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Evaluating Habitat Conditions for the Ringlet Butterfly (*Erebia pronoe glottis*) in a Multi-Use Mountain Landscape in the French Pyrenees

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Abstract

We conducted a mark–release–recapture study of the ringlet butterfly, *Erebia pronoe glottis*, in the Pyrenees to study population density, flight activity, dispersal, and nectar plant preferences. We found differences between both sexes in population density (males: 48/ha; females: 23/ha), sex ratio (2.1), and behaviour (75.4 vs. 20.5% flying). Both sexes used a wide range of nectar plants (Asteraceae, 40.6%; Apiaceae, 34.4%; Caprifoliaceae, 18.8%). However, local abundance appeared to be limited by the availability of nectar plants. Compared to a population of an extensively used pasture in the Alps, a significant increase in flight activity, but not in range, was observed. Movement patterns showed the establishment of home ranges, which significantly limited the dispersal potential, being low for both sexes (mean fight distances-males: 101 m ± 73 SD; females: 68 m ± 80 SD). A sedentary taxon such as *E. pronoe glottis* does not seem to be able to avoid the pressure of resource shortage by dispersal. As a late-flying pollinator, *Erebia pronoe* competes seasonally for scarce resources. These are further reduced by grazing pressure and are exploited by honey bees as a superior competitor, resulting in low habitat quality and, consequently, in comparatively low abundance of *E. pronoe glottis*.

Keywords: lepidoptera; mark–release–recapture; resource depletion; movement patterns; population demography

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1. Introduction

Worldwide, insect fauna is under increasing pressure, which is reflected in massive losses in diversity and abundance of many species [1–3]. One of the main causes is the loss of high-quality habitats [4]. The availability of resources is one of the most significant quality parameters of habitats, along with microclimate and vegetation structures [5,6]. In this context, a habitat should not be understood as a physically limited area of a certain vegetation type, but rather as a physically limited locality that meets the diverse biotic and abiotic requirements of a species in spatial and temporal succession [7]. The extent of this area is determined by the perceptual limits and specific mobility of the species [8]. Only if all its biotic and abiotic needs are met within a specific area, a species can survive, but these requirements may not remain the same. Specific requirements may differ for particular species among seasons or developmental stages and may be scattered across the landscape. Thus, high mobility can allow effective use of scattered resources and, subsequently, survival.

Likewise, high mobility is of great importance for many taxa to keep up with climate change and the associated shifts of range boundaries. However, even mobile taxa such as birds or butterflies cannot fully compensate for these effects, resulting in extinction debts. For example, an alpine species may follow the shift of the snowline and yet be subject to an increased risk of extinction. The earlier onset of snowmelt can result in asynchronous development of flora and fauna depending on it, disrupting biotic interactions and reducing resources, thereby increasing extinction risk [9]. This pressure can be met, especially by host plant generalists, partly through a shift in their requirements (i.e., resource evasion) [9].

Among insects threatened by climate change, alpine butterflies are under particular pressure due to their dependence on snow cover for the survival of their larvae [9–11]. In addition, the majority of alpine butterflies are not able to avoid stressors through dispersal in the often heterogeneous high mountain landscapes because of their mostly sedentary behaviour [12,13]. This further increases the risk of biodiversity loss of the alpine insect fauna. The sensitive response of butterflies to environmental conditions and their changes, as well as their high reproductive rates, make them excellent indicators of habitat quality and resource availability [5,14,15]. Therefore, the current status of local alpine butterfly populations needs to be surveyed to gain an understanding of the local ecological niche and ecological potential, and to assess the influence of various stressors.

We have chosen the alpine butterfly species *Erebia pronoe* (Esper, 1780) (Lepidoptera: Nymphalidae) as a typical representative of alpine rupiculous grasslands [16], a species of which several morphologically and genetically distinct lineages have been described throughout its distribution range [17–20]. It thrives on wet meadows, calcareous grasslands, and screes from the upper montane to the alpine zone [16]. *E. pronoe* is widespread and often common throughout the Alps. It is local in the Swiss and French Jura as well as in the Pyrenees, where high densities can be reached. Populations of *E. pronoe* become rarer in the Carpathians, including the High Tatras and the mountains of the Balkan Peninsula [21].

Erebia pronoe flies in one generation from the end of July to mid-September, which can fluctuate depending on the onset of snowmelt; it hibernates as L1 larva. The preferred larval food plants are *Festuca* species such as *Festuca ovina* L. (Poaceae), *Festuca rubra* L. (Poaceae), and *Festuca quadriflora* Honck (Poaceae), and to a lesser degree *Anthoxanthum odoratum* L. (Poaceae); breeding on *Poa annua* L. (Poaceae) was successful [22]. In a recent study performed in highly suitable habitats in high altitudes of the eastern Alps, *E. pronoe* was found to be a low-mobility species with opportunistic use of resources with established home ranges [23]. Phylogeographic analyses revealed a strong differentiation within this species among and even within high mountain systems [20], and it is unknown whether different phylogeographic lineages are ecologically similar. Furthermore, it is unknown whether populations in less suitable habitats and at lower altitudes behave similarly to the high-altitude populations analysed by Wendt et al. [23] in the highly suitable habitat of the eastern Alps. In the population ecology study presented here, we therefore investigated the demographic structure of a population in the French Pyrenees by applying mark–release–recapture (MRR). The studied population belongs to a phylogeographic lineage, i.e., *Erebia pronoe glottis* Fruhstorfer, 1920, strongly differentiated from the eastern Alps [20]. Furthermore, the Pyrenean study area had three times the size of the study area assessed by Wendt et al. [23] in the eastern Alps; besides the former, with only moderate perturbation by pasturing, our site in the Pyrenees was strongly impacted by a larger number of apiaries and intensive high-altitude pasturing by cows. Furthermore, in contrast to the site in the eastern Alps, the Pyrenean site was at the lower edge of the species' altitudinal distribution.

By studying the behaviour and mobility of both sexes, as well as the influence of weather on these factors, we address the following questions:

What is the abundance and sex ratio of the Pyrenean population at the lower altitudinal edge in the French Pyrenees, and what emerging patterns can be observed?

Do flight patterns and distances differ between the Pyrenean and the Alpine populations? How can these differences be explained?

2. Materials and Methods

2.1. Study Area

Our study area in the core of the distribution of *Erebia pronoe glottis* is located in the French Pyrenees near the "Parc national des Pyrénées" and close to the Station de Ski Cauterets-Le Lys (42°52′ N; 0°08′ W) in the arrondissement Argelès-Gazost, Department Hautes-Pyrénées. The studied steep slope is composed of two study plots of 5.45 ha and 5.77 ha, respectively, and extends 1400–1650 m asl, which is below the natural forest line [24]. The study plots are interspersed with gravel areas and represent a characteristic habitat of *E. pronoe*. Further suitable habitats exist within a radius of 200 m. To the east, our study plots border the protected area "Parc national des Pyrénées", where no capturing of butterflies was performed. The area to the west was too steep for performing MRR; the adjoining areas to the north and south were too heavily grazed for the occurrence of *E. pronoe glottis*, as it was grazed by ca. 50 cows, as well as occasionally a herd of horses (ca. 20) and a flock of sheep (>300). Five apiaries with 36–59 colonies each were located at 50–1500 m from our MRR plots (Figure 1).

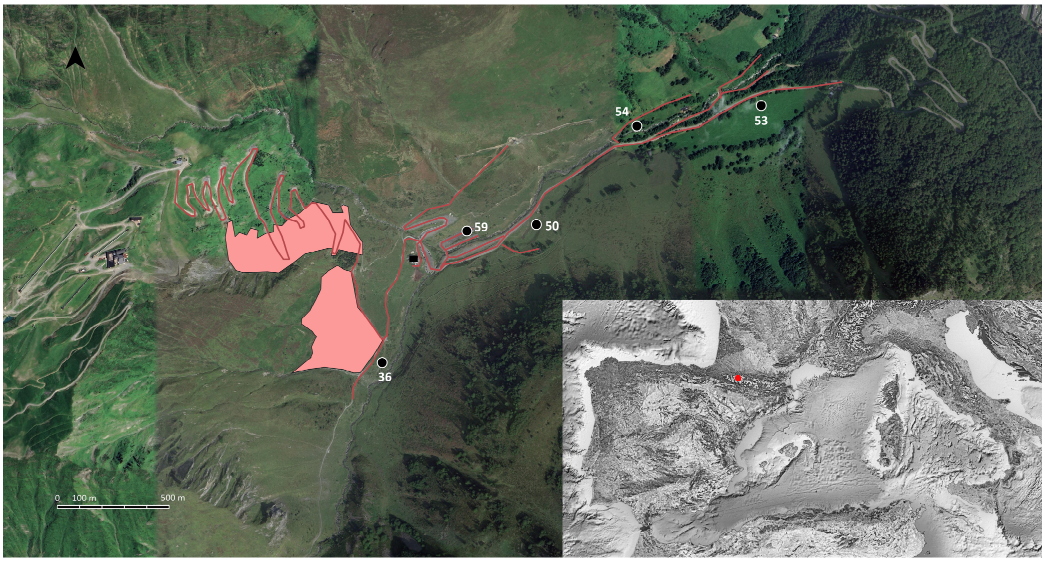

Figure 1. Sampling area of *Erebia pronoe glottis* in pink. Black circles mark the location of apiaries with the number of colonies given. The black square is the location of a cow shelter. For better orientation, roads and paths are given in red. The WGS-EPSG 3857 coordinate system was used.

2.2. Mark–Release–Recapture (MRR)

We conducted MRR for our analyses of the demographic structure and species-specific mobility patterns to identify specific adaptations to alpine habitats. The study was carried out from 20 July to 30 August 2019, covering most of the flight period of *E. pronoe glottis*. Butterflies were caught with a butterfly net (diameter: 40 cm) from 9 a.m. to 6 p.m. under suitable weather conditions [25]; to avoid daytime effects, sampling in the area was randomised, and we always started at a different point in the study plots. Each individual was marked on the underside of the hind wings with a fine, waterproof pen

(StabiloOHPen universal S) and provided with an individual code consisting of a letter for the day and a consecutive number. In addition, we recorded the following: GPS coordinates using the App Tourcount 3.1.1 on a Samsung S4 mini, sex, wing condition (scale 1 = wing seam completely preserved; up to 4 = wing heavily damaged [26]), behaviour when being captured, and current weather conditions [27]. In case of nectar uptake, plant species were noted. We collected the same data for each recapture, except recaptures on the same day to avoid capture-release trauma and theoretically allow for a complete intermixing of the whole population [28]. Potential sex-specific differences in behaviour and flower visits based on the species level were assessed by X^2 homogeneity tests. We analysed the influence of wind and cloud cover on the behaviour by applying X^2-tests.

2.3. Population Demography

Based on our MRR dataset, we conducted population modelling to calculate population size as a potential indicator of habitat quality and to study demographic structures for potential adaptations, like protandry and asynchronous emergence. The first five days of capture were not used for modelling as the low number of captures interfered with the modelling process. The program Mark 8.2 and its module Popan [29], based on the Jolly–Seber method, were used to estimate daily, sex-specific population size. Four parameters were estimated: ϕ (phi), the probability of survival; p, the probability of capture; pent, the proportional recruitment; and N, the size of the superpopulation. These parameters can be constant (.), sex-specific (g), time-factorial (t), linear (T), or quadratic (T^2) time-dependent and can have additive (g + t; g + T, . . .) or interactive relationships ($g \times t$; $g \times T$; . . .) [30]. Furthermore, sampling effort (i.e., the time spent in the field) was included as covariate for capture probability. A saturated model consisting of these parameters was verified by applying a goodness-of-fit test using the program RELEASE 3.0. Based on this, various parameter combinations were tested, and the best-supported model was selected using the corrected Akaike Information Criterion (AIC_C) [31].

2.4. Mobility Parameters

We analysed movement patterns in the habitat to infer the dispersal potential as well as resource use and availability. For the reconstruction of movement patterns, we used the collected GPS data of captures and recaptures. These were imported into QGIS 3.8.3 [32]. The direct geographic distance between capture and recapture was calculated for each individual by creating a linear distance matrix layer with the vector analysis tool in the WGS 84 (EPSG4326) Coordinate Reference System. We summed up the distances between all points of capture to assess the minimum total distance moved.

We performed a Shapiro–Wilk test to check for normal distribution of the movement distances by using the program R version 3.6.1 [33]. Since the datasets were not normally distributed (males p: 1.376×10^{-10}; females p: 0.023), we used the Mann–Whitney U test to determine differences in distances travelled by males and females and the two-sided Spearman's rank correlation to analyse the influence of days since first capture on the distances moved. In addition, an ANOVA was carried out using R to investigate whether the distances travelled differed between sexes over time. The travelled distances were divided into distance classes (20 m, 30 m, and 50 m intervals), separately for each sex. The inverse cumulative percentage of these classes was determined, which corresponds to the probability density function, i.e., the dispersal kernel [13]. To check for any potential artefacts caused by the chosen interval sizes, we analysed and compared three different interval size classes.

Based on these classes, the probabilities of dispersal flights were investigated through distance extrapolation. Two frequently applied regression analyses were used, the negative exponential function (NEF) and the inverse power function (IPF) [34–36]. NEF tends to underestimate rare long-distance movements, whereas IPF may encounter problems with "zero" movements [37]. The data were linearly transformed with a semi-ln plot for NEF analyses or with a double-ln plot for IPF analyses. In both equations, "P" stands for the proportional probability that an individual will travel at least as far as the distance D, and "a" stands for the intercept of the regression. NEF operates with the dispersal constant K as slope, whereas IPF uses the variable n as slope, which represents the effect of distance on dispersal [13].

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

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

We selected the best model and the most suitable interval size, based on stability indices R^2 of the calculated curves. This allowed extrapolations of the population's proportion that should travel distances exceeding the size of the study area. The calculations were performed separately for males and females.

3. Results

During 20 field days (20 July–30 August 2019), we marked 323 *E. pronoe glottis* individuals (261 males; 62 females); 120 of these were recaptured (106 males; 14 females) (see Supplementary Figures S1 and S2). This translates into a recapture rate of 37.2% (males: 40.6%; females: 22.6%). We achieved up to six recaptures for males; two females were recaptured twice.

3.1. Demography

The best-supported model with the lowest $\mathrm{AIC_C}$ value and the lowest number of parameters yielded a group effect on the survival probability phi, an interactive effect of sex and factorial time on the capture probability p, a constant proportional recruitment pent, and an effect of sex on the number of individuals (Tables 1 and 2 and Supplementary Figure S3). This model estimated a population size of 529 males (±38 SE, 95% CI 454–604) and 207 females (±41 SE, 95% CI 90–325); see Supplementary Figures S4–S9 for real parameter estimates. This corresponds to a theoretical density of 48 males/ha and 23 females/ha. The estimated sex ratio was 2.1 males per female. The modelled demographic structure showed no signs of protandry (see Supplementary Figure S10), but the higher ratio of males with deteriorated wing wear can indicate an earlier eclosing part of the male population (see Supplementary Figure S11).

Table 1. Comparison of the three best models of Popan 5.0 analyses for daily population size estimates of *Erebia pronoe glottis*: Akaike Information Criterion ($\mathrm{AIC_C}$) and number of parameters used; basic variables: probability of survival (Phi), probability of capture (p), proportional recruitment (pent), and size of the superpopulation (N).

Model-Nr.	Model	$\mathrm{AIC_C}$	Parameters
1	{Phi (g) p (g x t) pent (.) N (g)}	2161.8740	35
2	{Phi (g + T) p (t) pent (.) N (g)}	2163.9	36
3	{Phi (g + T^2) p (g x t) pent (.) N (g)}	2164.4757	37

Table 2. Median parameter estimates of the best supported model for both sexes of *Erebia pronoe glottis*.

	Phi	Min	Max	SE	p	Min	Max	SE
male	0.90 ± 0.02	0.87	0.92	0.03	0.16 ± 0.05	0.02	0.3	0.03
female	0.78 ± 0.07	0.73	0.81	0.07	0.06 (0.02, 0.18)	0	0.26	0.04

3.2. Mobility and Movement Patterns

Mobility was low in the studied *E. pronoe glottis* population. The average movement distance from capture to recapture was 101 m (± 73 SD; n = 175) in males. Females moved significantly less (68 m ± 80 SD; n = 16) (Mann–Whitney U test: W = 1950, $p = 0.009$). In the majority of cases, both sexes moved distances less than 150 m, but the percentage of males exceeding this distance (17.6%) was considerably higher than for females (6.3%) (Figure 2). The longest observed distances were 430 m for males and 340 m for females.

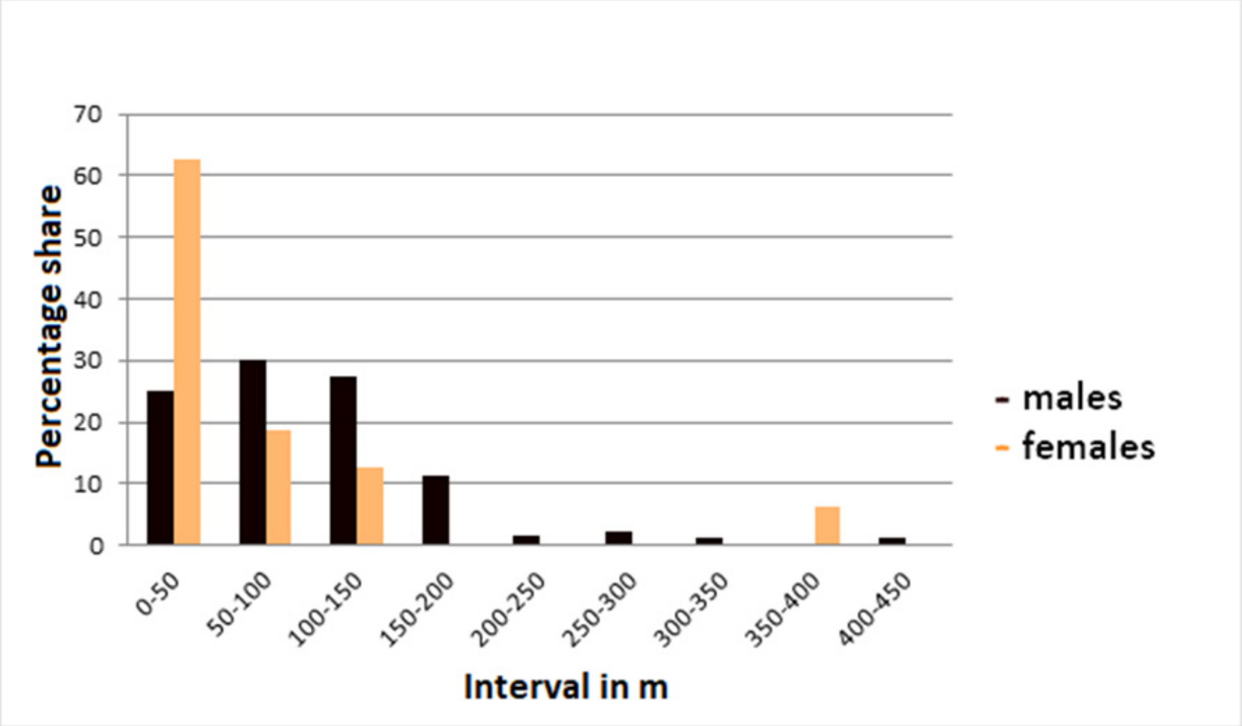

Figure 2. Dispersal of *Erebia pronoe glottis* differentiated by sex. The percentage of captured individuals observed dispersing in one of the 50 m distance classes is given.

We applied NEF and IPF functions for extrapolating the potential for long-distance dispersal. For both functions, the highest stability indices (R^2) were obtained for 50 m intervals (Table 3; see Supplementary Figures S12 and S13). The fit of NEF was better than that of IPF for both sexes. Following NEF, dispersal of 1 km or more would be largely impossible (males: 7.07×10^{-7}%; females: 3.66×10^{-6}%). However, the estimated values for IPF were also low (males: 0.25%; females: 0.40%), and the estimated proportions dispersing distances of more than 2, 3, or 5 km were still much lower (Table 4). A Spearman rank correlation revealed a positive correlation between flight distance and the number of days between capture and first recapture for females (rho = 0.570, $p = 0.033$) but not for males (rho = −0.040, $p = 0.68$).

Table 3. Stability index (R^2) of the inverse power function (IPF) and the negative exponential function (NEF) based on calculations with 20, 30, and 50 m intervals of the covered distances of *Erebia pronoe glottis*.

	20 m Intervals		**30 m Intervals**		**50 m Intervals**	
	IPF	**NEF**	**IPF**	**NEF**	**IPF**	**NEF**
males	0.85	0.98	0.87	0.98	0.90	0.98
females	0.88	0.91	0.89	0.88	0.95	0.99

Table 4. Percentage of *Erebia pronoe glottis* individuals expected to disperse more than 1, 2, 3, or 5 km calculated with the inverse power function (IPF) and the negative exponential function (NEF) based on 50 m intervals.

Distance	**IPF Males**	**IPF Females**	**NEF Males**	**NEF Females**
1 km	0.25	0.40	7.07×10^{-7}	3.66×10^{-6}
2 km	0.05	0.11	2.32×10^{-15}	5.46×10^{-14}
3 km	0.02	0.05	7.6×10^{-24}	8.15×10^{-22}
5 km	0.01	0.02	8.17×10^{-41}	1.82×10^{-37}

3.3. Behavioural Differences Between Sexes

We observed both sexes with almost equal frequency taking up resources (feeding refers to nectar uptake while drinking refers to water uptake) (Table 5, Figure 3). While males were considerably more engaged in flight activity, females were primarily encountered resting. In general, both sexes differed highly significantly in their behaviour (χ^2 = 129.6, df = 4, $p < 0.001$). With increasing cloud cover, male behaviour became more passive ($p = 0.021$), although this effect was only detectable for cloudiness of 60% or more; no significant effect was observed for females ($p = 0.267$). There was no significant effect of wind intensity on the behaviour of both sexes ($p > 0.1$).

Table 5. Percentage of individuals of *Erebia pronoe glottis* in five different behavioural categories distinguished by sex. Feeding refers to the uptake of nectar, while drinking refers to the uptake of water.

	Flying	**Resting**	**Feeding**	**Drinking**	**Egg Deposition**
males	75.4	13.3	5.3	5.8	0
females	20.5	59.0	12.8	0	7.7

3.4. Use of Nectar Plants

Asteraceae species were used as nectar sources in 40.6% of the cases, and we most frequently observed visits to *Carlina acaulis* L. (25.0%), *Carduus defloratus* L. (9.4%), *Leontodon hispidus* L. (3.1%), and *Cirsium eriophorum* L. (3.1%). In addition to Asteraeceae, the families Apiaceae with *Eryngium bourgatii* Gouan (34.4%) and Caprifoliaceae with *Scabiosa columbaria* L. (18.8%) were used frequently. Sex-specific differences in the preferences of nectar plants were not observed (χ^2 = 4.354, df = 7, $p = 0.74$).

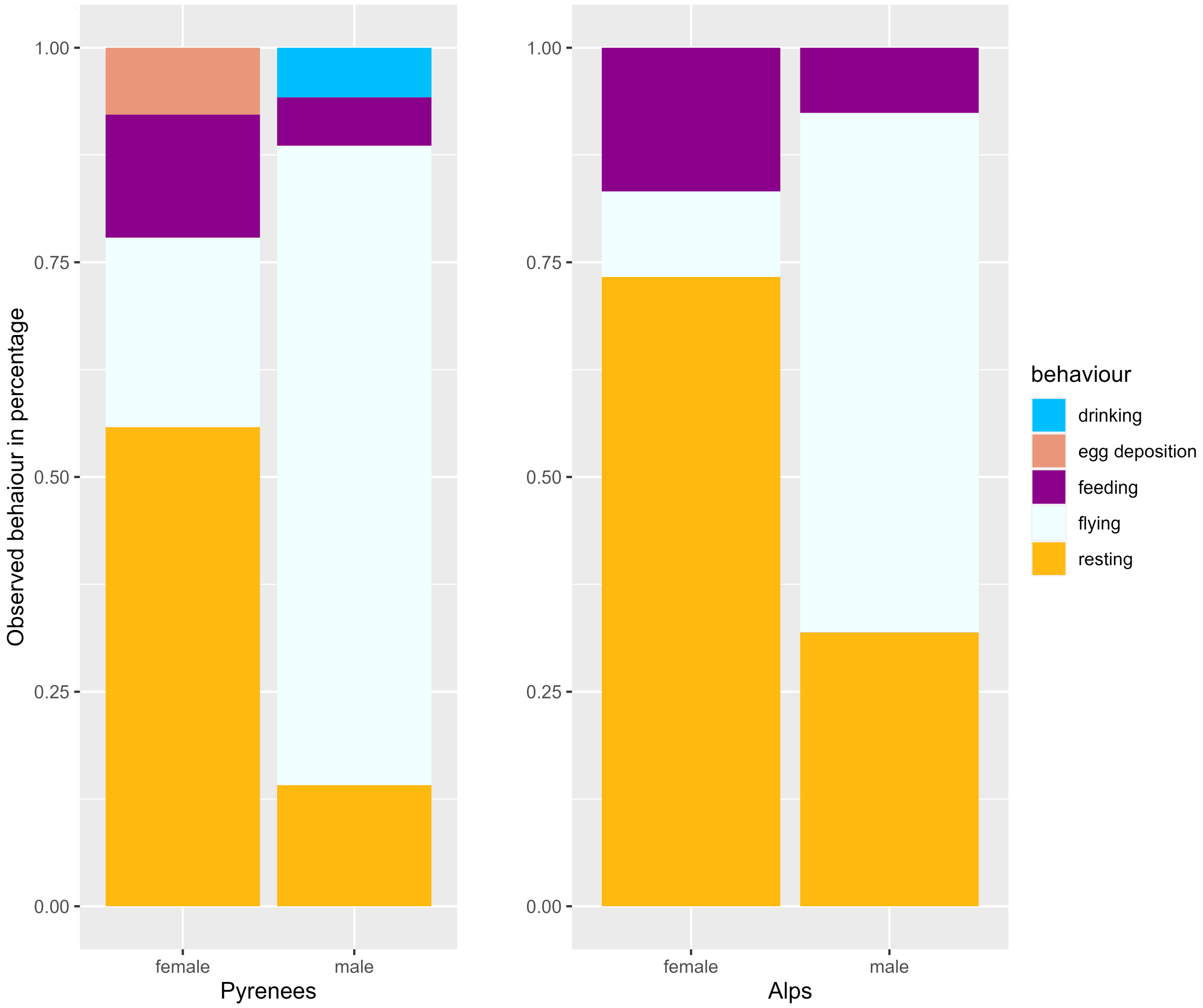

Figure 3. Behavioural comparison between populations of *Erebia pronoe glottis* in the Pyrenees and in the Alps. We distinguished five different behavioural categories, which were separated by sex and population. "Pyrenees" refers to the research area in Cauterets, and Alps refers to Hohe Tauern National Park, Salzburg, Austria [23].

4. Discussion

4.1. Population Density

With an estimated population size of about 800 individuals and a population density of about 70 individuals per hectare, the population studied in the central Pyrenees is only about 20% of the size and less than 10% of the density of the eastern Alps population studied by Wendt et al. [23]. The low number of captures early in the flight period made it difficult to model the actual demographic structure. The population peak appears to fall on the last days of the survey, which are always subject to greater uncertainty in the modelling. The absence of a pronounced peak in the graph of the estimated population size suggests a delayed flight period of *E. pronoe glottis* extended well into September 2019. Therefore, the actual population size is likely to exceed the modelled one.

Another possible shortcoming of this model is the calculated sex ratio. Such an unbalanced ratio would be rather unlikely considering the high level of infection with the Gram-negative bacteria *Wolbachia pipientis* (Hertig, 1936 (Ehrlichiaceae)) [20] and its influence on the demographic structure [37].The reported uneven sex ratio might be caused by differences in flight activity between sexes, affecting capture probabilities [13]. The patterns observed here also seem to suggest this, given that the higher flight activity in the Pyrenees is associated with a more balanced estimated sex ratio than in the Alpine population. Therefore, the population size of females is likely to have been underestimated in both cases.

Nevertheless, the observed population size and density are well below those of comparable studies. Comparing our results against other MRR studies in *Erebia* (i.e., *E. nivalis* > 1.200 individuals per hectare in the eastern Alps [13], *E. epiphron* > 400/ha, and *E. sudetica* > 1200/ha in the Sudeten Mts., northern Czech Republic [38] reveals a low population size and density of the here studied *E. pronoe glottis* population. Other common alpine and arctic–alpine butterfly species also had mostly higher densities in suitable habitats, such as *Boloria pales* (Denis & Schiffermüler, 1775) (Lepidoptera: Nymphalidae), *Boloria napaea* (Hoffmannsegg, 1804) (Lepidoptera: Nymphalidae) [39], etc. However, in a comparative study of *B. pales* on grazed and ungrazed habitats in the southeastern Carpathians, the density on the grazed sites (low habitat quality) was about 55 individuals per hectare and thus comparable with the density determined in our study, but it was about 250 at a flower-rich and thus more suitable ungrazed site [40].

Certainly, the abundance of a species is subject to many different influences and may fluctuate over the years. A large part of the differences between the various species can be explained by their respective characteristics. Nevertheless, demographic trends are most influenced by the rate of development. This, in turn, is determined by microclimate and nutrient availability during larval development [41]. Consequently, the low density of *E. pronoe glottis* in our Pyrenean population, compared with other *Erebia* species and alpine butterflies in general, most likely is the result of prevailing unfavourable conditions, which affect larval development or the overall fertility of the studied population.

4.2. Mobility and Movement Behaviour

The studied population had a very sedentary behaviour, and flight was only observed over rather short distances. However, no significant difference in flight distance was obtained if compared with the eastern Alpine population (Mann–Whitney U test: males, $W = 22284$, $p = 0.58$; females, $W = 91$, $p = 0.39$) [23]. This indicates a sufficient size of our study area and contradicts the widely accepted assumption that observed flight distances are positively correlated with the size of the study area [42]. Hence, the tendency of males to establish home ranges, as already observed in the Alps and now also in the Pyrenees (Figure 4), may lead to a spatial restriction to a sector of the study area and thus results in a limitation of the dispersal distances [43]. The lack of a correlation between flight distance and number of days between capture and first recapture underlines the sedentary character of our male *E. pronoe glottis*. The positive time-dependence of dispersal distances in females might be explained by successive movement away from the place of origin. This behaviour can increase egg-laying possibilities by the spatial distribution of eggs in low-resource habitats [36,44] and consequently the overall fecundity. In addition, avoidance of male harassment after successful mating may also lead to an increase in female mobility as a function of time [45]. Furthermore, sex-specific adaptation to low- or high-energy flight styles can result in a selective effect of a topographically structured habitat, as seen in *Phengaris* butterflies (Lycaenidae) [35]. The females of this genus avoid active, energy-consuming flight and prefer passive, low-energy gliding flight [35], leaving more energy for reproduction. This energetic aspect could be another explanation for the low flight activity and smaller mean flight distances of females compared to males observed in *E. pronoe glottis*, as females avoid active, energy-consuming vertical flight in this structured habitat.

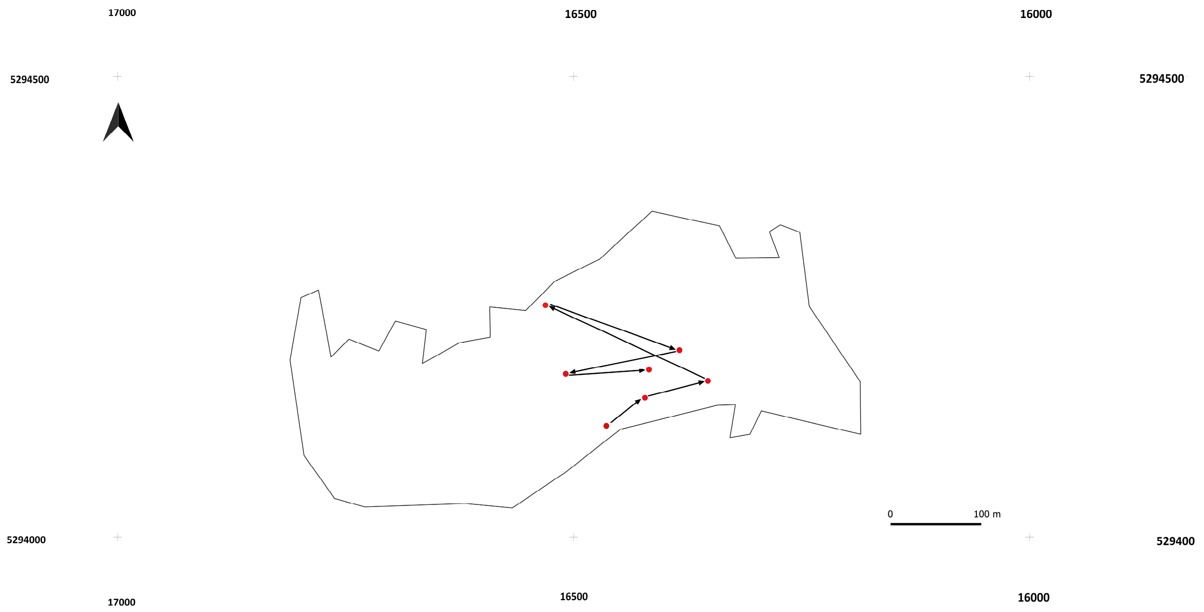

Figure 4. The movement pattern of a male *Erebia pronoe glottis* recaptured six times. Capture points are indicated by red dots and the movements between them by black arrows. The black outline indicates the boundaries of the survey area. The WGS 84-EPSG4326 coordinate system was used.

Males were significantly more flight active than females, as commonly observed for patrolling species [40]. Overall, the studied Pyrenean population engaged more in active flight than the eastern Alpine one (Figure 3). In the Pyrenees, we observed a behavioural change for both sexes compared to the Alpine population, with less time invested in feeding and more in flying. This trend has also been observed in other species on resource-poor sites [40,44], but without the frequently observed increase in average flight distance in our case. The higher flight activity of males on the one hand might be due to an increased effort in the search for nectar sources, but on the other hand, it is an indirect effect of the increased female flight activity because the activity of males changes with the appearance of females [46]. Thus, the increased flight activity of females might also increase the flight activity of males. Overall, the potential for the establishment of strong metapopulation structures is considered relatively low, given the philopatry and low flight distances of both sexes.

4.3. Environmental Stress on Alpine Species

Alpine species are increasingly suffering from the loss of high-quality habitats. This loss is mainly driven by changes in the formerly extensive use of alpine landscapes [47–50]. Habitat quality is a significant factor influencing behaviour [40,44] and population size [51] of butterflies. The high flight activity of both sexes of the here analysed *E. pronoe glottis* population in combination with its low population size indicates a population suffering from environmental stress. This environmental stress is most likely caused by low habitat quality, resulting from a more intensive use of our study area.

Thistle-like flowers (species from the genera *Cirsium*, *Carduus*, and *Eryngium*) represented the most important nectar sources of our Pyrenean *E. pronoe glottis* population. This might be due to the low grazing pressure on thistles [52,53], allowing that, in contrast to most other non-thorny flowering plants, many of them continuously flowered in our study area, characterised by high grazing intensity by cow and sheep herds. However, even without high grazing pressure, thistles can be the prevalent nectar resource supporting large and stable *E. pronoe* populations as in the Alps. Grazing reduces the amount of flowering resources [54] and, depending on the grazing animal, can also contribute to a change in plant community structures through selective browsing and nitrogen input [55], which can affect the availability of larval host plants. In addition to the general decline in flowering plants, further negative effects on population density can arise from trampling damage and browsing of larval host plants [47,50]. Conversely, grazing can prevent scrub encroachment and the succession of open grasslands. This is particularly important below the tree line, as it can help preserve habitats for grassland species [50].

The intensive use of our study area by beekeepers poses another threat through the depletion of nectar supply, causing further reduction of habitat quality. Honey bees (*Apis mellifera* Linné, 1758 (Hymenoptera: Apidae)) are superior nectar foragers, which fly earlier in the day, exploit resources selectively, and also take up nectar faster than butterflies [56–58], resulting in strong competition [59]. Honey bees have a large range of action and exert enormous competitive pressure on the respective local insect fauna, especially near their colonies [59]. Each of the five recorded apiaries was located within a distance of less than 2 km from our study site, which is well within the average foraging distance of honey bees. Consequently, distances less than 2 km are considered high influence areas [59,60]. As a result, minimum distance thresholds were not kept, and upper density limits of apiaries were exceeded in our study area, a situation for which massive impacts on the wild insect fauna have been documented [60]. Thus, the exploitative competition exerted by honey bees could have caused increased effort on nectar foraging, increased mobility, and lower population sizes of the native pollinator fauna [59]. Furthermore, the buzzing of honey bees triggers defensive behaviour to protect against predators in caterpillars. This protective behaviour is leading to a massive decrease in the feeding rate and thus also reduces the reproductive success of a population [61]. Therefore, the high flight activity and low population size of *E. pronoe glottis* in Cauterets might also be a consequence of honey bee-induced or intensified resource scarcity.

4.4. Conservation Implications

Late-flying pollinators compete seasonally for the decreasing amount of available nectar [62]. In our study area, this scarce resource is further reduced by high grazing pressure. The remaining nectar plants are then exploited by a superior competitor, to the point that only a comparatively small population of *E. pronoe* with low population density can survive in a supposedly natural landscape and in proximity to the Pyrenees National Park.

Such small populations are at risk of being trapped in a negative feedback loop, in which low population density makes mate finding more difficult and thus favours emigration [35,63], which further weakens the population. In the future, this effect could be enhanced by an asynchronous development of both sexes. Alpine species rely on compact snow covers not only for overwintering larvae and pupae [64,65] but also for terminating diapause [11]. Shorter winters and an earlier onset of snowmelt can result in prolonged flight duration with less distinct population peaks in a protandric, univoltine population, as shown for *E. epiphron* [11]. This desynchronised adult emergence can decrease the likelihood of successfully locating a mate.

The population studied here, apparently weakened by various stressors, must be strengthened to warrant its stability. The low dispersal capacity might impede the formation of a metapopulation structure, making recolonisation less likely in the case of a population collapse. Therefore, the population must be supported by improving habitat quality. This can be achieved by reducing grazing pressure, which would increase resource diversity and reduce impacts such as browsing and trampling damage. In addition, indirect exclusion of competition from honey bees needs to be mitigated, especially in late summer, a phase with generally lower nectar availability. This should be accomplished by maintaining minimum distances and density ceilings [60]. These measures would be beneficial for the here studied population of *E. pronoe glottis* but also for nectar-dependent insects living in alpine rupiculous grasslands.

Supplementary Materials: The online version contains supporting information available at downloaded : https://www.mdpi.com/article/10.3390/d17080554/s1.

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