 *Erebia* species occur there (Tolman & Lewington 2012, Neumayer et al. 2005). For this study I chose alpine meadows located at an altitude of 2300–2400 meters, distinctly above the natural tree line. These alpine mountain meadows were relatively homogenous regarding slope and resources with small fractions of open soil and rocks, relevant to ringlet butterflies. On all investigated meadows dwarf shrubs such as *Salix herbacea* occurred. A large road, the "Großglockner Hochalpenstraße", leads through the national park – connecting the Austrian states Salzburg and Carinthia – and cuts through these meadows. The Großglockner Hochalpenstraße was built in 1935 and 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 a negative impact on dispersal of ringlet butterflies, I examined two inhabited habitat plots on one side of the road and one plot on the other. The plots were arranged within these relatively homogeneous meadows with no natural elements determining the borders of the plots. The three plots formed a triangle. This setting was replicated a second time, so that I analysed six plots in total. Each plot had a size of 40 x 40 m^2 and the distance between plots was also 40 m. This is a distance *Erebia* species can easily overcome, as shown for *E. epiphron* and *E. sudetica* by Kuras et al. (2003). 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.

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.
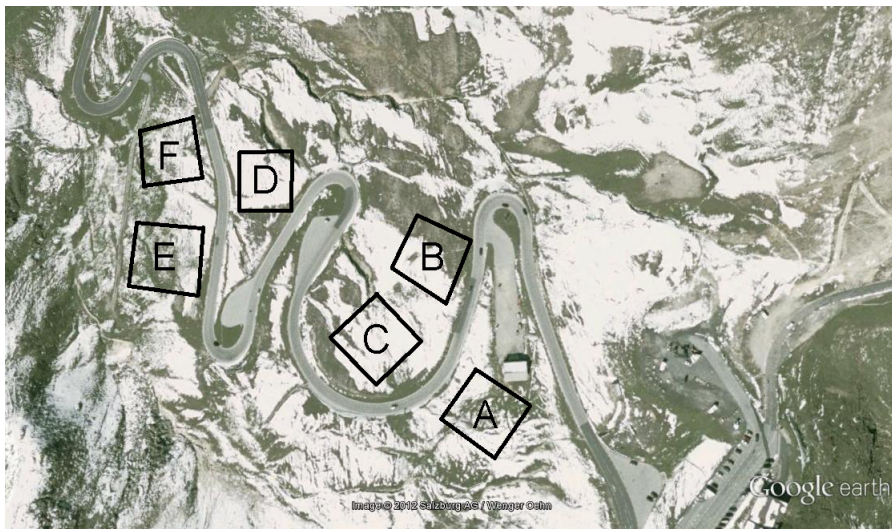

Figure 2: Schematic overview of the
"upper triangle" ABC and the "lower triangle" DEF.
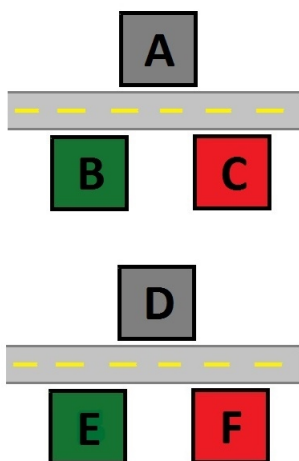
2.2 Data collection

I 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 and I spent six to eight hours per day at the study sites. Sampling time at each plot was about one hour. Butterflies

were captured with a hand-held net and individually marked with a consecutive number on the underside of one hind wing. I used a fine-point permanent marker (Staedtler Lumocolor) and a different colour for each patch (according to the colours used in the diagram in Figure 2). All individuals were released immediately after marking, handling time was less than one minute. Sex, age, hour of capture and location was noted for every butterfly. Age was estimated by wing-wear on an arbitrary scale (1 = fresh, 2 = pieces of wing missing, 3 = very damaged wings). The location was recorded with a GPS-device (Garmin Dakota 20) and the actual weather conditions were noted as well. I estimated wind intensity and the amount of clouds on a scale from 0–3. I also documented important resource features: once a week the available nectar sources (estimated on a scale from 1–4), the mean vegetation height (cm) and any tracks of grazing life stock (on a scale from 0–3) were estimated. At the end of my field study I quantified the vegetation cover by dwarf shrubs (in percent), which may serve as shelter during bad weather conditions. Also, I estimated the share of open soil, rock, rubble and other structures where butterflies can warm-up before resuming flight.

2.3 Data analysis

Mobility. I analysed the distance covered by butterflies by measuring the shortest line distance between the site coordinates of the first and the subsequent capture using Google Earth. I 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, I compared capture and recapure frequencies of the three most frequent species (*E. eriphyle, E. epiphron, E. pharte*) and the three categories by means of contingency tables. I calculated the Fisher test for these species in STATA 11 software. As the Boschloo test is uniformly more powerful than the Fisher test (Mehrotra et al. 2003), I also ran this test in the program R 2.15.2. This program has only implemented a version for two-by-two tables, therefore I compared two species and two categories and analysed every possible combination (in total 9). A rejection of the null hypothesis of no difference among

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the species meant that I would not be able to treat the three species as one with regard to their dispersal behavior. In this case, I would have to analyse every species individually in the following statistical analyses. I also compared *Erebia pandrose* and *Erebia gorge* to each other with respect to their mobility patterns using the Fisher and the Boschloo test. The Fisher and the Boschloo test were also used to find out if the road had an impact on the mobility of the three most frequently captured species *E. eriphyle*, *E. epiphron* and *E. pharte*. For this purpose, I compared if butterflies changed the plot less frequently if they were first captured at the separated plot A in contrast to butterflies that were first captured on the plots B or C. I also did this for the lower triangle DEF (for the design, see again Figure 2). I pooled the categories "same side" and "cross road" and named the newly established category "change plot". For this analysis I used the categories "sedentary" and "change plot". First, I compared the plot on one side of the road, plot A, to each plot on the other side of the road, plots B and C. Then I compared plot A to the pooled plots BC. That is, I analysed if butterflies changed the plot less frequently if they were first captured at the separated plot A in contrast to butterflies that were first captured at plots BC. The same was done for the other triangle DEF. Further, I compared the pooled plots AD to the pooled plots BCEF. If one had to reject the null hypothesis that butterflies captured on plots A and D, respectively, change the plot as frequently as butterflies captured on the other plots, the road would seem to have a negative impact on the butterflies' dispersal.

The impact of the road on the mobility was also tested using maximum likelihood estimation. This has the big advantage that one can control both for individual characteristics of the butterflies (e.g., age, sex) and characteristics of the plots (e.g., nectar availability). I used a logit and a probit model in the program STATA 11. First, I excluded those butterflies that had only been captured once (i.e. that were never recaptured). Second, I checked if the modelling results changed if I also included the butterflies that had only been captured once. In my 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. Further, I constructed a dummy variable that indicates 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. I did the same for the variable "plot D". I expected that butterflies captured on plot A or D, respectively, were more likely to stay on the same plots rather than crossing the road. I also tested whether modelling results changed if I constructed just one dummy variable "plot A or D", instead of using two dummy variables as described above. Again, I expected that if I recaptured a butterfly on the separated plots A or D, it was more likely that this butterfly had been initially captured on these same than on the other plots. This means, if I captured a butterfly on a separated plot, it is less likely that this butterfly had been on a different plot before, because otherwise it would have had to cross the road. I also controlled for the effect of nectar availability, age and species identity.[1] Nectar availability entered linearly into the regression equation. In contrast, I allowed age to enter quadratically into the regression equation to account for possible unimodal effects. In general, it was not feasible to have a symmetric design with two plots on each side of the road due to the shape of the road (Remember, there are two plots on one side of the road and one plot on the other side of the road.). Because of the triangular design of the plots, it did not make sense to use the covered distance of the butterflies as a dependent variable in our regression analysis. The reason is that a butterfly crossing the road had to cover a longer distance on average if recaptured than a butterfly changing between the non-separated plots (Pythagoras theorem of the right-angled triangle). Obviously, this countervailing effect is not important if I just compare the distance covered by recaptured butterflies per age across plots. I also checked if there was a difference among the species with respect to their age in the sense that, e.g. some species are more likely to be seen at age category 3 than others using a χ^2 test. I constructed a dummy variable for species identity, 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, BIC) and likelihood ratio tests were used for model selection. I started with a model containing a set of variables, considering collinearity between variables. Then I eliminated variables and selected the model

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[1]Other variables that I tested, but that always turned out to be nonsignificant were wind speed, clouds, sex and altitude. Also, I did not simultaneously include vegetation height and nectar availability in order to avoid multicollinearity between these two variables.

that could explain my data best according to information criteria.

Population size 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. I used the Jolly-Seber method as implemented in MARK: POPAN, because it is suitable for repeatedly sampled open populations (Schwarz and Arnason 1996). The method estimates daily population sizes and total population sizes. The four parameter index matrices (PIMs), phi (apparent survival), p (capture probability), pent (probability of entering into the population) and N (super-population size) may be constant or dependent e.g. on time. I selected the most appropriate model for each data subset based on the AIC-values corrected for small samples (White and Burnham 1999). In my chosen model I held phi and p constant. The only exception was the population size estimation for *Erebia gorge*, where according to the AIC-values my data could be best explained when phi was dependent on time and p was held constant.

3   Results

3.1   Mobility

In the six weeks of mark-release-recapture I marked a total of 316 individuals. 113 of these individuals were recaptured (Table 1). Roughly 62 % of the butterflies were recaptured within a distance of less than 30 metres from the location of their initial capture (Figure 3). I recaptured hardly any butterflies at a distance of more than 100 meters ($\approx 8\%$). My data indicates that neither body-size nor ecological specialization significantly influenced the mobility in *Erebia* butterflies. The road, however, seemed to be a barrier against dispersal.

Using the Fisher test I could not reject the null hypothesis of no difference in mobility between *E. eriphyle, E. epiphron* and *E. pharte* (p = 0.11), see Table 3. When I compared the three *Erebia* species and the three categories (sedentary, same side, cross road) using the Boschloo test and the Fisher test, I only found significant differences in two out of nine cases (Table 4). First, I found a difference between *Erebia epiphron* and *Erebia pharte* when I compared the categories sedentary and same side and second, when I compared these two species and the categories same side and cross road. Except for the two cases mentioned

before, I did not really find evidence that the species differ from each other with respect to their mobility patterns. I therefore did not distinguish between the three species in the further analysis. However, since it was not clear whether *Erebia epiphron* and *Erebia pharte* could be lumped with regard to mobility, I checked if the results changed in the further analysis if I treated these two species separately. I did not find differences in mobility between *Erebia gorge* and *Erebia pandrose* neither using the Fisher test (p = 0.60) nor using the Boschloo test (p = 0.57). The Fisher test and the Boschloo test suggested that butterflies captured on plot D seemed to change the plot less often than butterflies captured on plots E or F. However, I did not find evidence for such a mobility pattern for the upper triangle ABC. According to the logit model (Table 2) butterflies captured on plot D were significantly more likely to stay on the same plot than butterflies captured on the other plots. To put it differently, butterflies captured on plots E and F were more likely to change the plot than those captured on D. I also got this result using a probit model (Appendix, Table 8). The regression coefficient of the dummy variable plot D remained significant when I included butterflies that were captured only once (and not only the recaptured butterflies). I did not find analogous effects for plot A relative to B and C, i.e. in the triangle of plots at higher elevation. However, if I used just one dummy variable for plots A or D, I 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 on a plot, butterflies were significantly less likely to change the plot. I did not get this result if I included the butterflies that were captured only once. I allowed age to enter quadratically into the regression equation. I found significant evidence that very young butterflies were more likely to stay on the same plot. When they got older they were more likely to change the plot, and at the end of their flight period they were again more likely to stay on the same plot (Figure 4). As my earlier analyses suggested that *Erebia pharte* may behave differently than the other species, I controlled for *Erebia pharte* in the maximum likelihood estimation as well. Indeed I found that *Erebia pharte* was more likely to change between plots than the other species (Table 2).

Table 1: 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

Table 2: 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

Table 3: 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 I 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

Table 4: Analysed species and recapture rates for the categories "sedentary", "same side" and "cross road". Using the Fisher and the Boschloo test for differences among these species with respect to their mobility I could only reject the null hypothesis in these two cases (sedentary/same side: Fisher, p = 0.05, Boschloo, p = 0.04; same side/cross road: Fisher, p = 0.10, Boschloo, p = 0.05).

	E. epiphron	E. pharte		E. epiphron	E. pharte
sedentary	24	16	same side	3	9
same side	3	9	cross road	4	1

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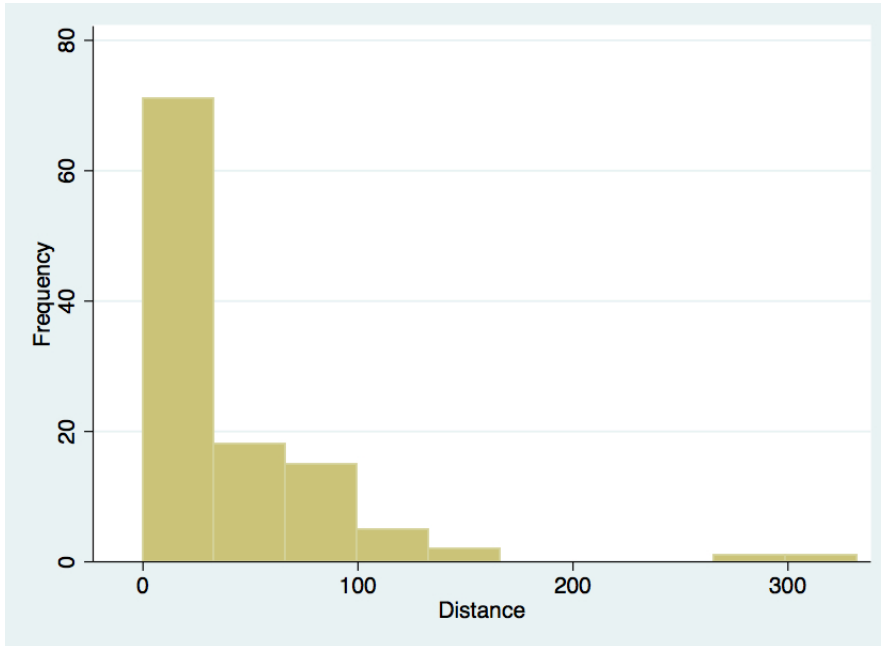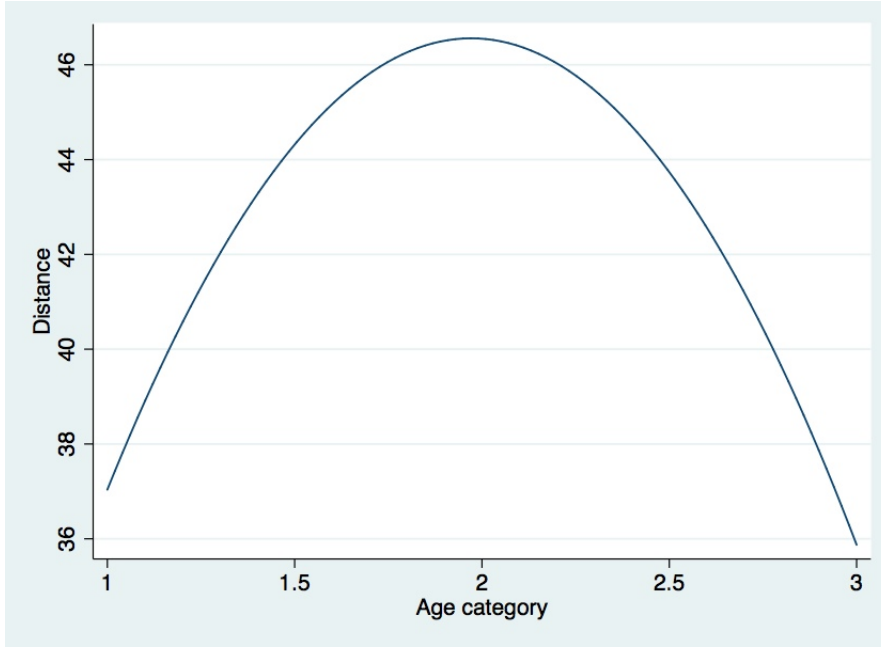

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Figure 4: Graph of the prediction for *Distance* [m] from a linear regression of *Distance* on *Age* [categories 1-3] and *Age squared.*

3.2   Population size and structure

155 of the 429 captured butterflies were females, 211 were males and for the remaining 63 the sex could not be determined. The most frequently captured species were *Erebia eriphyle* and *Erebia epiphron* (Table 5). *Erebia euryale* and *Erebia manto* were only captured once and therefore excluded from all analyses. Except for *Erebia pandrose* all the species occurred throughout the whole sampling time. The population of *E. pandrose* already collapsed at the end of July. We captured 200 individuals of age category 1, 157 of age category 2 and 72 of age category 3 (Table 6). I found differences in frequencies of captures among the species with respect to their age using a χ^2 test (p = 0.00). According to the POPAN model, total population sizes were ranging from 230 individuals (*Erebia pharte*) to 1316 individuals (*Erebia epiphron*) on roughly one hectare (one plot = 1 600 m^2, 6 plots in total = 9 600 m^2), see Table 7.

Table 5: Analysed species, the frequency and the percentage of captures. *Erebia euryale* and *Erebia manto* were only captured once and therefore not included in the analyses.

Species	Frequency	%
E. eriphyle	122	28.44
E. epiphron	106	24.71
E. pharte	69	16.08
E. gorge	58	13.52
E. pandrose	41	9.56
E. nivalis	31	7.23
E. euryale	1	0.23
E. manto	1	0.23

Table 6: Analysed species and the frequency of their captures in the respective age categories. Using a χ^2 test for differences in frequencies of captures among the species with respect to their age I rejected the null hypothesis of no difference (p = 0.00).

	E. eriphyle	E. epiphron	E. pharte	E. gorge	E. pandrose	E. nivalis
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

Table 7: Total population sizes estimated in the program MARK. Jolly-Seber-method implemented in POPAN; phi (apparent survival) and p (capture probability) were held constant, except for *Erebia gorge*, were phi was dependent on time and p was held constant.

Species	Total Population Size	Standard Error	95% Confidence Interval	
			Lower	Upper
E. eriphyle	1259.70	207.39	853.22	1666.18
E. epiphron	1316.41	205.23	914.16	1718.65
E. pharte	230.98	34.93	162.51	299.45
E. gorge	337.39	69.61	200.95	473.83
E. pandrose	796.55	258.39	290.10	1302.99
E. nivalis	497.08	137.30	227.97	766.19

4 Discussion

4.1 Mobility

Most of the marked alpine ringlet butterflies behaved rather sedentarily and did not move more than 40 meters ($\approx$ 69 % stayed within 40 meters) between two capture events (Figure 3). Kuras et al. (2003) also found that alpine ringlet butterflies *Erebia sudetica* and *Erebia*

epiphron in the Hrubý Jeseník Mountains in the Czech Republic were more likely to cross short distances rather than longer distances with most movements occurring within distances of 1 km. A similar mobility pattern was shown for an alpine population of *Euphydryas aurinia* by Junker et al. (2010). These authors suggested that a low mobility might be an adaptation of alpine butterfly species to a high elevation habitat. They argued that limited movement distances might prevent accidental drift events, e.g. by squalls, in these extreme high-altitude environments. Low mobility, however, has also been shown for lowland Satyrinae species, such as *Maniola jurtina* (Grill et al. 2006). Although these latter butterflies are physiologically capable of moving more than 2 km, most individuals are rather sedentary and spend their whole lifetime in a relatively small area.

Patch isolation. My data indicates that the Großglockner Hochalpenstraße may have a negative impact on the movement of ringlet butterflies. Contingency table tests suggested that butterflies captured on plot D were less likely to change the plot than butterflies captured on plots E or F. Butterflies captured on plot D had to cross the road to change the plot, which leads me to assume that the road is a decisive factor for the lower mobility of the butterflies captured on plot D. I did not find this pattern, however, for the upper triangle ABC. This might be due to a lower sample size and thus reduced statistical power for data from the upper triangle. When pooling the triangles and comparing the "separated" plots A/D to the plots BC/EF, I again found that butterflies captured on the separated plots were less likely to change the plot. The maximum likelihood estimation corroborated the results from the contingency table tests (Table 2). Collectively, these results confirm my 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. Thus, the road seems to constrain the mobility of alpine *Erebia* ringlet butterflies. Roads have previously been reported to restrain movements of sedentary butterfly species, while more mobile species were not affected (Munguira & 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* by Valtonen & Saarinen (2005) at a highway intersection in Finland showed that the highway significantly hindered

the butterfly's movement. In contrast to the present study, Valtonen & Saarinen investigated a highly anthropogenically influenced habitat, whereas my study was conducted in a widely intact landscape. Nevertheless, I showed that one large road can act as a major barrier for a butterfly's mobility. Mader et al. (1990) suggested that carabid beetles and lycosid spiders may be hampered in their dispersal by agricultural roads and railway tracks. Bhattacharya et al. (2003) found that bumble bees were hindered in their movements in a conservation area due to habitat fragmentation by a railroad. The bumblebees were reluctant to cross the barriers unless the resources were declining. I found a similar behaviour in *Erebia* butterflies, as they were less likely to change a plot and take the risk of crossing the road when nectar availability on a plot was high. This shows that besides resource availability, patch isolation is a limiting factor for the mobility of *Erebia* butterflies.

To preserve a butterfly's metapopulation structure, the ability of dispersal is a key process (Hanski et al. 2000). If the 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 is limited. Anthropogenic habitat fragmentation may cause *Erebia* butterflies to stay on the same habitat patch, which might ulitmately lead to reduced genetic variation. This, in turn, can result in a decrease in heterozygosity and an increased extinction risk (Saccheri et al. 1998). It is well-known that high mountain landscapes are heterogeneous due to naturally diverse topography, which results in a diversity of microenvironments and a mosaic of plant communities (Bliss 1963). In an environment that is already very heterogeneous and small-structured by nature, habitat fragmentation might be even more threatening to the organisms. If the butterflies' populations become more isolated due to anthropogenic fragmentation, the populations might run a higher risk of extinction (Hill et al. 1996).

Species identity. In contrast to my expectations, I 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 I compared larger species like *E. eriphyle* to smaller species like *E. pharte* – nor ecological specialization – when I compared a habitat generalist like *E. pandrose* to a habitat specialist like *E. gorge*. Although it has been suggested that habitat generalists and larger species (with a relative high investment in the thorax musculature) are more dis-

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persive (Quinn et al. 1997, Hill et al. 1998), other authors did not find a significant effect of body-size on mobility (e.g., Hanski et al. 2006). Since the butterfly species under study, however, are rather specialized – as they have to cope with extreme temperatures, strong winds and sudden weather changes – the results in the present study could be explained by the fact that all analysed *Erebia* species are adapted to a mountain habitat and therefore rather specialized. Also, the analysed species are rather homogeneous regarding morphology and ecological requirements 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. According to the Fisher test and the Boschloo test, *Erebia pharte* seemed to behave differently than the other species. Therefore we controlled for *Erebia pharte* in the maximum likelihood estimation as well. We found that *Erebia pharte* was more likely to change the plot than the other species. However, this weakly significant effect only emerged if I also included butterflies that were captured only once (Table 2). Hence, evidence for higher mobility in *Erebia pharte* remains mixed, which could be due to the small sample size. This trait deserves further study, and generally it would be worthwhile to explore species differences within the genus *Erebia* with regard to mobility using broader data from more sites and under more variable conditions.

Resource availability. Nectar availability influenced the mobility of *Erebia* butterflies, i.e. 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, I only got this result when I excluded butterflies that were only captured once. Loertscher et al. (1995) found that the microdistribution of *Melanargia galathea, Lysandra coridon, Ochlodes sylvanus* and *Zygaena loti* was strongly influenced by the distribution of their nectar plants. This is supported by Kuussaari et al. (1996) who found that a great abundance of flowers decreased the emigration rates of the butterfly *Melitaea cinxia*. Hence, I conclude that ringlet butterflies in alpine grassland tend to be sedentary when a suitable habitat is found and do not take the risk of entering the surrounding matrix.

Age. I found that 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 likely to change the plot, but towards the end of their flight period the butterflies

became again more likely to stay on the same plot. I did not find any studies which show a similar mobility pattern with respect to the age of the individuals. However, we measured age on wing-wear, which is not a perfect measure of age. This could cause some noise in the results. On the other hand, wing-wear is a common measure for age, since wings are not repaired as the butterflies age (Karlsson 1994, Kemp 2006). 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 *Pararge aegeria* and *Speyeria mormonia* had proportionally more flight muscle and a higher thorax ratio than younger ones, which can indicate that an individual is more mobile (Hill et al. 1998). The decrease in the mobility at the end of the flight period found in the present study could be explained by bad weather conditions. Towards the end of our sampling time it snowed at the study area. After a few days of bad weather in mid-August I noticed a sharp decline in captures and a few days later the *Erebia* butterflies at my 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.

4.2   Population size and structure

The total population sizes for *Erebia* species estimated using the program MARK ranged from 230 individuals for *Erebia pharte* to 1316 individuals for *Erebia epiphron* (Table 7). These findings match the results of a study by Slamova et al. (2012) on *Erebia aethiops* in a montane nature reserve in the Czech Republic and a study by Brussard & Ehrlich (1970) on *Erebia epipsodea* in montane central Colorado. Estimated population sizes of the studied *Erebia* species did not coincide with the frequency of captures of these species. According to the POPAN model *Erebia pharte* had the smallest population size of the six species under study. *E. pharte* was the third-most frequently captured species during my fieldwork and recapture rates were high (Table 1). Low recapture rates, in contrast, can lead to high numbers in population size estimations. This might be the case for *Erebia pandrose*. Apparent sex ratios were biased towards males for all *Erebia* species except for *Erebia eriphyle* and *Erebia pandrose*. Such a population structure has also been found for *Erebia epiphron* and *Erebia sudetica* by

Kuras et al. (2003). 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 male individuals in the number of captures. *Erebia pandrose* butterflies disappeared from my study site at the end of July. According to Stettmer et al. (2007) *Erebia pandrose* is the earliest appearing *Erebia* species in the Austrian alps with a flight period from May to August. The rather early disappearence of adult *E. pandrose* butterflies in the summer of 2012 might be due to bad weather conditions including snow, after which the population was not able to recover. The fact, that especially *Erebia pandrose* appears rather early may explain the differences in frequencies of captures among the species with respect to their age. I started my field study at the beginning of July and therefore I might have missed young individuals of *Erebia pandrose* and rather captured mid-aged and old individuals.

5   Conclusion

In conclusion, dispersal capacity of alpine *Erebia* butterflies in the Hohe Tauern National Park turned out to be limited. As expected, the Großglockner Hochalpenstraße further constrained the mobility of *Erebia* butterflies, i.e. individuals were significantly less likely to change a habitat patch if they had to cross the road. Contrary to expectation, I found but slight differences between *Erebia* species with respect to their mobility . Only *Erebia 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 to another side. The most remarkable finding was that age influenced the mobility of *Erebia* butterflies in a unimodal manner, i.e. during the first days after emergence the probability of changing the plot increased with age, but towards the end of the flight period the probability of changing the plot decreased. Further studies of age influencing mobility especially in alpine *Erebia* butterflies would be worthwhile. Generally, it would be interesting to further explore the genus *Erebia* with respect to mobility using data from more sites and over a longer period of time to account for movement patterns under more variable conditions.

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6 Appendix

Table 8: Maximum Likelihood Estimation, probit 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.

	(1)	(2)	(3)	(4)
VARIABLES	Probit - recaptured	Probit - recaptured	Probit - all	Probit - all
Plot A		0.404		0.596
		(0.733)		(0.467)
Plot D		1.512***		0.998**
		(0.571)		(0.437)
Plot A or Plot D	1.172**		0.836**	
	(0.472)		(0.343)	
Nectar	0.383**	0.418**	0.131	0.145
	(0.170)	(0.172)	(0.114)	(0.116)
Age	-2.348**	-2.294**	-1.894**	-1.914**
	(1.072)	(1.074)	(0.760)	(0.761)
Age squared	0.590**	0.575**	0.438**	0.444**
	(0.273)	(0.274)	(0.195)	(0.195)
Erebia pharte	-0.463	-0.462	-0.427*	-0.429*
	(0.322)	(0.323)	(0.224)	(0.224)
Constant	1.350	1.195	2.763***	2.735***
	(1.025)	(1.039)	(0.729)	(0.731)
Observations	113	113	427	427
LR chi-squared	14.17	15.72	20.67	21.10
LR-test p-value	0.0145	0.0153	0.000936	0.00176

Standard errors in parentheses

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

Abstract

Dispersal is a crucial feature for the preservation of butterfly metapopulations, which can be affected by habitat fragmentation. Each individual that leaves the habitat and 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. I conducted a mark-release-recapture study on six alpine *Erebia* species in the Hohe Tauern National Park in order to investigate if the Großglockner Hochalpenstraße – a large and highly frequented road in an alpine environment – acts as a barrier to movement for these relatively sedentary butterflies. By studying six species which differ in body-size and ecological requirements I aimed at analysing which of the following variables predict movement probability: (a) species membership, (b) ecological specialization, (c) resource availability, (d) age or (e) patch isolation. I also estimated the population sizes of the six analysed *Erebia* species.

I captured a total of 429 individuals, of which 113 were recaptured. My data indicates that neither body-size nor ecological specialization significantly influenced mobility patterns in these *Erebia* butterflies. The road, however, seemed to be a barrier for dispersal. I 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. Butterflies that were on a patch with a high nectar level were less likely to leave the patch. In addition age influenced mobility, with mid-aged butterflies being most likely to change between patches.

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

Zusammenfassung

Ausbreitung ist eine wesentliche Eigenschaft für den Erhalt von Schmetterlings-Metapopulationen, welche durch Habitatfragmentierung beeinträchtigt werden kann. Jedes Individuum, das das Habitat verlässt und in die Matrix eintritt, geht ein Risiko ein. Deshalb sind sogar oft geflügelte Organismen wie Schmetterlinge sehr sedentär und verbringen ihr gesamtes Leben auf einer relativ kleinen Fläche. Für solche Arten können große Straßen ein beträchtliches Hindernis für die Fortbewegung darstellen. Ich führte eine Fang-Wiederfang-Studie an sechs verschiedenen alpinen *Erebia* Arten im Nationalpark Hohe Tauern durch, um herauszufinden ob die Großglockner Hochalpenstraße – eine breite und hochfrequentierte Straße in alpiner Umgebung – eine Barriere für die Fortbewegung dieser relativ sedentären Schmetterlinge darstellt. Indem ich sechs Arten untersuchte, die sich in Körpergröße und ihren ökologischen Ansprüchen unterscheiden, beabsichtigte ich aufzuklären, welche der folgenden Variablen die Wahrscheinlichkeit für Fortbewegung voraussagen: (a) Artzugehörigkeit, (b) ökologische Spezialisierung, (c) Ressourcenangebot, (d) Alter oder (e) Habitatisolierung. Ich schätzte außerdem die Populationsgrößen der sechs untersuchten *Erebia* Arten.

Insgesamt wurden 429 Individuen gefangen, von welchen 113 wiedergefangen wurden. Meine Daten weisen darauf hin, dass weder Körpergröße noch ökologische Spezialisierung die Mobilitätsmuster in diesen *Erebia* Schmetterlingen signifikant beeinflussen. Die Straße jedoch schien ein Hindernis für die Ausbreitung zu sein. Ich fand heraus, dass Schmetterlinge, die die Straße überqueren mussten um zu einem anderen geeigneten Habitat-Patch zu kommen, mit geringerer Wahrscheinlichkeit den Habitat-Patch verließen als Schmetterlinge, die die Straße nicht überqueren mussten. Schmetterlinge, die sich auf einem Habitat-Patch mit einem hohen Nektaranteil befanden, verließen mit geringerer Wahrscheinlichkeit den Patch. Weiters beeinflusste das Alter die Mobilität dahingehend, dass Schmetterlinge mittleren Alters mit der höchsten Wahrscheinlichkeit zwischen den Patches wechselten.

Schlüsselwörter: Ausbreitung, Habitatfragmentierung, *Erebia*, Mobilität, alpine Schmetterlinge, Alter, Fang-Wiederfang, Metapopulation

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Sprachkenntnisse

Deutsch: Muttersprache
Englisch: Fließend
Spanisch: Intermediär
Latein: Grundkenntnisse
Französisch: Grundkenntnisse

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