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**Population ecology, mobility and adaption strategies of the ringlet species
Erebia eriphyle and *Erebia manto* in the Hohe Tauern National Park**

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Abstract

The climate of the high Alps poses a particular challenge for butterflies, which is why species living there must be well adapted to the environmental conditions in order to survive and reproduce. Using mark-release-recapture methods, the two butterfly species *Erebia manto* and *Erebia eriphyle* were studied in the Austrian Alps to determine their population structure, behaviour, dispersal ability, movement patterns and preferred nectar plants. The population size estimation revealed a higher number of males (*E. manto*: 322 ± 113 ; *E. eriphyle*: 199 ± 107) than females (*E. manto*: 46 ± 19 ; *E. eriphyle*: 25 ± 15). Both *E. eriphyle* and *E. manto* exhibited protandry. Compared to other *Erebia* species, *E. manto* showed a higher probability of long-distance dispersal, which is greater in females than in males. However, the small sample size does neither allow reliable conclusions to be drawn about the probability for long-distance dispersal in *E. eriphyle*, nor about the movement patterns, behaviour and preferred nectar plants of both species. Likewise, the analysis of wing conditions also failed to provide clear findings on the age structure of the populations of both species. However, the results suggest, at least in the case of male *E. manto*, that the imagines eclose simultaneously and the population ages in a linear fashion. This study provides preliminary indications that *E. manto* and *E. eriphyle* are well adapted to their high-alpine habitat, as they both exhibit protandry while maintaining their population under these challenging environmental conditions. Nevertheless, further research with a larger data set is needed in order to make valid statements and close remaining knowledge gaps.

Zusammenfassung

Das Klima der Hochalpen stellt für Schmetterlinge eine besondere Herausforderung dar, weshalb dort lebende Arten gut an die Umweltbedingungen angepasst sein müssen, um zu überleben und sich zu reproduzieren. Mithilfe von Fang-Wiederfang wurden die beiden Schmetterlingsarten *Erebia manto* und *Erebia eriphyle* in den österreichischen Alpen untersucht, um deren Populationsstruktur, das Verhalten, die Ausbreitungsfähigkeit, die Bewegungsmuster und die bevorzugten Nektarpflanzen zu ermitteln. Die Populationsgrößenschätzung ergab bei beiden Arten einen größeren Anteil an Männchen (*E. manto*: 322 ± 113 ; *E. eriphyle*: 199 ± 107) als Weibchen (*E. manto*: 46 ± 19 ; *E. eriphyle*: 25 ± 15). Sowohl *E. eriphyle* als auch *E. manto* zeigten Proterandrie. Für *E. manto* deutete sich im Vergleich zu anderen Erebien eine höhere Ausbreitungswahrscheinlichkeit an, die bei den Weibchen größer ist als bei den Männchen. Die geringe Stichprobengröße ermöglichte jedoch weder zuverlässige Aussagen zur Ausbreitungswahrscheinlichkeit von *E. eriphyle* noch zu den Bewegungsmustern, zum Verhalten und zu den bevorzugten Nektarpflanzen beider Arten. Auch die Analyse der Flügelzustände ergab keine eindeutigen Erkenntnisse zur Altersstruktur der Populationen beider Arten. Die Ergebnisse weisen allerdings zumindest bei den Männchen von *E. manto* auf einen gleichzeitigen Schlupf der Imagines und einen linear verlaufenden Alterungsprozess der Population hin. Die vorliegende Arbeit liefert erste Hinweise darauf, dass *E. manto* und *E. eriphyle* gut an ihren hochalpinen Lebensraum angepasst sind, da beide Arten Protandrie aufweisen und gleichzeitig ihre Population unter diesen schwierigen Umweltbedingungen aufrechterhalten können. Es sind jedoch weitere Untersuchungen mit einem größeren Datensatz erforderlich, um valide Aussagen zu treffen und verbleibende Erkenntnislücken zu schließen.

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List of abbreviations

Bft	wind force in Beaufort
<i>B. napaea</i>	<i>Boloria napaea</i>
<i>B. pales</i>	<i>Boloria pales</i>
<i>E. eriphyle</i>	<i>Erebia eriphyle</i>
<i>E. manto</i>	<i>Erebia manto</i>
<i>E. nivalis</i>	<i>Erebia nivalis</i>
<i>E. pronoe</i>	<i>Erebia pronoe</i>
GOF test	goodness of fit test
GPS	Global Positioning System
IPF	inverse power function
NEF	negative exponential function
SD	standard deviation
ssp.	subspecies

1. Introduction

Land use change and climate change are fundamental challenges that affect many species on our planet and contribute to the loss of biodiversity. Butterflies are susceptible to these threats as well and comprehensive knowledge about their way of life and their habitat requirements is essential to develop effective conservation strategies. Nevertheless, we still do not know enough about many butterfly species. One example is the hermit *Chazara briseis* (LINNAEUS, 1764), which was formerly widely distributed but habitat degradation in combination with high preoviposition mortality of the females caused rapid population declines all over Europe (Kadlec et al., 2010). Furthermore, species that have developed specific adaptations allowing them to inhabit extreme habitats are particularly threatened compared to more generalist species. High mountain ranges, such as the Alps, serve as a prime example of an extreme habitat. The short duration of the summer season accompanied by extreme weather conditions poses a challenge for butterfly species living there. Hence, butterfly species inhabiting these areas must adapt to the extreme environmental conditions to allow for survival and reproduction.

Mark-release-recapture is a proven method for investigating the adaptations of butterflies to their environment; previous studies already used this method to gain knowledge on the population structure, dispersal ability, movement patterns, behaviour, habitat use and nectar plant preference of various butterfly species (e.g. Ehl et al., 2019a; Junker & Schmitt, 2010; Junker et al., 2010; Kadlec et al., 2010; Wendt et al., 2021). Using this methodology, prior studies found out that some mountainous butterfly species like *Euphydryas aurinia* subspecies (ssp.) *debilis* (OBERTHÜR, 1909), *Boloria pales* ([DENIS & SCHIFFERMÜLLER], 1775) and *Boloria napaea* (HOFFMANNSEGG, 1804) are able to survive short-term cold spells under closed snow cover during the flight period without affecting population development or causing increased mortality (Ehl et al., 2017; Junker et al., 2010). Other butterfly species as for example *Erebia pronoe* (ESPER, 1780) and partly *Erebia nivalis* (LORKOVIĆ & DE LESSE, 1954) exhibit protandry (Ehl et al., 2018a; Wendt et al., 2021) meaning that males eclose prior to females. This phenomenon is common in butterfly species and has the adaptive advantage that females can be fertilised immediately after eclosion. The disadvantage is the longer flight period and the risk, that all males could die due to unfavourable environmental conditions before the females eclose, preventing reproduction. Due to erratic cold spells in mountainous regions, which can occur during the flight period, protandry carries a significant risk for butterfly species living there. The knowledge that *E. pronoe* and partly *E. nivalis* exhibit protandry suggests that

they are well adapted to their extreme habitats (Ehl et al., 2018a; Wendt et al., 2021). Other species, such as *E. pronoe*, additionally exhibit serial eclosion as a strategy to mitigate the risk of population extinction due to extreme weather events (Wendt et al., 2021). These risk spreading strategies can be evaluated by investigating into the age structure of the population, for example.

Apart from the chosen reproductive strategy, mark-release-recapture also helps to find out whether the species under consideration prefer specific nectar plants or choose opportunistically. Moreover, the availability of suitable nectar plants is an important factor for conservation measures. Previous research on *B. pales* and *B. napaea*, for example, revealed sex-specific nectar plant preferences (Ehl et al., 2018b; Ehl et al., 2019b). Contrary to that, *E. nivalis* is not adapted to specific nectar plants but rather chooses opportunistically, and also for *E. pronoe*, no sexual preference for nectar plants could be determined (Ehl et al., 2018a; Wendt et al., 2021).

Another crucial factor in times of climate change and altered land use is the ability to disperse over longer distances, which can also be investigated through mark-release-recapture. This ability determines if species can colonize new, more favourable habitats and recolonize after local extinctions. Especially if distribution ranges and suitable habitat patches of mountainous species shift towards higher altitudes due to climate change, the habitat and the populations become more fragmented. This enhances the importance of the ability to disperse over longer distances to colonize or recolonize suitable habitat patches and maintain metapopulations. Previous studies have shown that males are often more flight active than females (Ehl et al., 2018a; Ehl et al., 2019b; Wendt et al., 2021), but females rather disperse over larger distances (Weyer & Schmitt, 2013). However, also a higher probability of long-distance dispersal in males compared to females has been already demonstrated (Ehl et al., 2019b) For *Euphydryas aurinia* (ROTTEMBURG, 1775) in the Portuguese Algarve, dispersal and direction were shown to depend on habitat conditions and larger distances were predominantly covered along habitat structures (Junker & Schmitt, 2010). Therefore, a lack of habitat structures and habitat fragmentation negatively impacts the species' ability to disperse (Junker & Schmitt, 2010). Ehl et al. (2019b) also demonstrated that land management impacts mobility and population density in *B. pales*. Grazing resulted in higher population density and greater flight distances (Ehl et al., 2019b). Especially for *Erebia* species it is known that they are rather sedentary and predominantly move shorter distances (Polic et al., 2014).

Many high mountain butterfly species have not been extensively studied yet; however, the existing literature suggests considerable differences between the species regarding their ecology and strategy for surviving in this extreme habitat. These differences highlight the necessity to study each species individually, in order to understand its needs and determine the threats to ensure its long-term survival in times of changing climate and land use. The presented thesis seeks to enhance the knowledge about the ecology and the adaptations of butterfly species in the Alps towards their extreme environment. Therefore, the ringlet species *Erebia manto* ([DENIS & SCHIFFERMÜLLER], 1775) and *Erebia eriphyle* (FREYER, 1836) were studied within the High Tauern National Park of Austria. Previous studies on *E. manto* primarily investigated into the genetic structure (Cupedo, 1997; Cupedo & Doorenweerd, 2020; Jospin et al., 2023; Schmitt et al., 2014; Sonderegger, 2005). However, not much is known about its ecology and adaptations towards its extreme habitat. *E. eriphyle* is even less studied so far. As both species are closely related, this thesis additionally aims to assess the extent to which the ecological niches of both species are differentiated. Therefore, the study focuses on answering the following research questions:

- (1) How many individuals of each sex does the population of *E. manto* and *E. eriphyle* comprise?
- (2) How is the population structure of both species during the flight period?
- (3) Which movement pattern and dispersal behaviour do *E. manto* and *E. eriphyle* show?
- (4) Is there a behavioural difference between the sexes and the two species?
- (5) Which nectar plants are used by *E. manto* and *E. eriphyle*? Are there sex-specific preferences present within the two investigated species?

2. Materials and Methods

2.1 Species

2.1.1 *Erebia manto*

The yellow-spotted ringlet *Erebia manto* ([DENIS & SCHIFFERMÜLLER], 1775) belongs to the order Lepidoptera, the family Nymphalidae and the subfamily Satyrinae (Embacher et al., 2011). In Austria this species is listed as “Least Concern” (Höttinger & Pennerstorfer, 2005) and in the federal state of Salzburg as protected species (Salzburger Naturschutzgesetz 1999 - NSchG).

E. manto solely occurs in European mountain ranges and is a typical alpine-disjunct and cold adapted species (Schmitt et al., 2014). Its distribution is documented to cover the Cantabrian Mountains, the Pyrenees, the Alpes, the Massif Central, the Carpathians, the Vosges Mountains, the Jura, the Slovakian Carpathians (High Tatras and Mala Fatra), the southern and eventually eastern Carpathians, and Bosnia (Cupedo & Doorenweerd, 2020; Kudrna et al., 2015; Sonderegger, 2005; Tshikolovets, 2011). The current distribution of *E. manto* is caused by post-glacial recolonisation events originating from different glacial refugia (Cupedo, 1997; Schmitt et al., 2014). During the Pleistocene and thereafter intraspecific divergence of *E. manto* occurred (Cupedo & Doorenweerd, 2020), leading to ongoing debates about the number of subspecies and whether they should be considered as distinct species. An allozyme analysis of genetic samples collected in the immediate vicinity of the study area previously revealed that the investigated population is intermediate between the three genetic clusters of the Alps and the Slovakian Carpathians, which are less differentiated from each other (Schmitt et al., 2014). The smaller degree of differentiation between them might be caused by the more recent origin, probably in the Würm ice age, during which they inhabited different refuge areas around the Alpine ice sheet (Schmitt et al., 2014).

E. manto mainly inhabits the subalpine zone, primarily along the tree line or slightly below (Cupedo & Doorenweerd, 2020; Sonderegger, 2005). The species is also present in the alpine zone following the distribution of the green alder and occurs above the alpine tree line in pastures with high grasses (Sonderegger, 2005). Furthermore, the presence of this species is documented in the montane zone, specifically in shady valleys characterized by tall herbaceous vegetation (Sonderegger, 2005). The lower distribution boundary is situated at an altitude of 1,200 m above sea level (Sonderegger, 2005). Sometimes *E. manto* can be found up to 2,500 m above sea level or even higher if the habitat is suitable (e.g. pastures with high vegetation) (Sonderegger, 2005). For sleeping and during bad weather conditions, the species hides in dense

vegetation, often along streams or moist places (Sonderegger, 2005). *E. manto* prefers a southern exposition of the habitat, however, northwestern exposition is also documented (Sonderegger, 2005).

The species undergoes a biennial development with five larval stages (Sonderegger, 2005). The larvae are often found along the edges of green alder complexes or dry meadows, where they mainly feed on *Anthoxanthum odoratum*, but also *Carex ferruginea*, *Poa nemoralis*, and *Poa alpina* (Sonderegger, 2005). In contrast, Tshikolovets (2011) indicates mainly *Festuca rubra* and other *Festuca* species as larval plants. Male imagines eclose at the beginning of July, however, the main flight time is between 20th of July and 20th of August, in some years even until September (Sonderegger, 2005). According to Sonderegger (2005), the imagines often feed on *Centaurea*, *Kautia* and yellow Asteraceae.

2.1.2 *Erebia eriphyle*

The Eriphyle ringlet, *Erebia eriphyle* (FREYER, 1836), belongs to the order Lepidoptera, the family Nymphalidae, and the subfamily Satyrinae (Embacher et al., 2011) and is distributed in the Central and Eastern Alps (Kudrna et al., 2015; Sonderegger, 2005). In Austria *E. eriphyle* is listed as “Near Threatened” and is a protected species in the federal state of Salzburg (Höttinger & Pennerstorfer, 2005; Salzburger Naturschutzgesetz 1999 - NSchG). As a high proportion of the geographical distribution of this species is situated in Austria's mountainous regions, federal states such as Salzburg have a particularly high responsibility for its conservation (Gros, 2023).

The species mainly inhabits the subalpine zone and is distributed from 1,200 m until 2,250 m above sea level (Sonderegger, 2005; Tolman et al., 2012). With increasing elevation, *E. eriphyle* tendentially prefers a southern exposition (Sonderegger, 2005). The species is associated with tall herbaceous vegetation, frequently in combination with green alder, especially in areas above the tree line (Sonderegger, 2005). The preferred tall herbaceous vegetation often consists of *Adenostyles*, *Geranium silvaticum*, *Peucedanum ostruthium* and *Deschampsia caespitosa* (Sonderegger, 2005). *E. eriphyle* undergoes a biennial development with four larval stages (Sonderegger, 2005). The larvae use *Deschampsia caespitosa* as a forage crop and for overwintering but sometimes were found on *Carex ferruginea* and *Anthoxanthum odoratum* as well (Sonderegger, 2005). In early years, the imagines eclose already at the end of June, however, the main flight time is between beginning of July and mid-August (Sonderegger, 2005).

2.1.3 Differentiation between *Erebia manto* and *Erebia eriphyle*

E. manto and *E. eriphyle* are sibling species and therefore closely related (Schmitt et al., 2014). Both species have quite variable morphological characteristics and can easily be confounded with each other as well as with *Erebia melampus* (FUESSLY, 1775), *Erebia pharte* (HÜBNER, 1804) and other ringlet species (Sonderegger, 2005). Especially *E. manto* additionally shows geographical variation of its wing colouration throughout its distribution range (Sonderegger, 2005). Therefore, species identification solely based on wing patterning is challenging and can be misleading (Sonderegger, 2005). Fully reliable determinations consequently are only possible via the assessment of genital structures (Sonderegger, 2005). Given that the presented study is based on the mark-release-recapture methodology and the individuals needed to be kept alive, the study of genitalia was not possible. Consequently, the determination was performed based on wing patterns. The decision was made using the pattern of the wings' underside, as the most reliable differences are located there. For species identification, I used the literature of Tolman et al. (2012), Tolman et al. (1998) and Sonderegger (2005).

Within the study area, the basic colours of *E. manto* and *E. eriphyle* had the same range of variation. The spot colour of both species reached from light orange to red brown, however, the colouring faded out when wing condition deteriorated. In contrast to *E. eriphyle*, *E. manto* displayed a sexual dimorphism on the underside of the hindwing, i.e. females often had pale-yellow markings (Figure 1). In case of this typical female pattern, I classified the individual as *E. manto*. The males of *E. manto* had orange spots on the hindwing underside, which are only present in the postdiscal area and are arranged in a curved line (Figure 1). In *E. eriphyle*, these spots are not arranged in a curved line but the spot in cell M4 is slightly shifted towards the base (Figure 2). In *E. manto*, the colouration of the postdiscal band of the forewing underside is uniformly orange and well defined (Figure 1). In contrast, *E. eriphyle* has a less defined band extending more to the basis of the wing, often with a gradual colour shift from the postdiscal band to the brown basic colouration (Figure 2). Both species often had core spots within the orange postdiscal band of the lower forewing, hence not being a reliable trait for species determination, nevertheless they were mostly obscured in *E. eriphyle* compared to *E. manto*.



Figure 1: *Erebia manto* male (left, individual H3) and female (right, individual Q1).



Figure 2: *Erebia eriphyle* male (left, individual C4) and female (right, individual I5).

2.2 Study area

The fieldwork was conducted in the Austrian Central Alps of the federal state Salzburg (Figure 3). Climatically, the whole region belongs to the temperate zone and is strongly influenced by the mountain climate of the alpine altitudinal zone. Sudden changes in weather, especially towards heavy cloudiness, high wind speed, low temperatures, precipitation, and poor visibility, occurred often. The chosen study area is located at an altitude between 2,240 and 2,390 metres above sea level along the Großglockner High Alpine Road, adjacent to the Wilfried-Haslauer-Haus within the area called "Oberes Nassfeld". The study area is situated partially within the core zone of the High Tauern National Park (Nationalpark Hohe Tauern, 2018) (Figure 3) and the region's geological context places it within the broader Hohe Tauern window (Nationalpark Hohe Tauern, n. d.). The entire area is used for agricultural purposes, specifically grazing, during the summer months. From 8th of July 2022 to the end of fieldwork, thirteen cows were observed grazing on the study area. Additionally, the presence of sheep grazing in the

surrounding was noted; however, these animals were not observed within the study area. The topography of the study area features a southern slope and a plateau, which is crossed by two small and rarely used farm roads (Figure 3 and Figure 4), and was defined by fencing towards west, north, and east. The plateau is characterized by the presence of numerous meltwater channels that extend from east to west, with one of these channels delineating the southern border (Figure 3). At the time of the fieldwork, the meltwater channels were not filled with water but vegetation. Within the nutritious meltwater channels of the western plateau, tall herbaceous vegetation dominated by *Alchemilla vulgaris* and *Rumex alpinus* was present, creating a moist microclimate. Notwithstanding the presence of scree in certain regions of the study area, particularly in the southern slope, most of the area is covered by soil and vegetation. Exposed scree was observed in a limited number of small areas. The majority of flowering plant species were present at the southern slope and in smaller numbers also at the plateau outside the melt water channels, where vegetation was lower. The main plant species at the slopes were *Helianthemum alpestre*, *Anthyllis vulneraria*, *Aster alpinus*, *Crepis aurea*, *Trifolium pratense*, *Silene vulgaris*, *Leontodon hispidus* and *Scorzonerioides helvetica*. The predominant hue among the floral species was yellow. A total of 58 flowering plant species were identified in the study area, classified into 21 distinct plant families (Appendix 1).

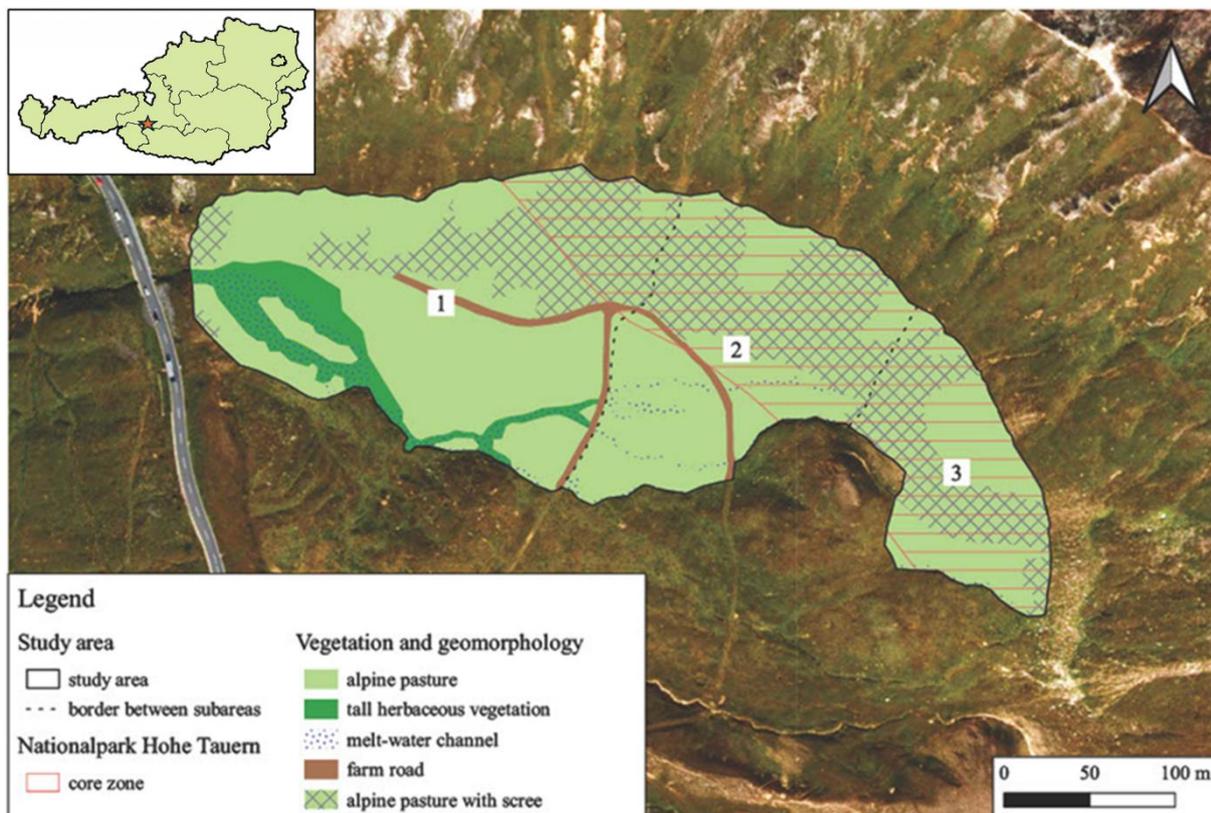


Figure 3: Overview map of the study area within “Oberes Nassfeld”. The location of the study area within Austria is indicated by the red star in the inlet map. The numbers from 1 to 3 indicate the three subareas.



Figure 4: Picture of the study area (“Oberes Nassfeld”) with southern slope and plateau.

2.3 Data collection

I collected data from 2nd of July 2022 to 8th of August 2022. During this time, the fieldwork was conducted only under suitable weather conditions for butterfly activity. In case of unsuitable weather conditions (i.e. high wind speed, heavy cloudiness, precipitation, fog, low temperatures), fieldwork was stopped. Consequently, on certain days, fieldwork was not feasible, or not the entire study area was surveyed. Data collected by then were still included in the analysis. The study area was divided into three subareas (Figure 3), with each subarea undergoing a single daily survey. The three subareas allow for six possible sequences in which they can be surveyed. These six combinations were applied in an alternating order to minimize the influence of daily fluctuations in butterfly activity on the dataset. The boundaries between the subareas were marked with wooden sticks if necessary. The methodical exploration of the study area was conducted in the form of serpentine lines through each subarea. This approach ensured the comprehensive coverage of the entire study area, with no section remaining unsurveyed.

During fieldwork, individuals encountered within the study area were captured using a butterfly net and the species was identified. Individuals that were captured, even in cases where the species identification was ambiguous, were photographed before and after marking at least

once. This process served to verify the species determination based on the pictures obtained. Even if the species identification was ambiguous, all data were collected in case this species can be assigned to either *E. manto* or *E. eriphyle* later. The determination of sex was made based on genital structure. Individuals with valvae were classified as males, while the others were categorised as females. The wing condition of each individual was classified into one of four categories (1 = wing completely preserved, 2 = fringe is missing, 3 = slight damage, 4 = serious damage). Intermediate wing conditions were classified as such (for example, a wing condition between 1 and 2 was classified as 1.5). Furthermore, the behaviour of every individual immediately prior to the capture event was recorded and classified into four categories: flying, resting, interaction with another butterfly or feeding. In case of an individual being observed feeding on a flower, the species of the flower in question was documented. Finally, each individual captured was marked with a unique identification code (ID) (Figure 5) at the time of first capture, which was also recorded every time the individual was recaptured. The ID was composed of a letter and a number. Each day of fieldwork with captured individuals was assigned a letter. Individuals captured on the same day were marked with the same letter. The numbering of individuals starts every field day from one and is ongoing. The letters were written on the undersides of both hindwings, and the complete ID on the undersides of both forewings, using a permanent marker (Figure 5). Following treatment, each individual was immediately released at the site of its capture.

In the event of an individual being recaptured, this was documented as a recapture event only if a minimum of one day elapsed since the individual's previous capture or recapture. This rule was implemented to mitigate potential bias in the collected data. This bias could arise from the impact of netting and handling on the butterflies' behaviour prior to the recapture event. If an individual was recaptured, the protocol was followed except for species identification, marking, photographing and sex determination.

The documentation of the recorded mark-release-recapture data during the fieldwork was done using a smartphone (Samsung Galaxy XCover 4s) equipped with the TourCount application (version 3.2.9; Stein, 2022). For each entered data point concerning a captured or recaptured individual, the application automatically recorded the Global Positioning System (GPS) coordinates of the location (longitude and latitude), the elevation, the uncertainty of the GPS position, the date, and the time. All other data concerning the captured or recaptured individuals (ID, species, sex, wing condition, behaviour, nectar plant, capture or recapture event) were entered manually. The application was also used for the manual recording of meteorological

data, including temperature [°C], wind force [Bft] (Beaufort), cloudiness [%], as well as the start and end time and the date of each field day.



Figure 5: Marked *Erebia manto* female (individual P2).

2.4 Data analysis

Subsequent to the completion of the fieldwork, the species identification of the individuals was initially verified through the analysis of the obtained photos before and after marking. In cases where the initial identification was found to be inaccurate, the classification was corrected accordingly. Individuals that could not be clearly assigned to either *E. manto* or *E. eriphyle* were excluded from all subsequent analyses. Moreover, the wing condition was examined once more to ascertain its accuracy, with any necessary corrections applied.

To analyse the obtained dataset, the software R (version 4.1.2 (2021-11-01); R Core Team, 2021) was used for the analysis of the population structure, the wing condition, the nectar plant preferences, and the behaviour. The following R packages were used in this study: Rcmdr (version 2.9.0), dplyr (version 1.1.2), patchwork (version 1.1.3), hrbrthemes (version 0.8.0), ggplot2 (version 3.4.3), lubridate (version 1.9.2), scales (version 1.2.1), ggpmisc (version 0.5.4.1) and tidyverse (version 2.0.0).

2.4.1 Estimation of population size

The collected mark-release-recapture data were used to estimate the population size of *E. manto* and *E. eriphyle* within the study area. First, the software Microsoft 365 Excel was used to convert the data into a different format for the subsequent population size estimation. The

obtained dataset is based on whether a specific individual was caught (1) or not (0) during each of the field days. This information was then used to create a capture history for each individual, consisting of a sequence of 1's and 0's, with each number representing a field day.

To analyse the adapted mark-release-recapture dataset, I used the software MARK (White, n. d.; version 9.0). The investigated population in this study is open, which means that individuals may leave (emigration or death) or join (immigration or eclosion of imagines) the population at any time. Therefore, the Jolly-Seber method implemented in MARK using the POPAN formulation was applied (Schwarz & Arnason, 1996). The POPAN model is based on encounter possibilities (days), intervals between encounter possibilities, and groups (i.e. males and females). The model estimates the four parameters Φ (local survival rate - probability that the individual survives and stays in the population), p (capture probability of a marked individual given the individual is alive and present in the study area), $pent$ (probability of entry into the population) and N (superpopulation size) (Schwarz & Arnason, 2020). These parameters can be constant (\bullet), depending on sex (g) or time in a factorial (t), linear (T) or quadratic manner (T^2) (White & Burnham, 1999) and act either additively ($g + t$, $g + T$, $g + T^2$) or interactively ($g*t$, $g*T$, $g*T^2$).

At first, the full model was created. Therefore, the data type (POPAN), the encounter occasions and the corresponding time intervals as well as the attribute groups were specified. Initially, the full model $Phi(g*t)p(g*t)pent(g*t)N(g*t)$ with the link function Parm-Specific, and the link values $Phi = \text{logit}$, $p = \text{logit}$, $pent = \text{mlogit}1/2$ and $N = \text{log}$ was created. A second attempt was made by employing the same full model and link function, but with the link values set to $Phi = \text{sin}$, $p = \text{sin}$, $pent = \text{mlogit}1/2$, and $N = \text{identity}$.

In order to perform the estimations in accordance with the methodologies outlined by Schwarz & Arnason (2020), the following assumptions must be taken into consideration: (1) Unmarked and marked individuals of the population are equally likely to be captured and are random samples of the population; (2) individuals keep their tags during the whole experiment; (3) the tags are recorded accurately; (4) the process of sampling occurs instantaneously; (5) the probability of survival for both marked and unmarked individuals between sampling occasions is homogeneous; (6) the capture probability remains constant for both marked and unmarked individuals and (7) the study area remains constant (Schwarz & Arnason, 2020). As the model makes the already mentioned assumptions, the goodness of fit (GOF) testing confirms that the full model fits properly to the dataset (Cooch & White, 2022). For this purpose, the inbuilt Program RELEASE was used, which consists of three tests (Cooch & White, 2022). Test one

is not really a GOF test and is only included, if groups are compared (e.g. male and female). This test compares the null hypothesis (all parameters of p_i and Φ_i of all groups have the same value) with the alternative hypothesis (at least values for p_i or Φ_i or both are different between the groups) (Cooch & White, 2022). Test two analyses, whether all marked and unmarked individuals have the same chance of recapture at any time (Cooch & White, 2022). Test three examines if marked individuals have the same probability of survival, regardless of when they were marked (Cooch & White, 2022). At this point, the previously described analysis with MARK was finalised. For more detailed information, see Chapter 3.1.

Instead, the total population size, with the respective standard errors, for *E. manto* and *E. eriphyle* males and females was estimated for the entire flight period according to du Feu et al. (1983). This approach involves the estimation of the population size \hat{P} , derived from the number of captures (N) and recaptures (R) within a designated session (du Feu et al., 1983). The session is defined as the time interval during which the overall population size is estimated, in this case, the entire flight period. The approach of du Feu et al. (1983) is based on certain assumptions: (1) The sampled population must be closed (du Feu et al., 1983); however, du Feu et al. (1983) recommend this method for butterflies as well, emphasizing that it produces in general reliable results for the majority of simple mark-release-recapture studies. (2) Individuals do not show trap-shyness or trap-happiness (du Feu et al., 1983). (3) The capture events should not impact the behaviour (du Feu et al., 1983). (4) The capture method is equally effective for all individuals within the estimated group (du Feu et al., 1983). (5) Finally, the handling time of the individual should not have an impact (du Feu et al., 1983). Detailed information on the calculation is given in du Feu et al. (1983).

2.4.2 Population structure

The obtained data was evaluated using the software R to assess the population structure over the whole flight period by calculating and plotting the count of *E. eriphyle* and *E. manto* per sex. The sex ratio per day was also calculated and plotted for both species. Furthermore, the percentage of males and females in relation to the total captures of the respective sex was plotted per day for *E. manto* and *E. eriphyle*.

2.4.3 Age structure

The wing conditions of *E. manto* and *E. eriphyle* were examined to identify the age structure of both species. In order to avoid overfitting caused by the relatively small sample size, a linear regression model was used instead of a higher-order polynomial model. Due to the consistent

methodology for assessing the wing condition and the subsequent validation based on the taken photos, normally distributed residuals can be assumed, as required in a linear model. The analysis was conducted on the wing condition data from capture and recapture events. For each species and sex, three distinct analysis variants were conducted: (1) The initial approach included the calculation of a daily mean wing condition for both species and sexes, respectively. Subsequently, a linear regression model was fitted, and the results were plotted. (2) The second approach adopted a similar methodology to the first one but was limited to data from days with at least three capture or recapture events per species and sex. This approach was selected to eliminate the impact of inadequate sample size at certain field days. (3) The third approach entailed the calculation of the mean wing condition over a five-day period (days without fieldwork are included) for both species and sexes, respectively. Five-day-periods with less than three capture or recapture events were excluded from further analysis. Afterwards, a linear regression model was fitted, and the results were plotted. The obtained results were evaluated based on the coefficient of determination R^2 and the p -value.

2.4.4 Estimation of long-distance dispersal

In order to estimate the percentage of individuals that disperse over long distances, the GPS locations of the recorded individuals were used. First, the linear distances between the capture and recapture locations were calculated for each individual by using the "Distance Matrix" function in QGIS (version 3.26.0; QGIS.org, 2022). Furthermore, the calculated distances of each individual between the capture and all recapture events were summed up to obtain the minimum total distance travelled.

The subsequent estimation of long-distance dispersal, as well as the plotting, was conducted using the software Microsoft Excel 365. During the analysis, male and female individuals of *E. manto* and *E. eriphyle* were treated separately. The analysis was done with the calculated linear distances between capture and first recapture. Prior to the implementation of the distance extrapolation, the movement distance of each individual was first categorized into distance classes (e.g., 0–20 m, 20–40 m, etc.) with intervals of 20 m, 30 m, or 50 m. Consequently, each distance class contained the number of individuals that had a movement distance within that class (e.g., 0–20 m: 8 individuals, 20–40 m: 5 individuals, etc.). Two distinct approaches were used in the evaluation of movement data: The first approach was to count the individual only in the distance class in which the movement distance value occurred (referred to as “occupied”; e.g., a calculated movement distance of 35 m would fall within the distance class 20–40 m). The subsequent approach involved the additional categorization of individuals in unoccupied

distance classes below their calculated movement distance value (referred to as "complete"; e.g., a calculated movement distance of 35 m would fall within the distance classes of 10–20 m and 20–40 m, if the distance class 10-20 m is not occupied). Both above mentioned approaches were performed with all three intervals.

The obtained data was subsequently analysed using the inverse power function (IPF) and the negative exponential function (NEF) (Baguette, 2003; Junker & Schmitt, 2010; Weyer & Schmitt, 2013). The relative likelihood that an individual reaches a certain distance is:

$$P_{NEF} = ae^{-kD} \quad \text{or} \quad \ln(P) = \ln(a) - kD$$

$$P_{IPF} = aD^{-n} \quad \text{or} \quad \ln(P) = \ln(a) - n(\ln D)$$

P describes the probability that an individual moves until a certain distance (D), a is the scaling constant, k is the dispersal constant describing the shape of the exponential curve and n is the variable, which determines the effect of distance on dispersal (Baguette, 2003; Junker & Schmitt, 2010). In order to assess the obtained results, the coefficient of determination R^2 was applied. The models with the highest R^2 -values best represent the data; consequently, these models have been employed for distance extrapolation (1 km, 2 km, 3 km and 5 km). In the subsequent interpretation of the results, models with $R^2 = 1$ were not considered, as in these cases only two distance categories were taken. Therefore, the mathematical formula of the curve is not meaningful enough to perform an extrapolation of the percentage of individuals that disperse over a certain distance.

2.4.5 Movement patterns

The movement patterns of *E. manto* and *E. eriphyle* males and females were assessed through maps created in the software QGIS (version 3.26.0; QGIS.org, 2022). Initially, the GPS locations of capture and recapture events were mapped. To assess movement patterns, the linear distances between capture and subsequent recapture events were visualized for each species and sex, respectively. A descriptive evaluation of the visualised movement patterns was conducted afterwards.

2.4.6 Behaviour and nectar plant preferences

The R software was once again used to conduct a comparative analysis of the behavioural patterns exhibited by the species *E. manto* and *E. eriphyle* across different sexes. In order to ascertain whether behavioural differences exist between the two species and sexes, the following combinations were tested against each other: *E. manto* males vs. females, *E. eriphyle*

males vs. females, *E. manto* males vs. *E. eriphyle* males, and *E. manto* females vs. *E. eriphyle* females. The analysis was conducted using behavioural data exclusively from the capture event, excluding data from subsequent recaptures. This was done to avoid pseudoreplication. Initially, a contingency table was created, followed by the conduction of a χ^2 -homogeneity-test, a statistical method that compares the tested groups and identifies disparities in the distribution of nominal data. The χ^2 -homogeneity-test is invalid if the expected values in the contingency table are below five and if the sample size is below sixty (Rudolf & Kuhlisch, 2020; Timischl, 2000; Hartung et al., 2009). In such cases, the dataset is too small to conduct a χ^2 -homogeneity-test, and a two-sided Fisher-test is a suitable alternative as it has no requirements regarding the sample size and can be used even if the expected values in the contingency table are below five (Rudolf & Kuhlisch, 2020). The Fisher-test is a statistical method that determines whether there is a significant association between categorical variables within a contingency table or not.

The statistical methodology applied for the behavioural analysis was also used for the analysis of the nectar plant preferences of males and females of *E. manto* and *E. eriphyle*. In this particular instance, data from the initial capture event and subsequent recapture events were analysed; however, each individual that was observed to visit a nectar plant was included only once with its first flower visit in the analysis.

3. Results

A total of 20 days were spent collecting data, with an average operation time of 3 hours and 14 minutes per day. Temperatures on these days ranged from 6 to 20 °C, and wind speeds from 1 to 4 Bft. However, 4 Bft was measured only once, and the work was stopped due to unfavourable weather conditions shortly afterwards. The level of cloudiness was predominantly within the range 0-60%. On certain days, the cloudiness levels were higher, and fieldwork was either stopped or had limited success. Comprehensive details concerning the respective field days, including meteorological information, can be found in the supplementary material (Appendix 2).

During the fieldwork, 80 individuals of *E. manto* (63 males, 17 females) and 42 individuals of *E. eriphyle* (33 males, 9 females) were marked and released (Table 1). More detailed information on the number of individuals of the respective species and sex that were recaptured once or twice, as well as the recapture ratio, is shown in Table 1. As demonstrated in the aforementioned table, the recapture rate for both species was found to be higher for females than for males. A total of 138 handling events of *E. manto* and *E. eriphyle* was documented during fieldwork. The longest recorded timespan between first capture and last recapture for *E. manto* was 3 days for males and 9 days for females. For *E. eriphyle*, it was 4 days for both males and females.

For all subsequent results it should be noted that the uncertainty of the recorded GPS locations of all capture events was very high (mean: 29 m, standard deviation $SD = 4$ m).

3.1 Estimation of population size

Initially, an attempt was made to estimate the population size per day and the corresponding parameters for *E. manto* within the software MARK, as outlined in the methods section (Chapter 2.4.1). However, it became apparent that the sample size of *E. manto* was too small for the GOF test to provide adequate information regarding the compatibility of the dataset with the model assumptions. A high proportion of the estimated parameters and the corresponding test statistics of the first GOF test were unidentifiable in both tested variants of link functions. Moreover, the processing of the subsequent two GOF tests was also not feasible with this dataset in both tested variants. Therefore, it remained unclear if the dataset of *E. manto* fits the model's assumptions. Consequently, it was not possible to further perform the analysis by using the POPAN model within the software MARK. Instead, the population size estimation according to du Feu et al. (1983) was applied. Given the considerably smaller size of the *E. eriphyle*

dataset in comparison to the *E. manto* dataset, the estimation of population size for *E. eriphyle* according to du Feu et al. (1983) was applied immediately.

Following the approach of du Feu et al. (1983), the total population size of *E. manto* was estimated at 342 ± 94 individuals, whereas for *E. eriphyle*, the total population size was estimated at 201 ± 82 individuals (Table 1). This method estimated approximately eight times more males than females for *E. eriphyle*. The estimate for *E. manto* was found to be seven times higher for males than for females.

Table 1: Number of captured and recaptured individuals and the corresponding percentages of *Erebia manto* and *Erebia eriphyle* as well as the recapture ratio and the estimation of the overall population size according to du Feu et al. (1983).

	<i>Erebia eriphyle</i>						<i>Erebia manto</i>					
	males		females		total		males		females		total	
capture	33	78.6 %	9	21.4 %	42	89.4 %	63	78.8 %	17	21.3 %	80	87.9 %
first recapture	3	60.0 %	2	40.0 %	5	10.6 %	6	63.6 %	3	36.4 %	9	12.1 %
second recapture	0	%	0	%	0	%	1	%	1	%	2	%
total number of capture and recapture events	36	76.6 %	11	23.4 %	47		70	76.9 %	21	23.1 %	91	
recapture ratio	9.09 %		22.22 %		11.90 %		9.52 %		17.65 %		11.25 %	
estimated population size and standard error	199 ± 107		25 ± 15		201 ± 82		322 ± 113		46 ± 19		342 ± 94	

3.2 Population structure

3.2.1 *Erebia manto*

The analysis of the population structure of *E. manto* revealed that most males were captured prior to the females (Figure 6). The first male was captured on the 3rd of July 2022 whereas the first female appeared 14 days later on the 17th of July 2022. The male's peak is approximately six days earlier than that of the females. These findings provide robust evidence for the occurrence of protandry in *E. manto*. An examination of the sex ratio of *E. manto* per field day revealed a notable trend (Figure 7). Initially, the majority of captured individuals were males, however, as time elapsed, the proportion of females among the daily captures increased. Figure

8 shows the percentage of captured *E. manto* males and females per field day in relation to the total captures of each sex over the entire flight period. Again, it is clearly visible, that most males emerge before the females.

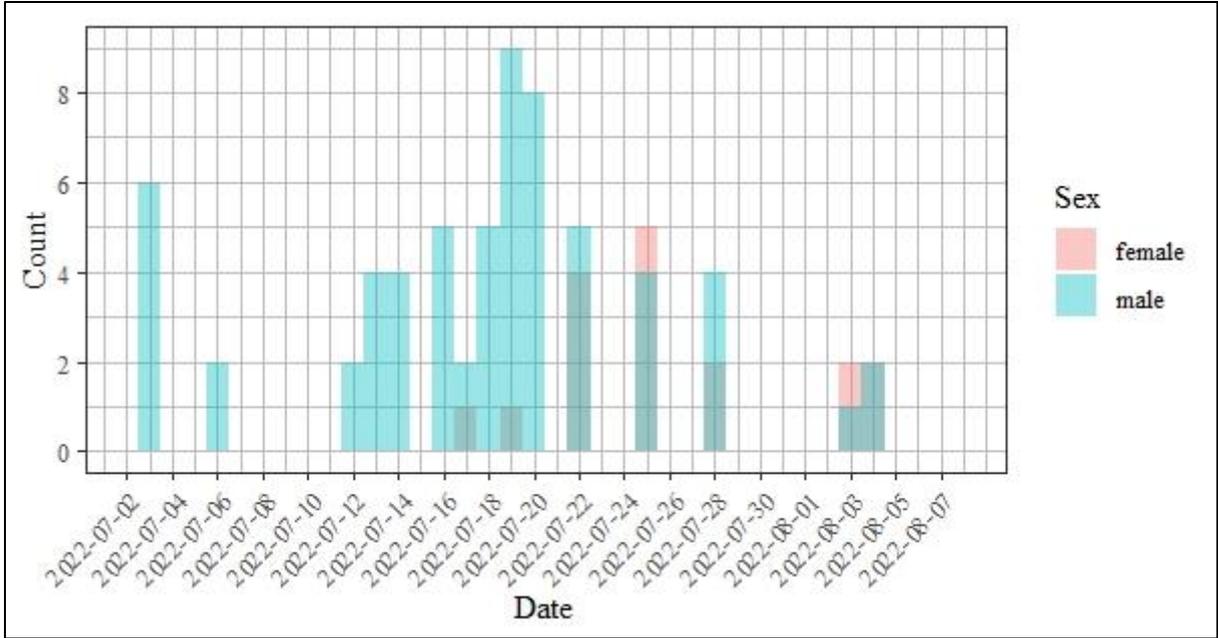


Figure 6: Count of *Erebria manto* males and females over the entire flight period.

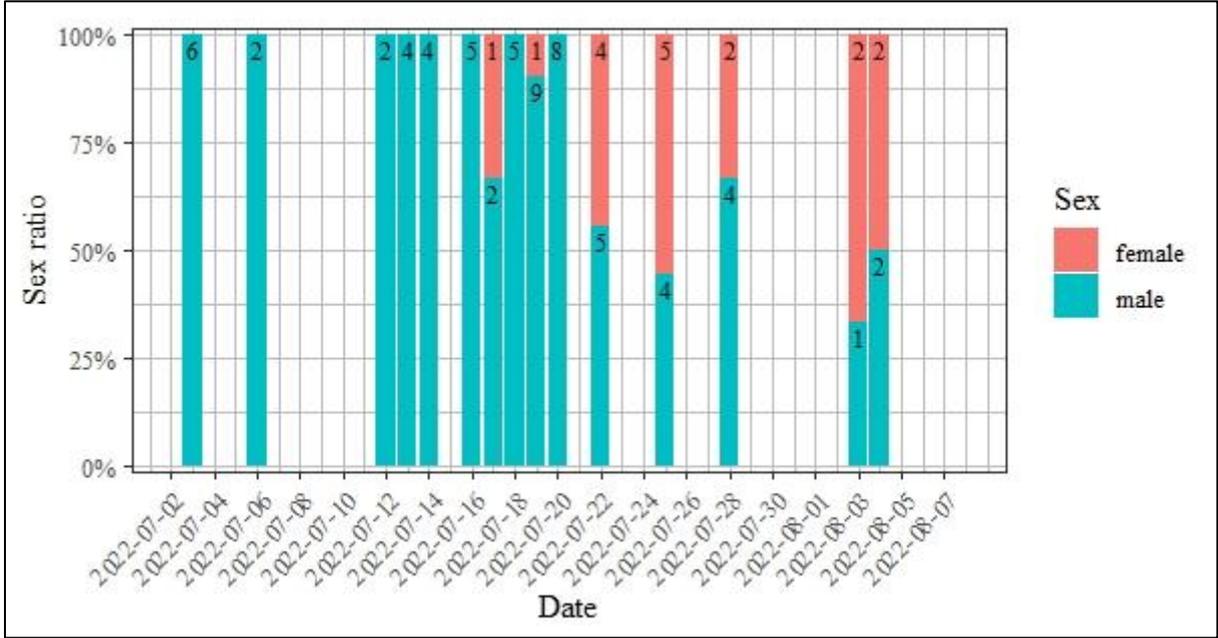


Figure 7: Sex ratio of *Erebria manto* males and females per field day during the entire flight period. The labelling at the columns shows the absolute numbers.

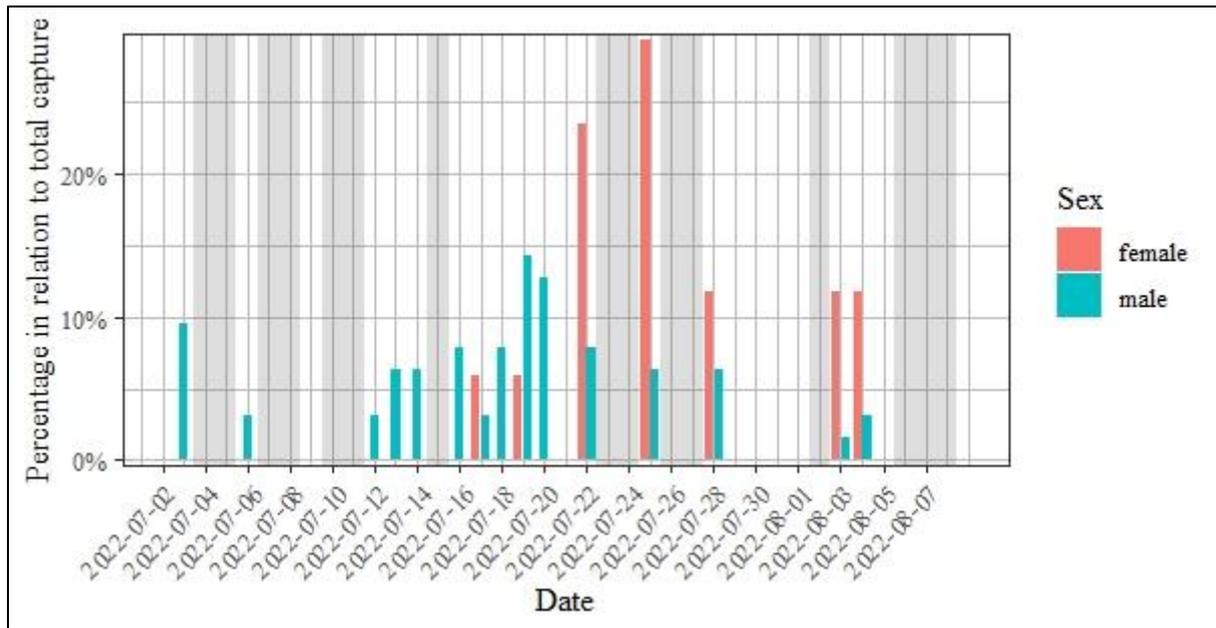


Figure 8: Percentage of *Erebria manto* males and females per field day in relation to the total captures of each sex over the entire flight period. The grey shading shows the days, where no fieldwork occurred due to unfavourable weather conditions. Please note that on days without grey shading, fieldwork took place; however, on certain days, no individuals of *Erebria manto* were captured.

3.2.2 *Erebria eriphyle*

An analysis of the count of *E. eriphyle* (Figure 9) reveals a single peak for males around 3rd of July 2022, followed by a second, less pronounced peak around 16th of July 2022. However, it should be noted that this split may be due to unfavourable weather conditions and the absence of fieldwork during the intermediate period. In the case of the female individuals, no pronounced peaks are evident. The first male individual was captured on 2nd of July 2022, with the first female specimen appearing the following day. The remaining female specimens were recorded from 16th of July 2022 onwards. The sex ratio of males and females of *E. eriphyle* per field day (Figure 10) clearly shows that, initially, almost only males were captured. However, from 16th of July 2022 onwards, the proportion of females considerably increased until, by the end, only females were captured. An analysis of the daily capture data for *E. eriphyle* indicates a trend in the sex ratio of captured individuals. The majority of males were captured during the initial phase of the fieldwork, while most females were captured during the latter phase (Figure 11). These findings suggest the presence of protandry in *E. eriphyle*.

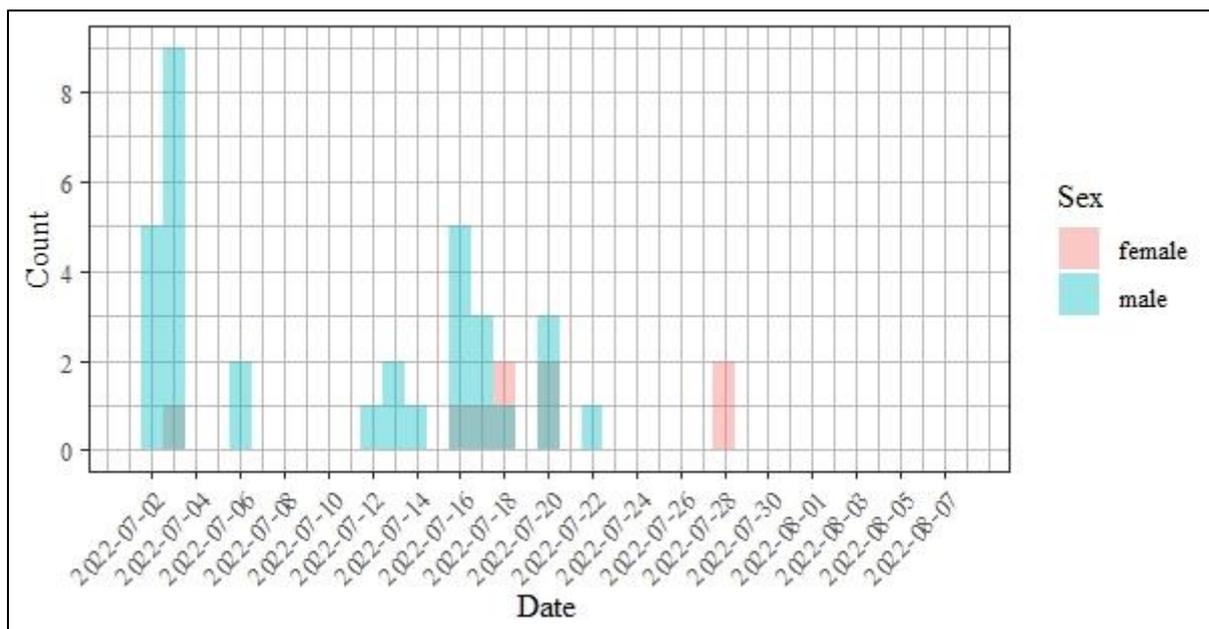


Figure 9: Count of *Erebria eriphyle* males and females over the entire flight period.

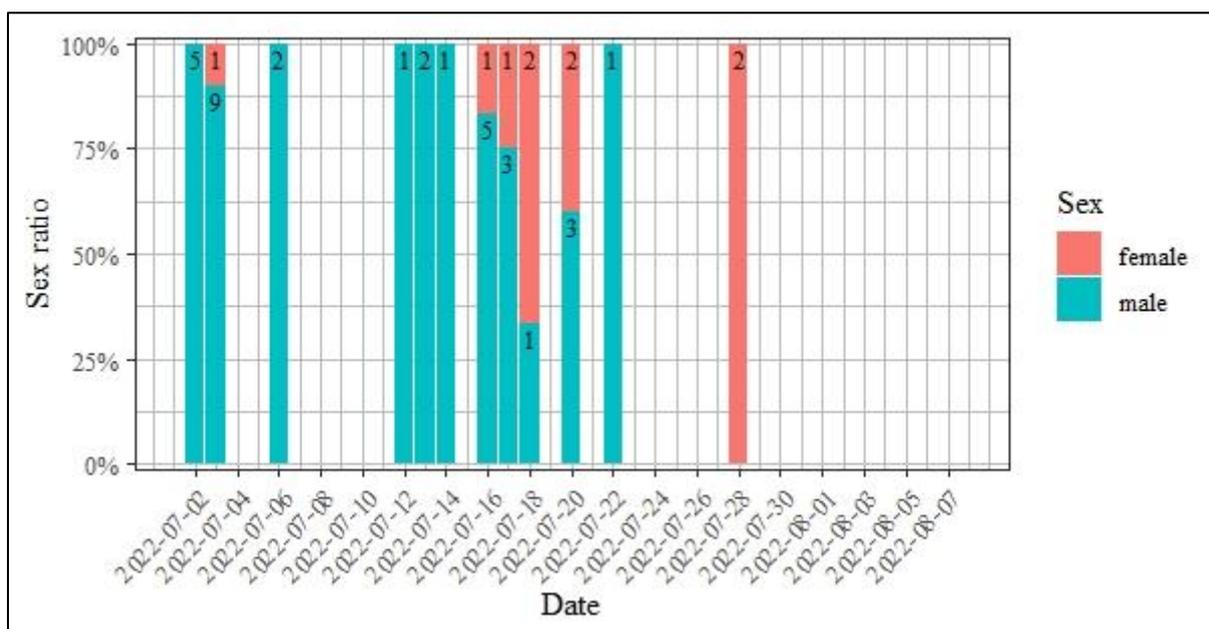


Figure 10: Sex ratio of *Erebria eriphyle* males and females per field day during the entire flight period. The labelling at the columns shows the absolute numbers.

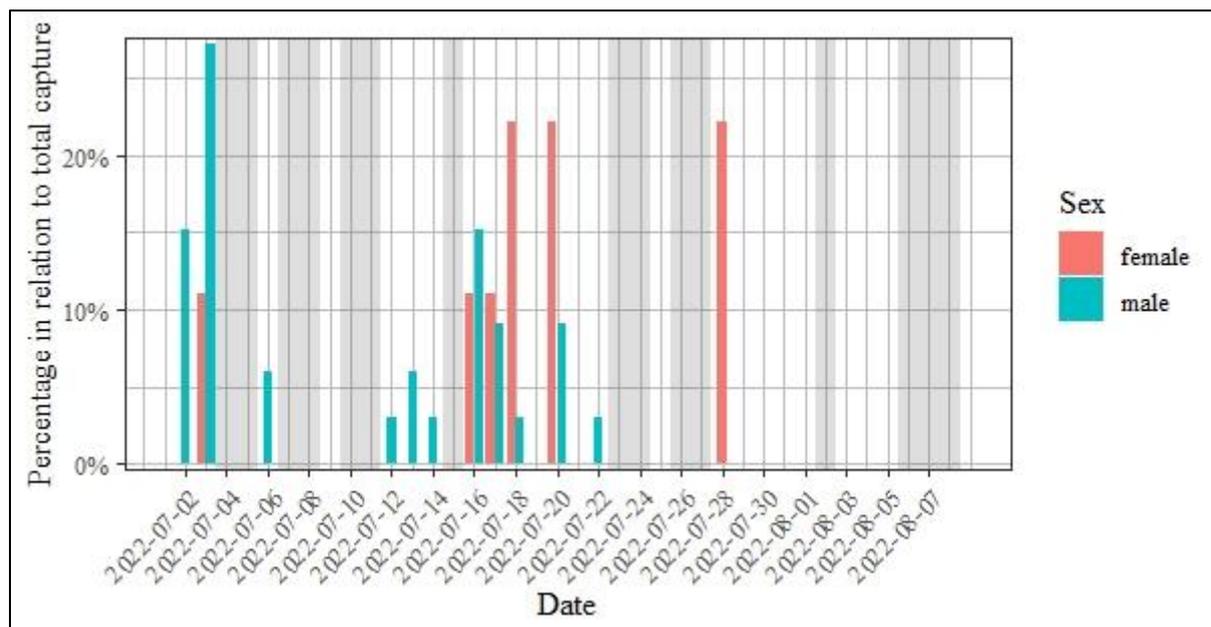
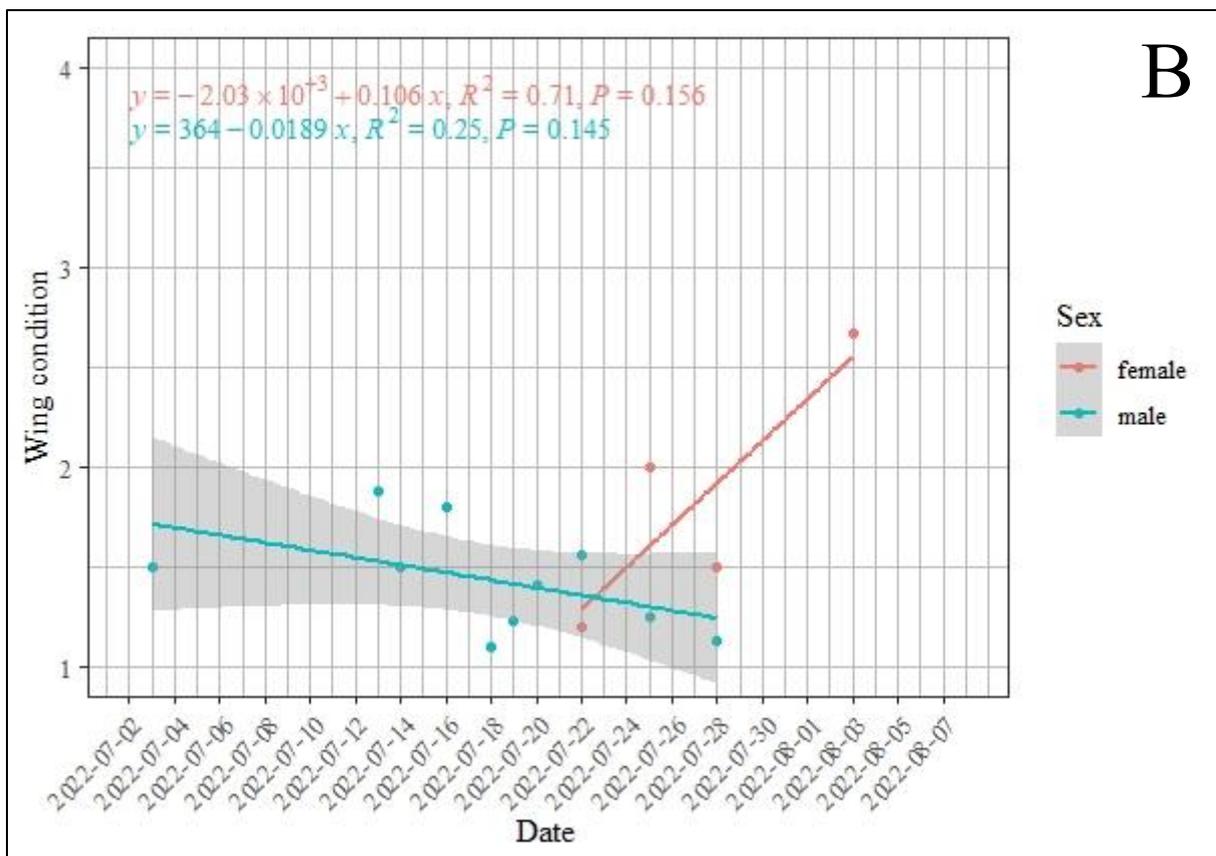
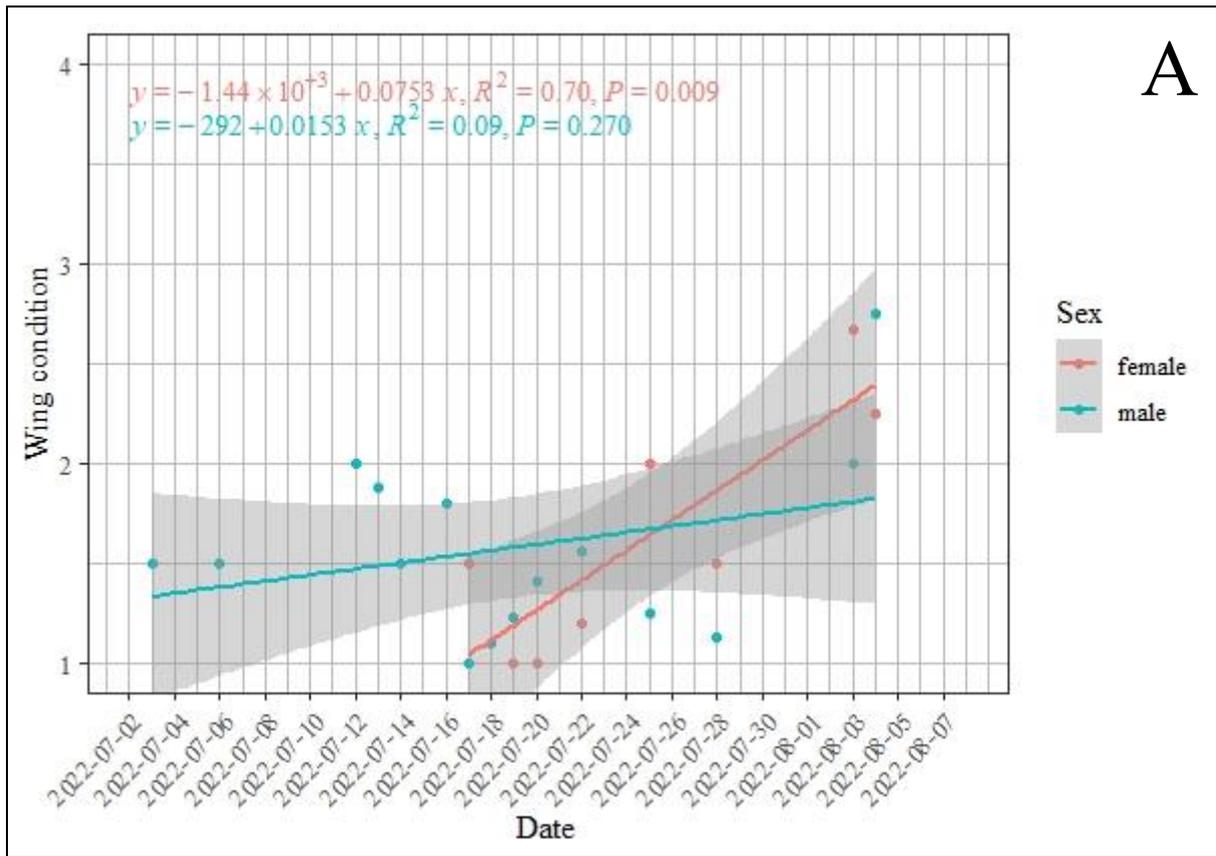


Figure 11: Percentage of *Erebia eriphyle* males and females per field day in relation to the total captures of each sex over the entire flight period. The grey shading shows the days, where no fieldwork occurred due to unfavourable weather conditions. Please note that on days without grey shading, fieldwork took place; however, on certain days, no individuals of *Erebia eriphyle* were captured.

3.3 Age structure

3.3.1 *Erebia manto*

The linear regression analysis of the complete dataset (69 males, 21 females) of *E. manto* revealed a significant deterioration in wing condition in the female individuals ($p = 0.009$, $R^2 = 0.70$), while no such deterioration was observed in the male individuals ($p = 0.270$, $R^2 = 0.09$) (Figure 12A). Even when performing the linear regression with the reduced dataset containing only days with at least three captures or recaptures (60 males, 16 females), there was no significant correlation between the wing condition and the progressing time for the *E. manto* males ($p = 0.145$, $R^2 = 0.25$) (Figure 12B). No significant correlation could be identified for *E. manto* females either ($p = 0.156$, $R^2 = 0.71$) (Figure 12B). Additionally, the calculation of the confidence interval was not feasible for the females due to the small number of data points (means). Using the mean values over five-day periods, the linear regression model did not reveal any significant correlations between wing condition and progressing time for either males ($p = 0.520$, $R^2 = 0.11$) or females ($p = 0.116$, $R^2 = 0.78$) (Figure 12C). For all these analysis variants, the R^2 -value for the linear regression models of the male individuals was very low, indicating that only a small proportion of the variance in wing condition of the males in this dataset can be explained by progressing time.



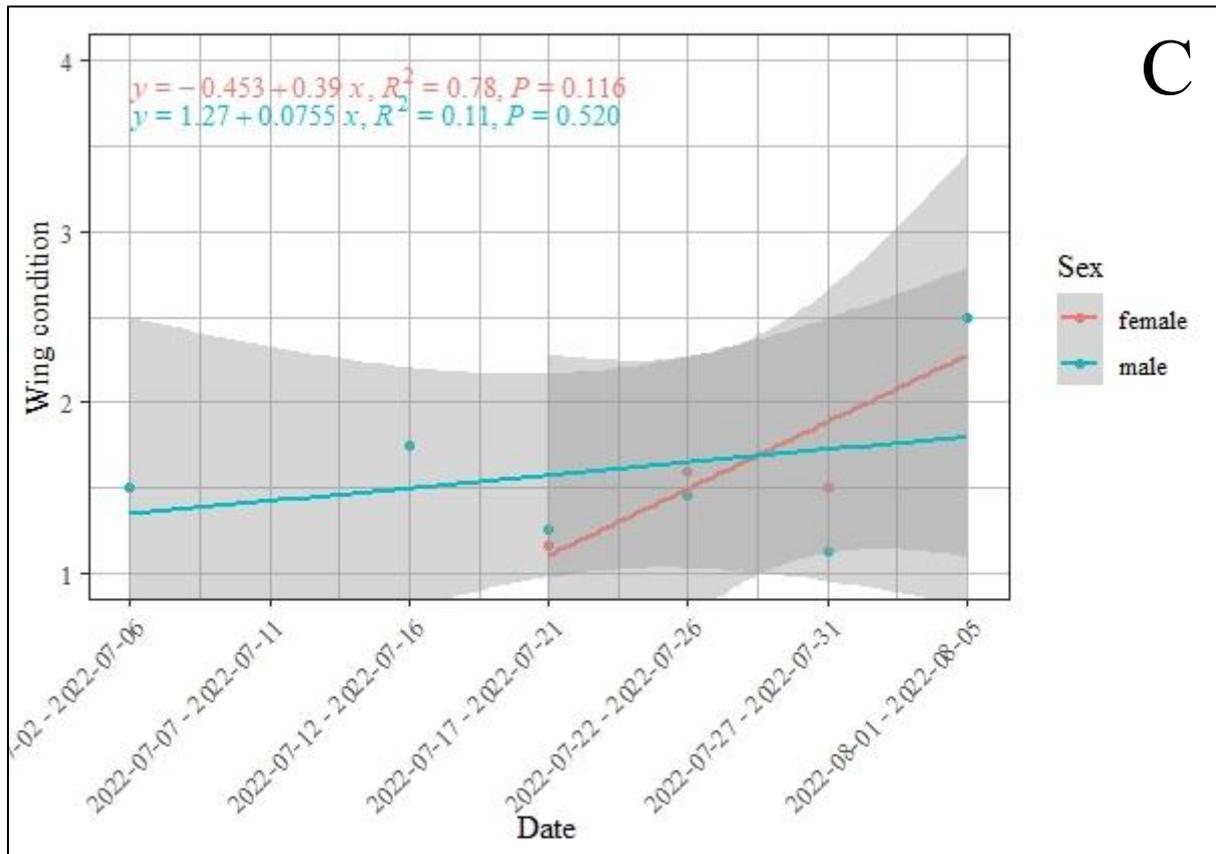
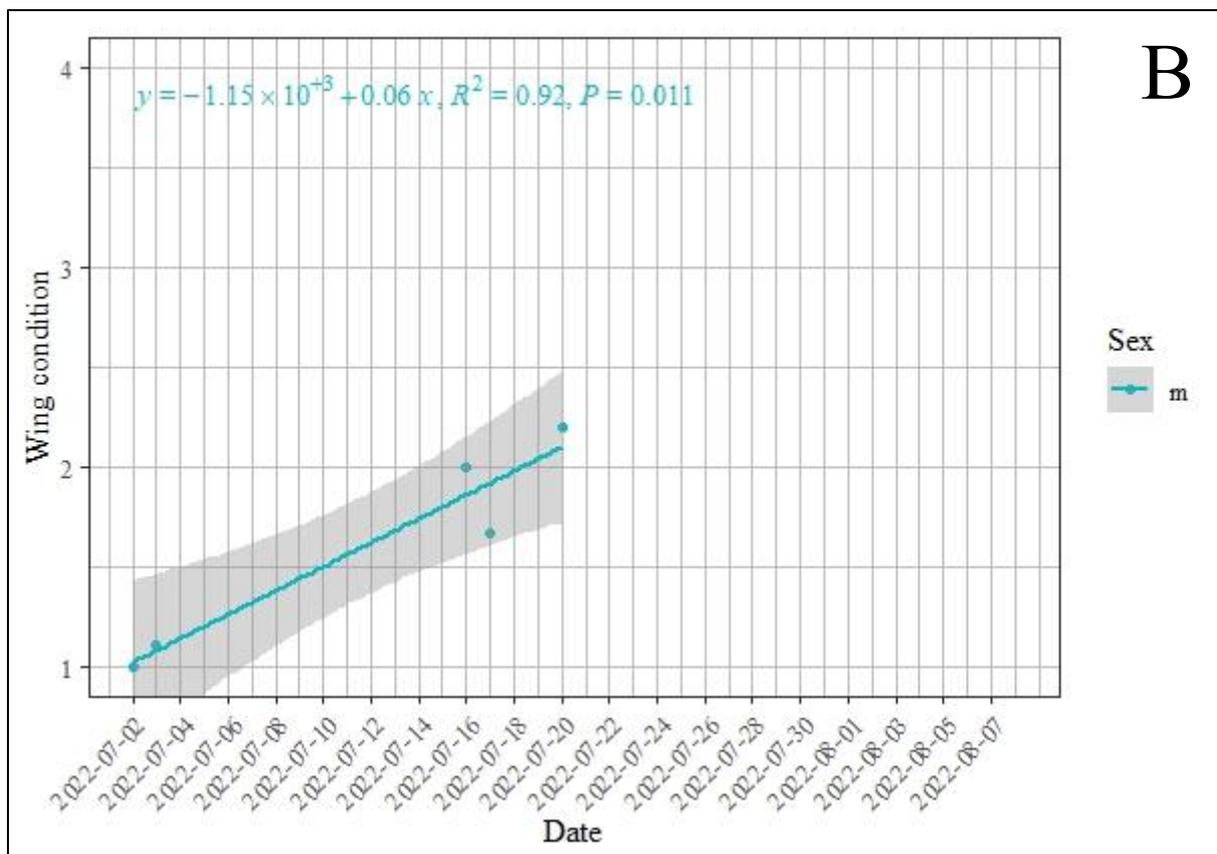
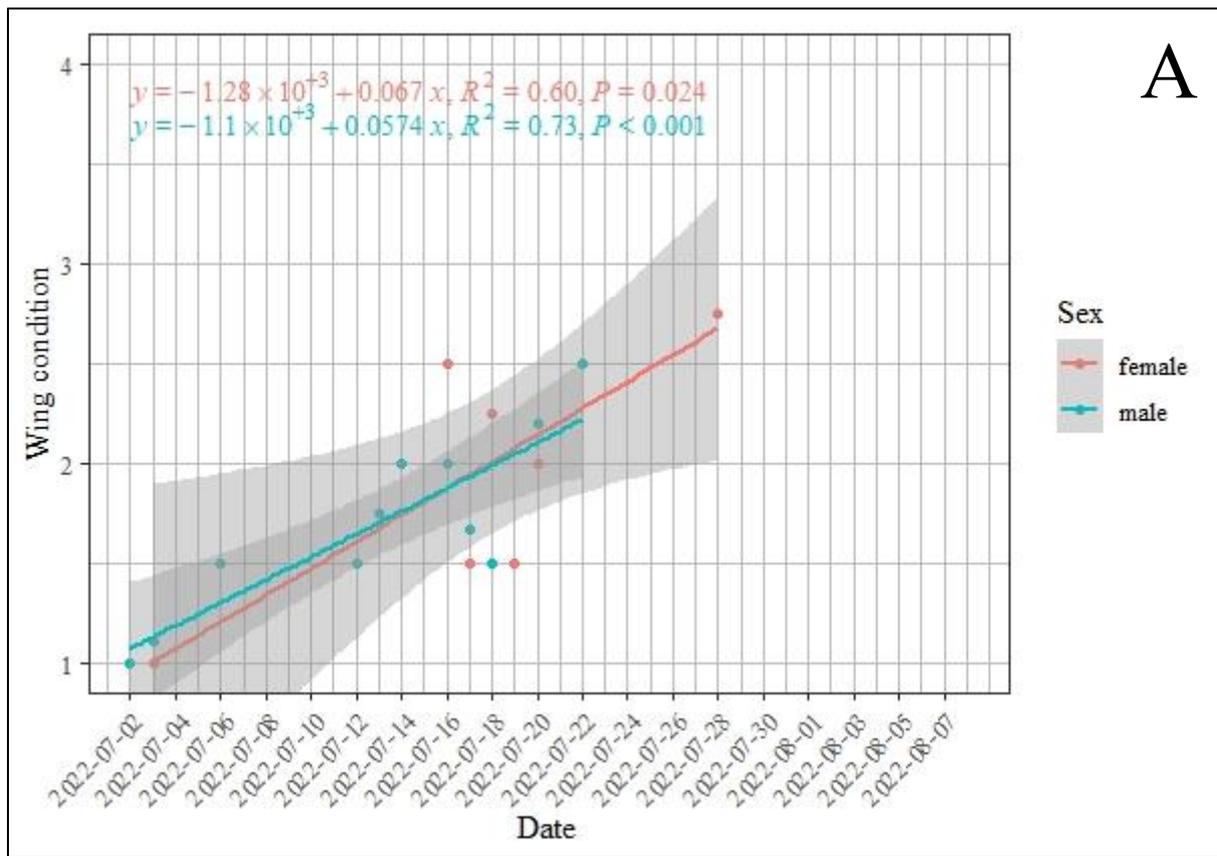


Figure 12: Linear regression models of the wing condition of *Erebia manto* over the entire fieldwork. These models were computed with (A) daily means, (B) daily means including only days with at least three captures or recaptures per sex and (C) means calculated over five-day-periods including only periods with at least captures or recaptures per sex.

3.3.2 *Erebia eriphyle*

A detailed examination of the linear regression analysis of the complete dataset (36 males, 11 females) of *E. eriphyle* revealed a statistically significant deterioration in the wing condition of males ($p < 0.001$, $R^2 = 0.73$) and females ($p = 0.024$, $R^2 = 0.60$) (Figure 13A). Both regression lines demonstrate a high degree of parallelism, suggesting a similar rate of deterioration in wing condition over time. As outlined in the methods (Chapter 2.4.3), the second approach reduced the dataset by only including days with at least three captures or recaptures per sex. This procedure resulted in the removal of all female individuals. The linear regression model of the remaining males (28 individuals) revealed a significant deterioration in wing condition over time ($p = 0.011$, $R^2 = 0.92$) (Figure 13B). The third approach (Chapter 2.4.3) reduced the dataset by calculating the mean over five-day-periods and included only periods with at least three captures or recaptures. However, for the females only one period (6 individuals) met this requirement; therefore, a linear regression model could not be fitted. The linear regression model of the males (32 individuals) displayed no significant correlation between wing condition and progressing time ($p = 0.182$, $R^2 = 0.92$) and the number of datapoints (means) within the linear regression model was too low for calculating the confidence interval (Figure 13C).



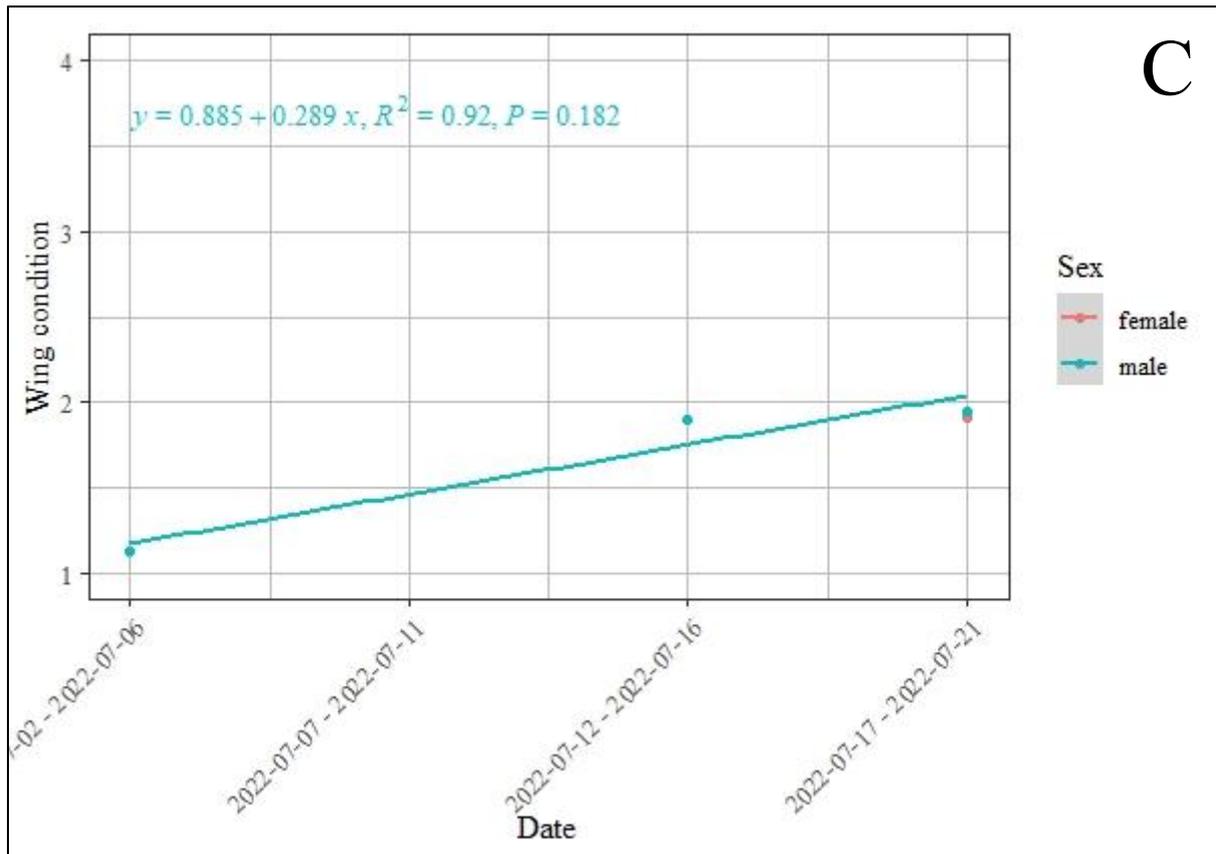


Figure 13: Linear regression models of the wing condition of *Erebia eriphyle* over the entire fieldwork. These models were computed with (A) daily means, (B) daily means including only days with at least three captures or recaptures per sex and (C) means calculated over five-day-periods including only periods with at least three captures or recaptures per sex.

3.4 Estimation of long-distance dispersal

3.4.1 *Erebia manto*

In total, the movement distance of six male and three female individuals of *E. manto* was documented. Figure 14 illustrates the percentage of individuals that moved a certain distance between the capture and the first recapture event. For the male individuals, the recorded movement distances ranged from 23 to 344 m (mean = 138 m, $SD = 127$ m). For the female individuals, the distances travelled between capture and first recapture ranged from 37 to 213 m (mean = 100 m, $SD = 98$ m). Only one female was recaptured twice, which dispersed over 220 m in total. One male individual was also recaptured a second time, but the GPS location of this second recapture is unknown. All other individuals of *E. manto* were recaptured only once.

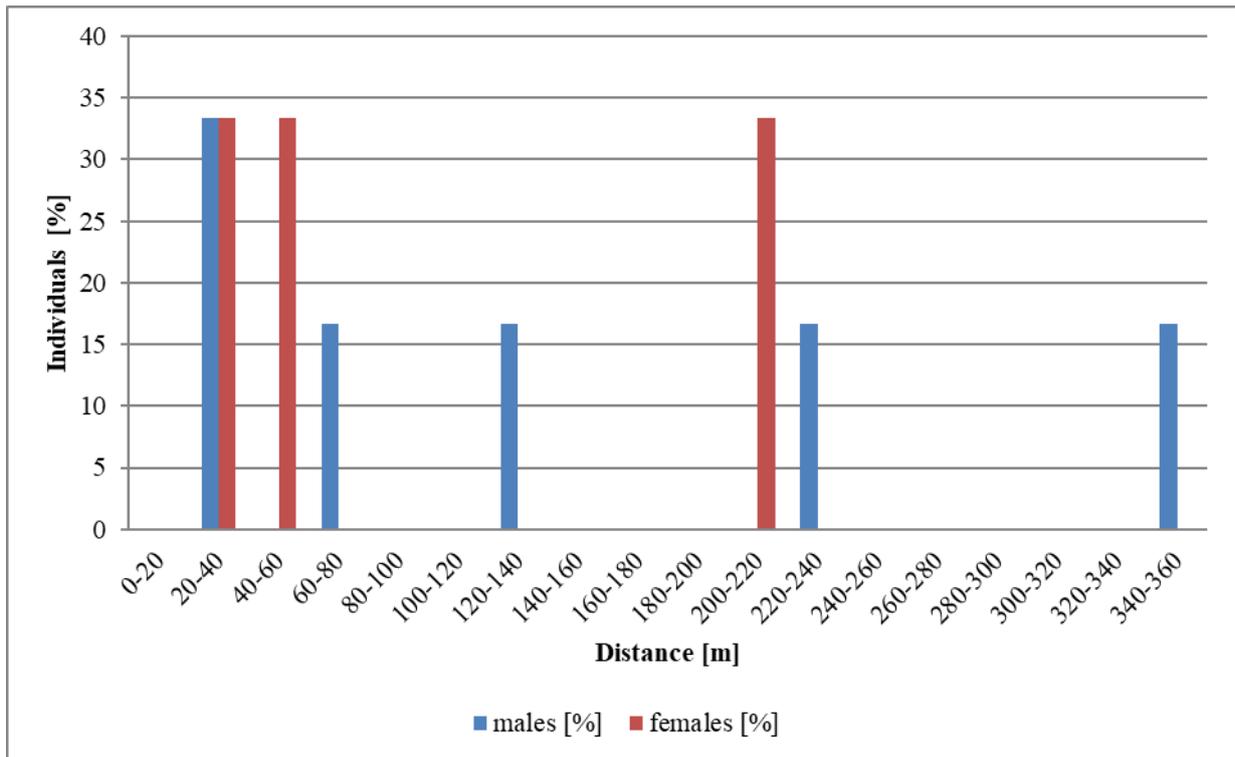


Figure 14: Percentage of females and males of *Erebia manto* that moved a certain distance between the capture and the first recapture event.

For the males of *E. manto*, the 30 m-interval, in combination with the “occupied” approach and the NEF model, showed the highest coefficient of determination ($R^2 = 0.99$) (Table 2). The females obtained the highest coefficient of determination ($R^2 = 0.97$) for the 20 m-interval with the “occupied” approach and the IPF model (Table 2). At least for the males, the R^2 -values of both model variants calculated with the three different intervals and with the “occupied” and the “complete” approach were similar in most cases. In contrast, there are clear differences in the R^2 -value for females between the three different intervals, the two model variants, and the “occupied” and “complete” approach. Table 3 shows how many percent of males and females disperse over a certain distance using the NEF and IPF model with intervals of 20 m and 30 m and the "occupied" approach. The corresponding curves can be viewed in Figure 15, 16 and 17. The data basis for females with the “occupied” approach and 30 m-interval was insufficient because only two distance classes were occupied. Therefore, no extrapolation with NEF and IPF is shown here. Overall, the estimates for the respective dispersal distances derived from the NEF model were consistently lower than those derived from the IPF model. The IPF model of the 20 m interval estimates a much higher probability of dispersal for the females compared to the males. Conversely, the NEF model indicates a slightly higher probability of dispersal for the males compared to the females. A comparison of the results from the 20 m and the 30 m interval for the males showed that the estimated percentages for the NEF are about the same;

for IPF, the percentages are slightly higher in the 30m interval. The complete distance extrapolation with IPF and NEF for all intervals and approaches can be found in Appendix 3.

Table 2: R^2 -values obtained from the negative exponential function (NEF) and the inverse power function (IPF) for *Erebia manto*, for both sexes and for different intervals, as well as for the “occupied” and “complete” approach.

Mathematical approach	Interval	Occupied/ complete	Male	Female
NEF	20 m	occupied	0.966	0.8698
		complete	0.9449	0.715
	30 m	occupied	0.9942	1
		complete	0.9774	0.6814
	50 m	occupied	0.9829	1
		complete	0.9812	0.6099
IPF	20 m	occupied	0.969	0.9671
		complete	0.8314	0.8249
	30 m	occupied	0.8991	1
		complete	0.869	0.7629
	50 m	occupied	0.9607	1
		complete	0.9449	0.828

Table 3: Percentage of *Erebia manto* females and males that disperse over a certain distance. These percentages were calculated using the negative exponential function (NEF) and the inverse power function (IPF) with the “occupied” approach. There are no percentages displayed for the 30 m-interval of the females, as the data basis was insufficient.

Sex	Distance	20 m-intervals		30 m-intervals	
		NEF	IPF	NEF	IPF
Male	1 km	0.584	9.579	0.566	11.167
	2 km	0.003	5.649	0.003	6.936
	3 km	1.61×10^{-5}	4.147	1.41×10^{-5}	5.250
	5 km	4.43×10^{-10}	2.810	3.51×10^{-10}	3.696
Female	1 km	0.488	12.836	-	-
	2 km	0.002	8.370	-	-
	3 km	9.95×10^{-6}	6.517	-	-
	5 km	2.03×10^{-10}	4.755	-	-

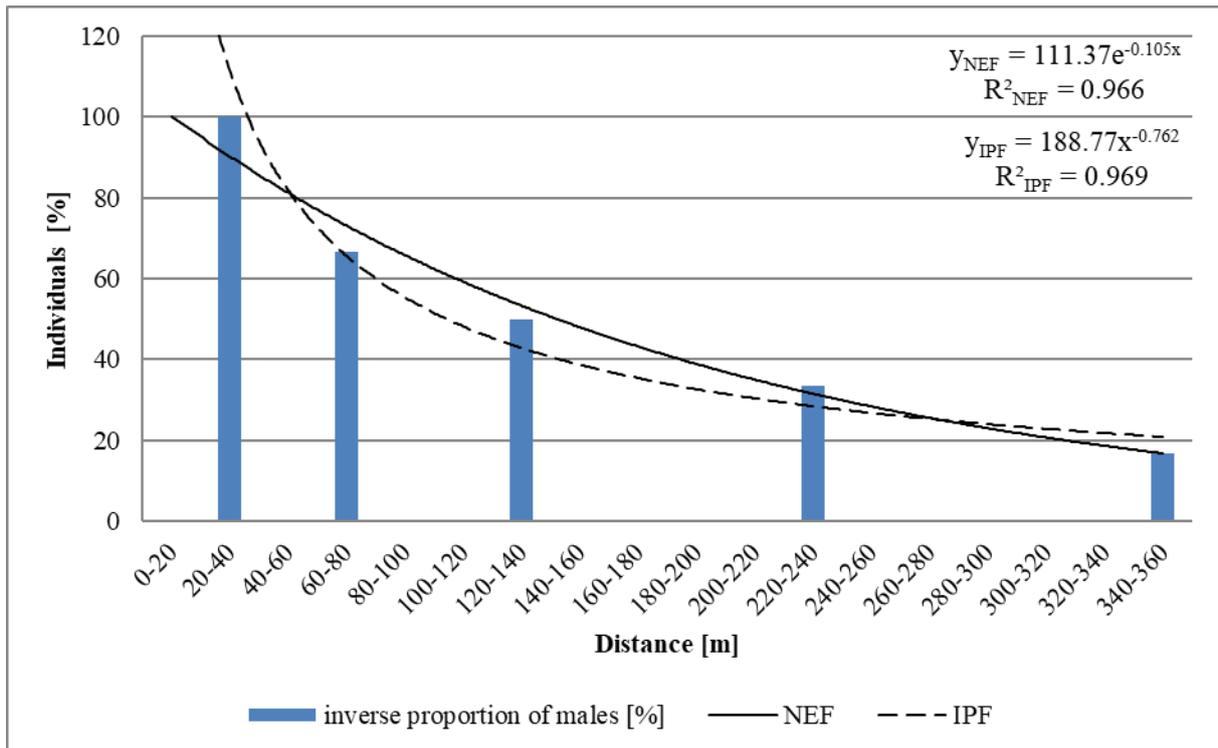


Figure 15: Inverse proportion of *Erebia manto* males of the “occupied” approach that moved a certain distance between the capture and the first recapture event. The distance is shown with an interval of 20 m, and the two curves depict the negative exponential function (NEF) and the inverse power function (IPF).

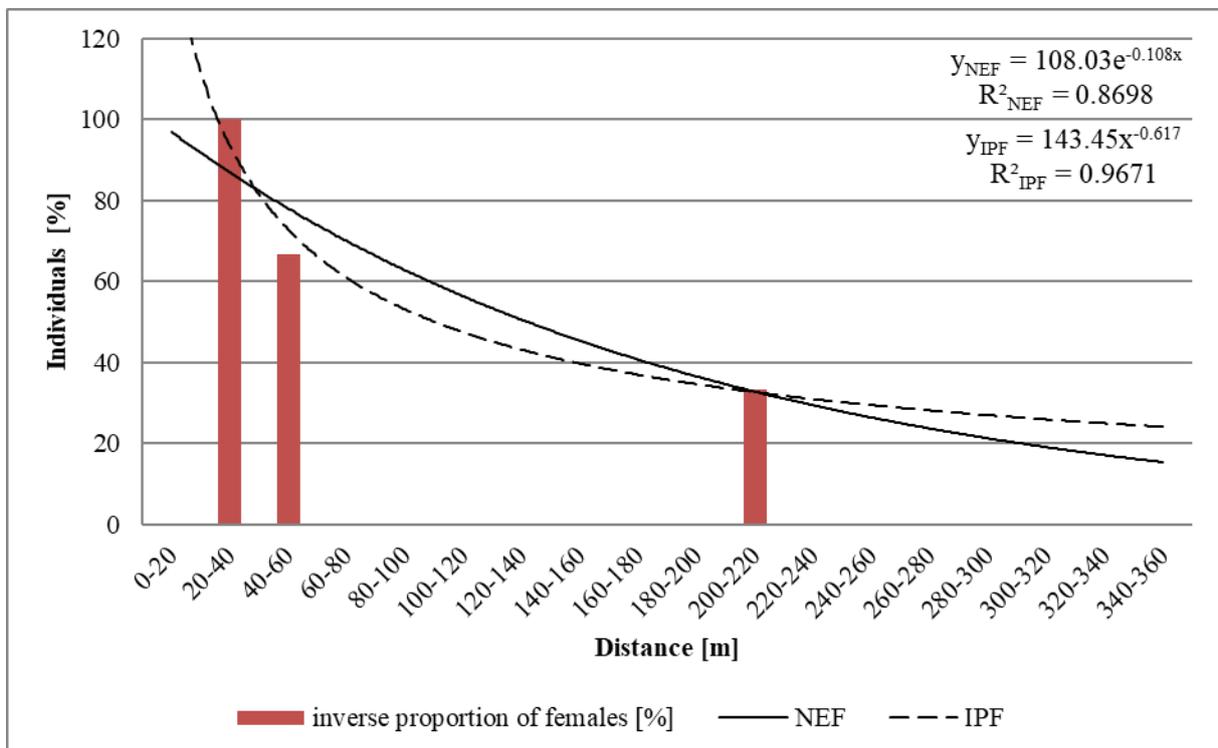


Figure 16: Inverse proportion of *Erebia manto* females of the “occupied” approach that moved a certain distance between the capture and the first recapture event. The distance is shown with an interval of 20 m, and the two curves depict the negative exponential function (NEF) and the inverse power function (IPF).

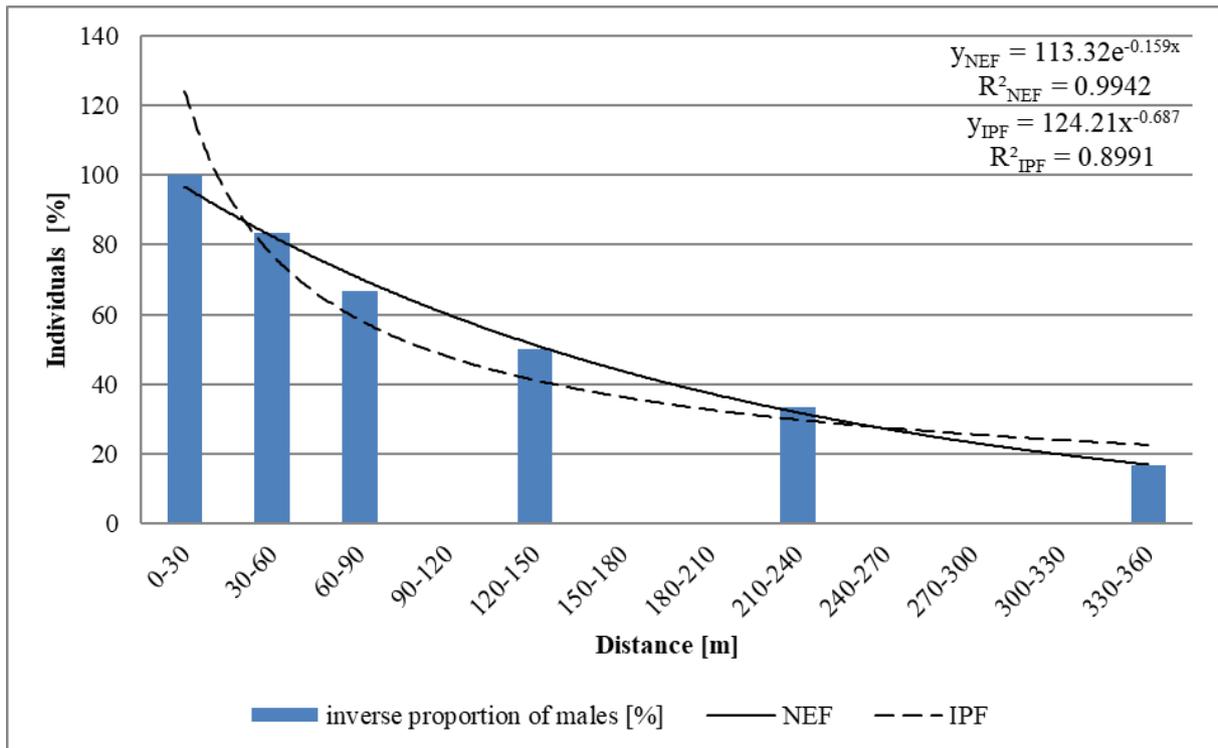


Figure 17: Inverse proportion of *Erebia manto* males of the “occupied” approach that moved a certain distance between the capture and the first recapture event. The distance is shown with an interval of 30 m, and the two curves depict the negative exponential function (NEF) and the inverse power function (IPF).

3.4.2 *Erebia eriphyle*

In total, the movement distance of three male individuals and two female individuals of *E. eriphyle* was measured. All of them were recaptured only once. The graph presented in Figure 18 illustrates the percentages of males and females, that moved a certain distance from the capture to the subsequent recapture event. The males travelled 58 m, 59 m and 73 m (mean = 63 m, $SD = 8$ m) whereas females moved 35 m and 72 m (mean = 53 m, $SD = 26$ m). Given the small sample size, the performed distance extrapolation is not reliable enough for meaningful interpretation. Further information and results on the distance extrapolation carried out for *E. eriphyle* can be found in Appendix 4.

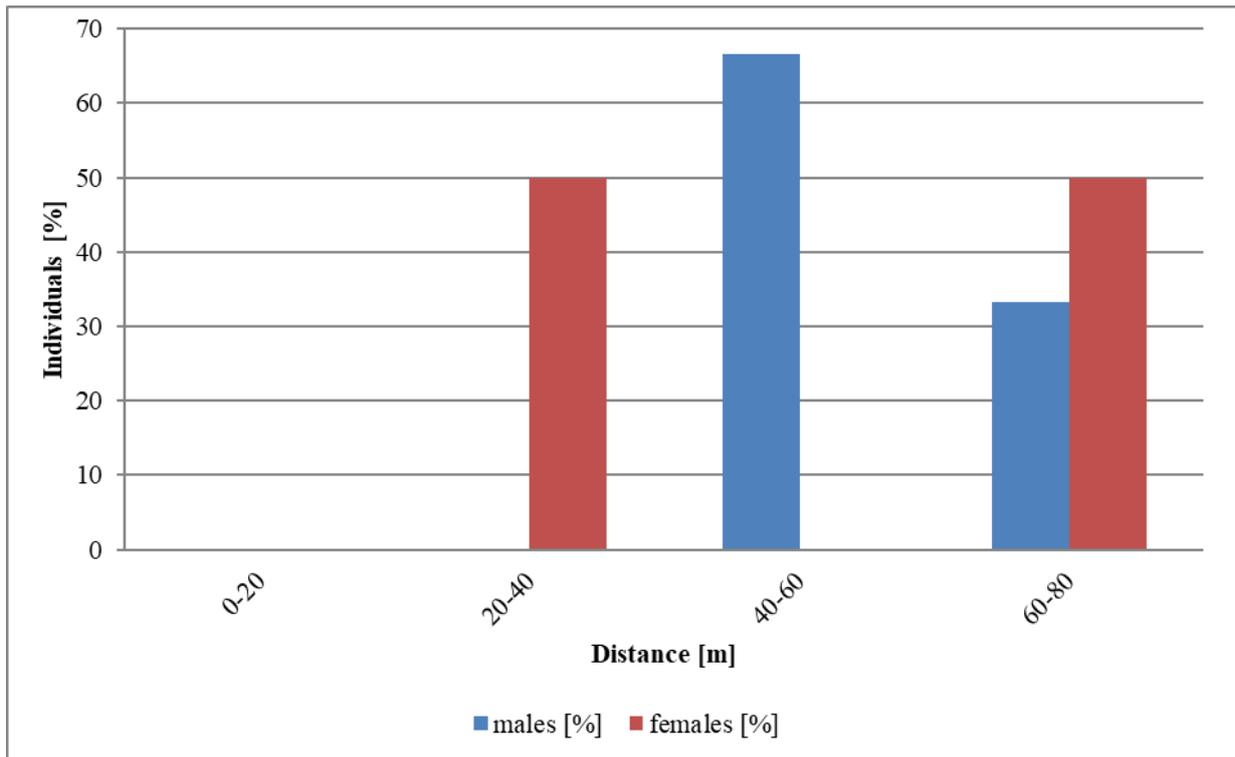


Figure 18: Percentage of females and males of *Erebia eriphyle* that moved a certain distance between the capture and the first recapture event.

3.5 Movement patterns

The majority of *E. manto* individuals was captured or recaptured in subarea one, with a smaller number also captured in subarea two (Figure 19). No recaptures and almost no captures occurred in subarea three. Most individuals of *E. eriphyle* were captured or recaptured in subarea one and very few captures occurred in the subareas two and three (Figure 20). Based on these capture and recapture locations, the movement patterns of a total of nine individuals of *E. manto* (six males and three females) and five individuals of *E. eriphyle* (three males and two females) were recorded. For the majority of these individuals only one recapture event occurred. Only two individuals were recaptured twice, but the GPS location of the second recapture could only be determined for one of these two individuals. Due to the small number of recorded recapture events per individual, the dataset does not allow conclusions about the movement patterns of males and females of *E. manto* and *E. eriphyle* within the study area. For more information on the recorded movement patterns, see Appendix 5 (the numbers one to three on the supplemented maps indicate the three subareas).

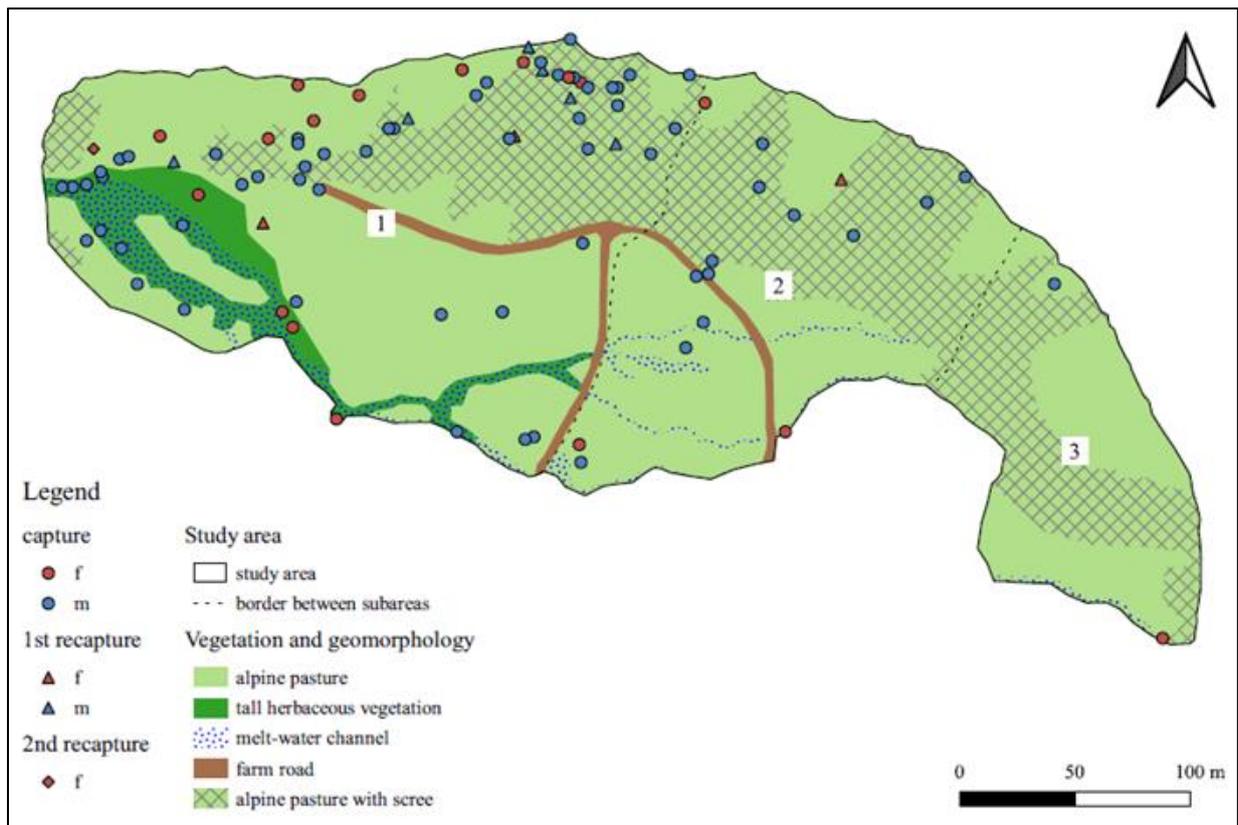


Figure 19: Mark-release-recapture locations of *Erebria manto* males and females. The numbers from 1 to 3 indicate the three subareas.

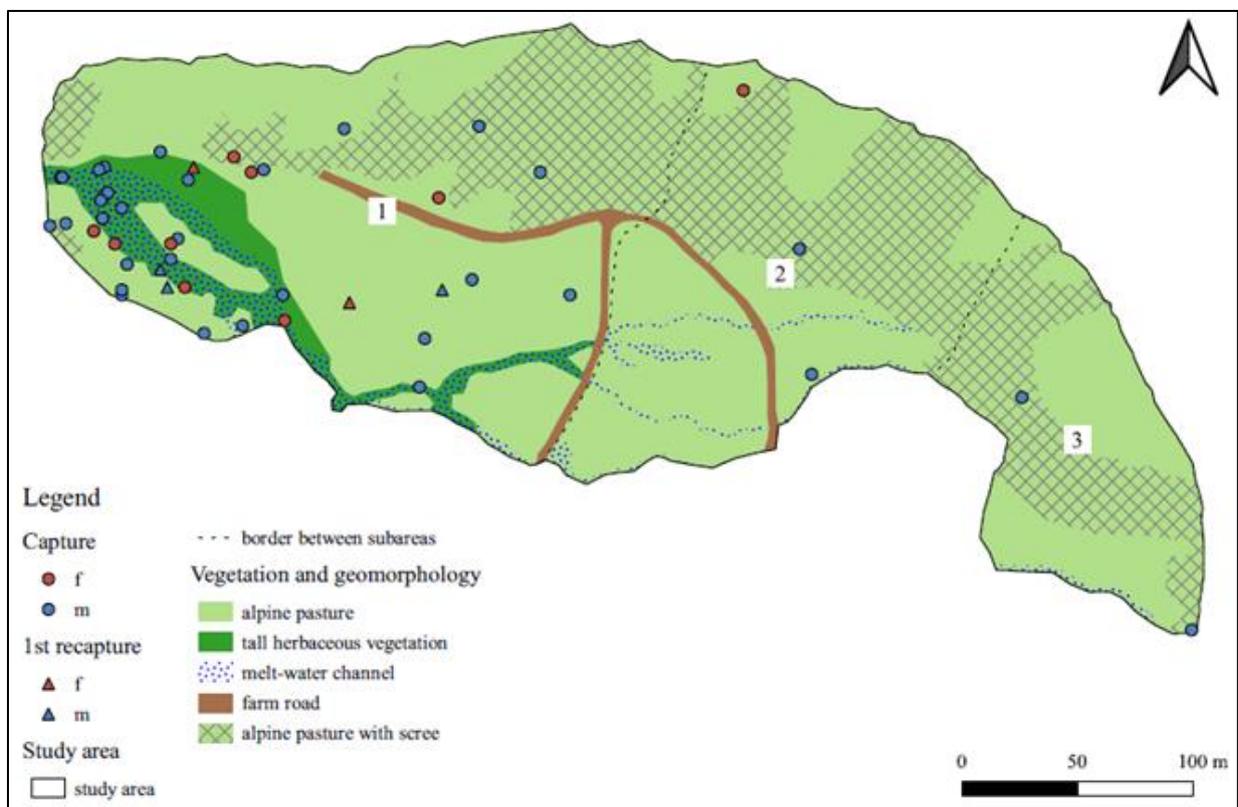


Figure 20: Mark-release-recapture locations of *Erebria eriphyle* males and females. The numbers from 1 to 3 indicate the three subareas.

3.6 Behaviour

In total, the behaviour of 80 individuals of *E. manto* (63 males and 17 females) and of 42 individuals of *E. eriphyle* (33 males and 9 females) was recorded when captured. Overall, flying was the most frequently recorded behaviour in both species and sexes (Table 4). Interaction behaviour was only observed for two *E. manto* males, which were captured together. The performed Fisher-test detected no significant behavioural differences between the sexes of the same species (Table 4). Nevertheless, the dataset hints towards a higher percentage of flying behaviour in males compared to females for both species, however, the difference is higher in *E. eriphyle* than in *E. manto* (Table 4). Furthermore, no significant behavioural differences between individuals of different species but the same sex were found (males: $p = 0.5103$, females: $p = 0.4794$).

Table 4: Absolute numbers and percentages of observed behaviour in *Erebia manto* and *Erebia eriphyle* females and males, as well as the results of the Fisher-tests. These statistical tests were used to determine whether there were any statistically significant behavioural differences between the two sexes of the same species.

Fisher-test	Sex	Resting	Interaction	Feeding	Flying	p -value
<i>E. eriphyle</i>	female	3 (33.3 %)	0 (0 %)	1 (11.1 %)	5 (55.6 %)	0.3206
	male	5 (15.2 %)	0 (0 %)	2 (6.1 %)	26 (78.8 %)	
<i>E. manto</i>	female	2 (11.8 %)	0 (0 %)	3 (17.7 %)	12 (70.6 %)	0.7194
	male	5 (7.9 %)	2 (3.2 %)	7 (11.1 %)	49 (77.8 %)	

3.7 Nectar plant preferences

A total of 12 visits of nectar plants was recorded for *E. manto* (5 females and 7 males). The nectar plant preference of *E. manto* males and females was evaluated by using a Fisher-test, but there was no statistical evidence for differences between both sexes (Table 5). However, when considering the absolute numbers, both sexes appear to prefer *Scorzoneroideis helvetica*. The majority of nectar plant visits of both species occurred on yellow flowers, but also visits on yellow to orange, white to pink and purple flowers were observed (Table 5). For *E. eriphyle*, individuals feeding on flowers of nectar plants were observed three times. One male was feeding on *Leontodon hispidus*, one male on *Taraxacum sp.* and one female on *Scorzoneroideis helvetica*, all three species have yellow flower heads. As the sample size of observed nectar plant visits for *E. eriphyle* was very low, no statistical test was performed. Both species were mainly found feeding on flowers of the plant family Asteraceae.

Table 5: Absolute numbers and percentages of visited nectar plant flowers of *Erebia manto* males and females and the result of the Fisher-test. The statistical test was used to determine whether there is a statistically significant difference in nectar plant preference between males and females.

Sex	<i>Crepis aurea</i>	<i>Scorzoneroideis helvetica</i>	<i>Trifolium pratense ssp. nivale</i>	<i>Helianthemum alpestre</i>	<i>Carduus defloratus</i>	p-value
colour of the flower head	yellow to orange	yellow	white to pink	yellow	purple	
female	0	3	1	0	1	0.4874
male	2	4	0	1	0	

4. Discussion

4.1 Sex ratio

The number of marked individuals as well as the estimation of the population sizes according to du Feu et al. (1983) showed an uneven sex ratio for both species. For *E. eriphyle* males, the estimated population size was found to be eight times larger than that of the female population. The number *E. manto* males was estimated to be about seven times higher than the number of females. Likewise, the absolute number of marked individuals of both species showed an uneven sex ratio, with more males than females. A variety of other mark-release-recapture studies also documented uneven sex ratios, with a preponderance of males over females, in butterfly species inhabiting mountainous regions (Ehl et al., 2018a; Ehl et al., 2019a; Habel et al., 2010; Wendt et al., 2021; Weyer & Schmitt, 2013). On the one hand, the imbalanced sex ratio could be caused by a low population size of females through an uneven sex ratio in the offspring or different survival rates of larvae and pupae. Another explanation could also be different and unbalanced immigration and emigration rates of males and females. In this particular instance, the most plausible explanation appears to be a methodical bias. Although no significant behavioural differences were found between the sexes of both species, the percentages of the observed behaviour (Table 4) suggest that females of both species are less flight active than males. The difference in flight activity would implicate that females are probably discovered less frequently and therefore get captured less often than males. This would lead to an underrepresentation of females in the dataset and result in a lower population size estimation for females compared to males in both species. Consequently, a considerably higher population size of females than estimated can be assumed for both species.

4.2 Protandry

Protandry is a common phenomenon in many butterflies and also known in some mountainous species e.g. *E. nivalis* (Ehl et al., 2018a) and *E. pronoe* (Wendt et al., 2021). Using this reproductive strategy, males eclose prior to females and benefit from maximizing their own reproductive success by mating with as many females as possible; females benefit from getting fertilized immediately and thereby reducing their risk of prereproductive death, hence reducing mating failures (Fagerström & Wiklund, 1982; Nève & Singer, 2008; Larsen et al., 2013). The disadvantage of protandry is the longer flight period and the risk, that all males could be killed due to unfavourable environmental conditions before the females eclose, preventing reproduction. Especially in mountainous regions this reproductive strategy is risky, as erratic cold spells regularly occur during the flight period.

In the case of *E. manto*, an earlier emergence of the males, occurring approximately two weeks prior to the females, has been observed. This phenomenon, accompanied by a distinct separation of male and female emergence peaks, provides evidence that protandry is present in this species. Therefore, it can be assumed, that *E. manto* is sufficiently well adapted to the environmental conditions at this altitude to benefit from protandry while maintaining the population even under the unpredictable weather conditions at the upper limit of its altitudinal range.

In contrast, the majority of *E. eriphyle* males emerge also two weeks earlier than the females, but a single female was captured already 13 days prior to the other females during the onset of the flight period. Due to the small sample size, the obtained population structure of *E. eriphyle* precludes a clear statement on the reproductive strategy of this species. One possible interpretation would be that the prior emergence of one female compared to all other females constitutes an outlier. Excluding this outlier, *E. eriphyle* would be considered as clearly protandrous. Another interpretation of the findings might be that *E. eriphyle* displays a rather soft protandry as most males emerge considerably earlier than the females, but a few females appear simultaneously with them. This phenomenon could be interpreted as a risk spreading strategy, which combines the advantages of protandry with an adaptation to the inconsistent environmental conditions in alpine habitats. Through the partly simultaneous eclosion of some males and females, mating failures in more hostile years would be mitigated and a complete temporal mismatch between both sexes would be avoided. Risk-spreading strategies are already known to exist in other butterfly species inhabiting alpine habitats (Ehl et al., 2018a; Ehl et al., 2019b; Wendt et al., 2021). Therefore, it is plausible that a risk spreading strategy might be present in *E. eriphyle* as well; however, this is not reflected in the dataset due to the limited sample size. In order to draw definitive conclusions on this question, further studies with an expanded dataset are necessary.

4.3 Age structure

Investigating into the wing condition of butterflies helps to understand the ageing of the population over the flight period. Moreover, the development of the wing condition over time within a population can be an indicator for the chosen reproductive strategy, as it sets the rejuvenation through eclosion of individuals in relation to the process of ageing in already present individuals (Ehl et al., 2019b). For example, a linear and parallel deterioration of wing condition in both sexes, but with a delay in females, would indicate concentrated eclosion and protandry. If the deterioration of wing condition can be divided into an initial phase, an equilibrium phase, and an aging phase, as has been proven for *B. pales* in the Romanian

Carpathians, this would suggest a risk-spreading strategy through an extended emergence period (Ehl et al., 2019b).

Unfortunately, the analysis of the obtained wing conditions of *E. manto* and *E. eriphyle* did not allow clear conclusions on the age structure within the investigated populations. The analysis of the entire dataset revealed a significant deterioration in wing condition for *E. eriphyle* and *E. manto* females, as well as for *E. eriphyle* males, throughout the entire flight period. However, after reducing the dataset by eliminating days with fewer than three recorded wing conditions, a significant deterioration was only found for *E. eriphyle* males. When the mean wing conditions were calculated over five-day periods (periods with less than three recorded wing conditions excluded) and used for linear regression, no significant correlations could be determined for any of the species or sexes studied. A comparison of the obtained statistical results indicates that the significant correlation observed in the analysis of the complete dataset for *E. manto* and *E. eriphyle* females is primarily attributable to the wing conditions of single female individuals. These single females may not be representative for the whole investigated female population of the respective species. The significant deterioration in wing condition found for *E. eriphyle* males in two of three analysis variants hints towards a simultaneous eclosion and a continuous aging of them. However, this should be further investigated as the results of the linear regression based on the means of five-day-periods do not support these findings. Nevertheless, it is overall plausible that a deterioration in wing condition occurs over time for both species and sexes in one way or another, since damage to the wings of the individuals accumulates as time passes. Moreover, the correlation between deterioration in wing condition and progressing time is already known in different butterfly species (Ehl et al., 2018a; Ehl et al., 2019a; Ehl et al., 2019b; Wendt et al., 2021; Ehl et al., 2017). Further investigation into the wing condition of both species is recommended. Doing so would ensure the validity of the results for *E. eriphyle* males and facilitate the understanding of the age structure in *E. eriphyle* females as well as both sexes of *E. manto*. This knowledge may also help to answer the question if distinct protandry is present in *E. eriphyle* or if the species additionally shows a risk diversification approach.

4.4 The impact of grazing

It is well established that the presence of adequate habitats has a substantial impact on the distribution patterns of species. As Ehl et al. (2019b) already demonstrated for *B. pales* in the Romanian Carpathians, the intensity of land use is one important factor determining the habitat quality for butterflies and therefore also affects their population density and movement

behaviour. Especially if butterflies are adapted to specific nectar or larval food plants, the alteration of plant species composition through permanent overgrazing might be an additional problem in the long run.

In the present study, the grazing of cows started a few days after the onset of the fieldwork and continued until the end on the entire study area. It is plausible that this grazing had a large impact on habitat quality and nectar plant availability for the present butterfly species and thus impacted the quality and extent of the dataset. It was observed that the quantity of floral heads within the grazed area diminished over time, but outside the grazed area and especially further up the slope still a huge amount of flower heads was present during the entire fieldwork. However, a quantitative or statistical analysis of this difference in flowering aspect was not conducted. Unfortunately, the ungrazed area was entirely outside the initially defined study area and therefore not sampled. Initially, both investigated species and other butterfly species were observed within the study area. Once grazing had begun, increasingly stronger evasive movements of all present butterflies were observed as the grazing duration increased; however, this is not visible in the movement patterns, as only a few recapture events occurred for both investigated species and sexes. Most butterflies, including *E. manto* and *E. eriphyle*, increasingly stayed in higher altitudes at the slope outside the fenced alpine pasture and thus also outside the study area. By the end of the fieldwork, hardly any butterflies were present in the grazed area and nearly all of them stayed in the ungrazed one.

My experience during fieldwork suggests, that *E. manto* and *E. eriphyle* prefer the ungrazed area over the grazed one and grazing seems to have a negative impact on habitat quality for them. However, this aspect has not been explicitly investigated in this study and needs further research. On the one hand, moving towards the ungrazed area is a favourable strategy for individuals as more resources (e.g. nectar plants and mating partners) are available; on the other hand, competition becomes stronger. At the same time, staying in the grazed area also might have advantages as the competition for the remaining resources is lower, however, this seems not to be the chosen strategy of *E. manto* and *E. eriphyle*. Indeed, a previous study already showed that nectar plant availability impacts the mobility of ringlet species as the individuals tend to stay on patches with high flowering aspect and leave patches with low availability of nectar plants (Polic et al., 2014). Therefore, it is assumed that grazing on the study area had a huge impact on the quality and quantity of the data collected, thereby also exerting a substantial impact on the results of this study. Based on this experience, further research on *E. manto* and *E. eriphyle* in ungrazed areas is suggested to mitigate the impact of grazing. Nevertheless, these

observations draw attention to the importance of an adapted grazing management for conservation and emphasize the need for areas with low or absent grazing to maintain a good habitat quality for the two investigated butterfly species.

4.5 Behaviour and movement patterns

The analysis of the behavioural patterns in *E. eriphyle* and *E. manto* revealed, that flying was the most recorded behaviour of males and females of both species when looking on the absolute numbers and the percentages. However, flying individuals might be overrepresented in the behavioural data, as they are easier to detect and therefore get caught more often. Despite no statistically significant differences in butterfly behaviour were found between the sexes and the species, the data show a tendency towards more flying behaviour in males compared to females for both species. Especially for *E. eriphyle* this difference is very prominent when looking on the percentages, but it is also visible for *E. manto*. The higher share of flight behaviour in males compared to females fits to the theory, that both sexes have different functions: Males are overall more mobile as they permanently look for females to mate with, but do not necessarily show more dispersal behaviour (Ehl et al., 2018a). As opposed to this, females focus on the production of eggs and search for suitable oviposition sites (Ehl et al., 2018a). Therefore, females invest their time in collecting nectar more often, saving energy and flying around less (Ehl et al., 2018a). Due to the low number of recapture events in *E. manto* and *E. eriphyle*, the spatial analysis of the recorded GPS positions gave no insight about the movement patterns of both species and sexes to address this aspect. However, it is known for other butterfly species, that males show typical back and forth movement patterns with rather short flight distances and only longer ones when establishing new home ranges; contrary to this females fly less frequently, but when they do, they travel greater distances (Ehl et al., 2018a; Heitzler, 2022; Wendt et al., 2021; Weyer & Schmitt, 2013). Further research with an extended dataset is necessary in order to draw conclusions about whether the movement patterns of males and females fit this theory and to make reliable statements on whether behavioural differences occur.

4.6 Estimation of long-distance dispersal

Investigating the linear movement distances of *E. manto* using the inverse power function revealed that females are more likely to disperse over long distances than males. By contrast, the analysis using the negative exponential function yields similar probabilities for both males and females. However, it must be taken into account, that the negative exponential function is

known for rather underestimating the probability of long-distance dispersal, and the inverse power function is more reliable for this purpose (Baguette, 2003). When interpreting the results of the long-distance extrapolation, it is important to note that the TourCount application, in conjunction with the specified smartphone model, caused a high degree of uncertainty in the recorded GPS locations. Furthermore, the movement distances of only a few individuals were recorded. Both aspects limit the informative value of the obtained results. Nevertheless, the higher dispersal of females compared to males in *E. manto* fits to previous studies on the related ringlet species *E. nivalis* and *E. pronoe* (Ehl et al., 2018a; Wendt et al., 2021). Higher dispersal ability in females is biologically reasonable, as this enables them to occupy suitable and vacant habitat patches, thereby increase their reproductive success and potentially establish a new population (Ehl et al., 2018a). In contrast, leaving a populated habitat patch and dispersing over long distances would not be a reasonable strategy for males, given their aim to mate with as many females as possible. Unfortunately, the data of *E. eriphyle* were insufficient for reliable estimates of the long-distance dispersal. However, the obtained linear movement distances are similar in magnitude to the ones from *E. manto*. Therefore, the percentage of individuals dispersing over longer distances might be similar for both species; nevertheless, this needs further investigation.

Previous research on the mobility of several ringlet species in the immediate vicinity to my study area predominantly revealed no significant differences among them (Polic et al., 2014), however, only *E. eriphyle* but not *E. manto* was included in this study. The research of Polic et al. (2014) additionally underlined that *Erebia* species are rather sedentary, and their movement distances are short with more than 50 % of the individuals moving a maximum of 25 m between the capture events (Polic et al., 2014). Contrary to this, the obtained estimates of long-distance dispersal for *E. manto* hint towards a particularly high dispersal ability compared to other *Erebia* species (Ehl et al., 2018a; Wendt et al., 2021). This would implicate that *E. manto* is able to recolonize formerly inhabited patches, which is useful under the unpredictable weather conditions in the alpine region. Moreover, *E. manto* would be able to effectively colonize new suitable habitats in the surrounding, which is an important ability in terms of climate change and land use alteration. On the other hand, dispersal from a suitable habitat patch towards the surrounding matrix implicates the risk of death without having previously reproduced. Nevertheless, further research involving a more expansive dataset with precise GPS locations for both species is required to confirm the findings for *E. manto* and make reliable statements on the ability for long-distance dispersal in *E. eriphyle*.

4.7 Nectar plant preferences

The investigation into the nectar plant preference showed, that *E. eriphyle* only visited yellow flowers and *E. manto* mainly yellow but also pink flowers. However, these observations as well as the preferred nectar plant species must be interpreted with caution, as the sample size is limited and the statistical validation of the results is lacking. Nevertheless, the observed colour preferences of *E. manto* and *E. eriphyle* in this study largely align with previous findings (Neumayer & Spaethe, 2007). Although, the choice of nectar plants for many alpine butterfly species cannot be explained solely by flower head colour and its abundance or nectar content (Neumayer & Spaethe, 2007). Neumayer & Spaethe (2007) also supposed an impact of innate and learned preferences on nectar plant choice as well as an effect due to concurrence with other pollinators (e.g. bumblebees). Moreover, the scent, the nectar quality and concentration (Rusterholz & Erhardt, 2000), the presence of other resources in the surrounding and the flower morphology might have an impact.

Indeed, previous investigations on *Lysandra bellargus* [ROTTEMBURG, 1775] showed already that the nectar plant choice can even vary between conspecific males and females (Rusterholz & Erhardt, 2000). Males of this species preferably choose nectar plants with a high sugar content, in particular sucrose, whereas females favoured flowers with high contents of fructose and amino acids (Rusterholz & Erhardt, 2000). These preferences might be caused by the higher energy demand for patrolling behaviour in males and the nutritional needs for egg production in females (Rusterholz & Erhardt, 2000). Nevertheless, the investigation into the existence of sex-specific nectar plant preferences did not reveal statistically significant differences for *E. manto*. Furthermore, the statistical result for *E. manto* should be viewed with caution as the sample size is low. Due to the absence of sufficient data, sex-specific nectar plant preference has not been tested for *E. eriphyle*. Consequently, it is not possible to draw definitive conclusions regarding the presence or absence of such preferences in both investigated species and further investigation is recommended.

5. Conclusion

This master thesis represents another step towards understanding the ecology and the adaptations of the two butterfly species *E. manto* and *E. eriphyle* and provides a starting point for future research to gain a more comprehensive understanding. The findings demonstrate that protandry is present in both species. However, further investigation is necessary to make a definitive statement whether risk spreading strategies are present in *E. eriphyle*. Nevertheless, both species overall seem to be well adapted to the environmental conditions in their alpine habitat. The existing age structure of *E. manto* and *E. eriphyle* could not be clearly determined with the available data set. Nevertheless, the results suggest that for *E. eriphyle* males simultaneous eclosion in combination with a linear ageing process is present within the population.

The estimation of long-distance dispersal suggests more frequent dispersal events in *E. manto* females than in males. Moreover, *E. manto* seems to be less sedentary than other *Erebia* species. Due to the low sample size, no reliable statements can be made about the probability for long-distance dispersal in *E. eriphyle*. Unfortunately, the low number of recaptures also prevented meaningful conclusions about the movement patterns of males and females of both species and further studies are needed to address this aspect. Based on this dataset no significant behavioural differences between both sexes and species were found. Nevertheless, the results suggest the tendency towards more flight behaviour in males than in females, but this needs to be further investigated. Likewise, the low sample size precluded valid statements on the nectar plant preference. Repeating this study with a more extensive dataset obtained from an ungrazed area and with more precise GPS locations is recommended in order to verify the results of this study and address remaining knowledge gaps.

6. References

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8. Selbstständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter oder unerlaubter Zuhilfenahme anderer als der angegebenen Quellen und Hilfsmittel angefertigt habe. Die den benutzten Quellen wörtlich oder inhaltlich entnommenen Stellen sind als solche kenntlich gemacht.

Die „Richtlinie zur Sicherung guter wissenschaftlicher Praxis für Studierende an der Universität Potsdam (Plagiatsrichtlinie) - Vom 20. Oktober 2010“, im Internet unter https://www.uni-potsdam.de/fileadmin/projects/ambek/Amtliche_Bekanntmachungen/2011/ambek-2011-01-037-039.pdf, habe ich zur Kenntnis genommen.

Ludwigsfelde, den 18.08.2025

Ort, Datum

Miriam 

Unterschrift