Variable hostplants of mountain populations of *Phengaris alcon* (Lepidoptera: Lycaenidae): flexibility in different habitats and possible adaptations to climate change

Moritz Kahnert, Melanie Brandmeier and Gregor Markl

Moritz Kahnert and Gregor Markl, Fachbereich Geowissenschaften, Universität Tübingen, Schnarrenbergstrasse 94–96, D-72076 Tübingen, Germany, corresponding author: markl@uni-tuebingen.de

Melanie Brandmeier, Technical University of Applied Sciences Würzburg-Schweinfurt, Röntgenring 8, D-97070 Würzburg, Germany

Abstract: Myrmecophilous *Phengaris alcon* is a well-studied example of intraspecific variation, colonizing wet and dry, lowland to high-Alpine meadows. In different habitats, different ant species and different larval foodplants of the family Gentianaceae are used. Two montane populations (around 1000 m a.s.l.) in Styria (Austria) live on three different foodplants: *Gentiana asclepiadea, G. cruciata* and *Gentianella germanica* agg. Gentian plants were mapped and eggs were counted several times on selected Gentian shoots. Oviposition occurred on all three plant species, but *G. cruciata* was by far preferred (4.5 times more occupied shoots, 6 times more eggs per shoot than on *G. asclepiadae,* similar for *Gl. germanica* agg.), although plants of *G. asclepiadea* grew over a larger area and were more abundant. No eggs were found outside the habitats with *G. cruciata*. During the flight period, the buds of *G. cruciata* were in suitable stage for oviposition. *G. asclepiadea* and *Gl. germanica* agg. had a later phenology and only prominent shoots with mature buds were used for oviposition, increasingly towards the end of the flight period. This testifies to the importance of bud phenology on oviposition choice. The montane populations could represent important, intermediate stepping stones between lowland and high-Alpine populations, helping the species to adapt to new larval foodplants. This flexibility allows the populations to become more resilient against climate change, when synchronization with the "normal" foodplant gets out of phase, as using different foodplants with different phenologies eases adaptation to the changing environmental conditions.

Keywords: *Phengaris alcon, Phengaris rebeli,* larval hostplants, variability, oviposition, adaptation, climate change, *Gentiana cruciata, Gentiana asclepiadea, Gentianella germanica* agg.

Variable Futterpflanzen bei bergbewohnenden Populationen von *Phengaris alcon* (Lepidoptera: Lycaenidae): Flexibilität in verschiedenen Habitaten und mögliche Präadaptation an Klimawandel

Zusammenfassung: Die myrmekophile Bläulingsart *Phengaris alcon* ist ein gut untersuchtes Beispiel für intraspezifische Variation; sie besiedelt feuchte und trockene Habitate vom Flachland bis hin zu hochalpinen Wiesen. In verschiedenen Habitaten werden unterschiedliche Ameisenarten und unterschiedliche Futterpflanzen der Familie Gentianaceae benutzt. Zwei montane Populationen (um 1000 m ü. NN) in der Steiermark (Österreich) leben dort hauptsächlich an drei verschiedenen Futterpflanzen: *Gentiana asclepiadea*, *G. cruciata* and *Gentianella germanica* agg. Die Enzianpflanzen in den Biotopen wurden kartiert und die abgelegten Eier mehrfach auf festgelegten Pflanzentrieben gezählt. Die Eiablage erfolgte an allen drei Pflanzenarten, aber *G. cruciata* wurde stark bevorzugt (4,5mal häufiger benutzte Triebe, 6mal mehr Eier pro Pflanze als bei *G. asclepiadae,* ähnlich bei *Gl. germanica* agg.), obwohl die Pflanzen von *G. asclepiadea* auf größerer Fläche vorkamen und häufiger waren. Keine Eier fanden sich auf Flächen außerhalb des Bereichs, wo auch *G. cruciata* vorkam. Zur Flugzeit der Falter waren die Blütenknospen von *G. cruciata* gerade im richtigen Reifezustand für die Eiablage. *G. asclepiadea* und *Gl. germanica* agg. hatten etwas spätere Blühphänologie, und nur große Pflanzen mit blühreifen Knospen wurden besonders gegen Ende der Flugzeit genutzt. Dies bestätigt die Wichtigkeit der Blühphänologie für die Auswahl der Eiablagestellen. Solche montanen Populationen der Falter können in der Evolution wichtige Trittsteine zwischen hochalpinen und Tieflandpopulationen darstellen, die den Bläulingen die Anpassung an neue Raupenfutterpflanzen erleichtert. Diese Flexibilität erlaubt den Populationen, gegenüber Klimaveränderungen reagieren zu können, wenn die „normalen" Futterpflanzen asynchron zu den Faltern werden.

Introduction

Because of its interesting parasitic larval development in ant nests and its importance for nature conservation, the genus *Phengaris* (Doherty, 1890) has attracted considerable interest over the past decades both by scientists (Nash et al. 2008, Ugelvig et al. 2011, Boe et al. 2022), and by nature conservation authorities, as they are considered to be "flagships of insect conservation in Europe" (Thomas 1995, Thomas & Settele 2004, Nowicki et al. 2019) and are regarded as indicator species for the biotope quality and the occurrence of other threatened species due their complex life cycle and specific needs (Maes & van Dyck 2005, Settele et al. 2005).

In Europe, four *Phengaris* species occur in mostly different, rarely overlapping habitats (Tartally et al. 2019): *Phengaris arion* (Linnaeus, 1758), *P. alcon* ([Denis & Schiffermüller], 1775), *P. nausithous* (Bergsträsser, 1779) and *P. teleius* (Bergsträsser, 1779). The populations of all four European *Phengaris* species are declining in many countries (van Swaay et al. 2011). Conservation efforts to preserve the species are necessary and effective, as shown by extinction events and successful reintroductions in individual cases (Thomas 1980, Wynhoff 1998, Thomas et al. 2009).

Populations of *Phengaris* are often small and part of a metapopulation (Maes et al. 2004, WallisDeVries 2004, Radchuk et al. 2012, Nowicki et al. 2019). Their habitats are located in extensively cultivated and open landscapes. Habitat loss and degradation due to intensification, abandonment or change of use and the fragmentation of the landscape pose major threats to the survival of the species (WallisDeVries 2004, van Swaay et al. 2010). On a European level, *P. arion* is considered as 'Endan-

gered', *P. teleius* as 'Vulnerable', the other two species as 'Near threatened' (*P. nausithous*) and 'Least Concern' (*P. alcon*). However, *P. alcon* is considered 'Near Threatened' for the EU-27 (van Swaay et al. 2010). *P. arion*, *P. teleius*, *P. nausithous* are included in Annex IV of the Habitats Directive (92/43/ EEC) and are thus "species of Community interests requiring strict protection" (Council of the European Union 1992).

Taxonomic background

The various taxa of the genus *Phengaris* are genetically complex (Pech et al. 2004, Fric et al. 2007, Bereczki et al. 2014). While genetic diversity within a population is rather low, genetic differences between populations of the same species can be large (Pecsenye et al. 2007). Genetic studies have shown intraspecific substructuring, the existence of subspecies or possibly cryptic species in several species (Als et al. 2004, Fric et al. 2007, Ugelvig et al. 2011), and this has been particularly discussed with regards to the species *P. alcon* (Sielezniew et al. 2012, Czekes et al. 2014, Tartally et al. 2016, Bereczki et al. 2018).

Populations of *P. alcon* occupy different habitats. They can be found in damp meadows, where larvae live prior to ant adoption on *Gentiana pneumonanthe* L., in rather dry, calcareous, nutrient-poor meadows, where the larvae use *Gentiana cruciata* L. as their main foodplant (Sielezniew et al. 2012, Czekes et al. 2014, Settele et al. 2015, Bereczki et al. 2018) and in mountain meadows in Styria and adjacent Salzburg (Austria), where they use *Gentianella germanica* subsp. *rhaetica* as their foodplant, recently described by Tartally et al. (2014). Further gentian species are known to be used by some populations, the most important being *G. asclepiadea* in Southern France (Bence & Richaud 2020) and other areas of the southern Alps and northern pre-Alpine foothills (Bräu et al. 2006, Bolt et al. 2010, Carleial et al. 2018).

All forms parasite different ant species of the genus *Myrmica* (Latreille, 1804) (Hymenoptera: Formicidae). The hygrophilous type adapted to humid habitats, hereafter **"*P. alcon* H",** uses *Myrmica scabrinodis* (Nylander, 1846), *Myrmica ruginodis* (Nylander, 1864) and *Myrmica rubra* (Linné, 1758) in most locations. The xerophilous type adapted to dry habitats, hereafter **"*P. alcon* X",** generally has a greater variety of host ants. Populations of this form are often found as parasites of *Myrmica schencki* (Viereck, 1903) or *Myrmica sabuleti* (Meinert, 1861), and sometimes also of *Myrmica scabrinodis* (Nylander, 1846) (Tartally et al. 2019). The mountain form, finally, appears to use exclusively *Myrmica sulcinodis* (Tartally et al. 2014, Tartally et al. 2019).

Until quite recently, the form in humid habitats and the one colonizing dry habitats were considered to be different species, *P. alcon* and *P. rebeli* (Elmes & Thomas 1987, Thomas 1995, Settele et al. 2015), but the use of the species name '*rebeli*' for *P. alcon* X turned out to be incorrect (Habeler 2008, Kudrna & Fric 2013): according to the original description by Hirschke (1905), *P. rebeli* refers to an Alpine form of *P. alcon*, which occurs in habitats of the Eastern Alps between 1500 and 2100 m, where *G. cruciata* as a foodplant is lacking and which differ greatly from the typical habitats of *P. alcon* X (Habeler 2008). This high mountain form of *P. alcon* was long lost and described again from the Styrian Alps in 2014 (Tartally et al. 2014).

The parasitisation of a specific host ant species *Myrmica sulcinodis* (Nylander, 1846) and genetic studies show that the Alpine form of *P. alcon* is a separate form that can be distinguished from *P. alcon* X and *P. alcon* H (Tartally et al. 2014, Bereczki et al. 2018). This high-altitude form, hereafter *P. alcon* '*rebeli*', has also been described from the Swiss Alps (Jutzeler 1988, 1989, Tartally et al. 2019).

Hence, there existed some taxonomic confusion related to this species. In a genetic analysis of the genus *Phengaris*, however, Als et al. (2004) showed that all studied populations of *P. alcon* X and *P. alcon* H can be assigned to a common genetic clade and all adaptions to different habitats, ant hosts and foodplants have occurred within the last one million years, starting from a common ancestor. These results also showed that the 'hygrophilous' form from humid habitats is the 'original form'. From this original form, xerophilic populations adapted to dry habitats have developed several times independently of each other (Fric et al. 2007, Kudrna & Fric 2013, Tartally et al. 2016). Hence, various populations of *P. alcon* X cannot be assigned to a monophyletic group (Sielezniew et al. 2012, Bereczki et al. 2018). Moreover, geographically close populations of different ecotypes are more closely related to each other than geographically distant populations of the same ecotype (Bereczki et al. 2005, Tartally et al. 2016, Koubínová et al. 2017, Bereczki et al. 2018).

Unfortunately, there are no genetic studies on the origin of *P. alcon* '*rebeli*'. However, the difficult gene exchange due to the Alpine topography suggests that populations of the '*rebeli*' form have arisen several times independently of each other through the adaption of local lowland populations to the Alpine conditions, comparable to the emergence of xerophilous populations as described by Bereczki et al. (2018).

For different ecotypes to develop within a species, the exchange of genes between two populations has to become more difficult due to the adaption to different ecological niches (Rundle & Nosil 2005). This 'ecological speciation' can, for example, be started by using different larval hostplants ('host-associated genetic differentiation (HAD)', Drès & Mallet (2002), Hinojosa et al. 2023, Tilmon 2008). If Lepidoptera populations of the same species adapt to different foodplants, isolation could, for example, occur due to different phenologies of the foodplants and, associated with this, different flight periods of the imagines (Hinojosa et al. 2023). Differentiation due to the utilisation of different larval foodplants is also known for another *Phengaris* species, namely *P. arion*,

which has two phenotypes using either early-flowering or late-flowering Lamiaceae for oviposition (Bereczki et al. 2014, 2022).

Some studies indicate that specialisation due to the use of different larval foodplants could also occur in *P. alcon*. The flight periods of syntopic populations of *P. alcon* X and *P. alcon* H near Cluj-Napoca in Romania (Timuş et al. 2013, Czekes et al. 2014, Tartally et al. 2016) are shifted about one month, which makes mating between them much more difficult (Timuş et al. 2013). The hatching of the imagines is adapted to the phenology of the gentian species used in each case (*G. pneumonanthe* and *G. cruciata,* occurring only about 100 m apart from each other, Czekes et al. 2014).

The complex lifecycles of the myrmecophilic genus *Phengaris*

The European species of *Phengaris* have a highly complex life cycle. During the first three larval instars, the larvae feed on the young seeds of their hostplants (Thomas et al. 1989). With the moult to the fourth larval instar (L_4) they change from phytophagous to an obligate myrmecophilous lifestyle. The larvae, which at this point only have 1–2% of their final body weight (Thomas & Wardlaw 1992, Thomas et al. 1998), drop from the feeding plants to the ground. With the help of chemical and acoustic signals, they deceive workers of the genus *Myrmica* (Hymenoptera: Formicidae) so that they believe to recognise them as part of their ant brood and carry them into the ant nest (Akino et al. 1999, Sala et al. 2014), where the larvae live parasitically.

The larvae of *P. arion* and *P. teleius* are exclusively predatory, feeding on ant brood, while *P. nausithous* and *P. alcon* are "cuckoo pararsites", fed by the ants and only partly feed on their brood (Als et al. 2004, Thomas & Settele 2004). The larvae of *P. alcon* are fed by the workers through trophallaxis (Elmes et al. 1991a, 1991b, Thomas & Elmes 1998). Compared to the predatory species, the adaption to ants is more extensive in "cuckoo parasitic" species. This form of parasitism requires a higher degree of integration into the ant nest and is associated with a closer coevolutionary adaption to specific ant species (Sala et al. 2014). In contrast to predatory species, they are more dependent on individual ant species at a particular site (Thomas & Settele 2004) and they also parasite the same ant species at different, faraway sites (Tartally et al. 2019).

Although the 'cuckoo' strategy requires greater adoption, it is also much more efficient than the predatory lifestyle, as four to five times as many butterflies can develop per ant nest. Which *Myrmica* species is used depends not only on evolutionary adaption, but also on which species is present in the specfic habitat (Pech et al. 2007). Populations of *Phengaris* are specialised on individual *Myrmica* species occurring at their location (Witek et al. 2008) and they use them more or less exclusively (Tartally et al. 2019).

Different growth rates were observed for the larvae in the ants' nest. Some of the larvae pupate the following summer and emerge after 11 months, while another part of the larvae grows more slowly and requires a further year with a total of two overwintering periods for their development (Thomas et al. 1998, Schönrogge et al. 2000). The females copulate within hours after emergence and lay eggs just one hour later (van Dyck & Regniers 2010). As larval foodplants, *P. arion* uses Lamiaceae, *P. nausithous* and *P. teleius* Rosaceae and *P. alcon* *Gentiana*ceae (Elmes & Thomas 1987, Ugelvig et al. 2011).

Oviposition on different *Gentiana*ceae

P. alcon uses various Gentianaceae for oviposition. *G. cruciata,* a typical plant of calcareous grasslands, is the most common foodplant of the larvae of *P. alcon* X (Elmes et al. 1996, Thomas & Elmes 2001, Arnyas et al. 2006, Kőrösi et al. 2008, Sielezniew et al. 2012, Czekes et al. 2014, Tartally et al. 2014, Settele et al. 2015, Osváth-Ferencz et al. 2016, Tartally et al. 2016, Vilbas et al. 2016).

G. pneumonanthe, which occurs in wet meadows, is the typical foodplant of the larvae of *P. alcon* H (Maes et al. 2004, WallisDeVries 2004, Küer & Fartmann 2005, Nowicki et al. 2005, Bräu et al. 2006, Sielezniew et al. 2012, Arnaldo et al. 2014, Tessier 2015, Nowicki et al. 2019, Dziekańska et al. 2020, Boe et al. 2022). In and around the Alps, also *Gentiana asclepiadea* L. is used as foodplant. This also grows on pre-Alpine wet meadows and in sub-Alpine mixed mountain forests (Oberdorfer 2001). Some populations of *P. alcon* H use, in addition to their main foodplant *G. pneumonanthe,* also *G. asclepiadea* (Krismann 2000, Bräu et al. 2006, Bolt et al. 2010). Interestingly, populations using *G. asclepiadea* as their only hostplant comprise *P. alcon* H populations (Lake Mindelsee and Upper Swabia, SW Germany: Marktanner 1985, Carleial et al. 2018) and *P. alcon* X from Bulgaria (Kolev 2002).

However, Bräu et al. (2006) found *G. asclepiadea* to be less suitable as foodplant than *G. pneumonanthe,* because of their less voluminous buds and ovulas. In addition, Bräu et al. (2006) suggested, that it is difficult for the larvae to penetrate the relatively tough buds. In sympatry with *G. pneumonanthe,* a bud of *G. asclepiadea* was occupied with fewer eggs and a smaller proportion of the larvae managed to successfully complete development in the bud (Bräu et al. 2006). Nevertheless, according to Bräu et al. (2006), *G. asclepiadea* is a foodplant of considerable importance for *P. alcon,* especially in the Bavarian and Austrian pre-Alpine and in the Southern Alpine region (Gros 2002, Bence & Richaud 2020).

Also plants of the genus *Gentianella* are used for oviposition: This has been described for *P. alcon* H (Bräu et al. 2006, Bolt et al. 2010, Sielezniew et al. 2012, Tessier 2015) and *P. alcon* X (Fartmann 2004). Bräu et al. (2006) reported successfully completed larval development on *Gl. germanica* agg. (Bräu et al. 2006). In addition, *Gentianella rhaetica* (subspecies of *Gl. germanica* agg.) has been documented as larval foodplant for *P. alcon* '*rebeli*'

in the limestone alps of Styria (Tartally et al. 2014). Lastly, Bereczki et al. (2005) report on a population of *P. alcon* X in Slovenia with oviposition on *Gentiana lutea* L. (Bereczki et al. 2005).

The oviposition behaviour of *P. alcon*

The females freshly hatched from the ant nests are immediately ready to mate and one hour after copulation, the females begin to lay eggs (van Dyck & Regniers 2010). The females search for suitable shoots of foodplant in flight and usually lay several eggs on one plant (Kőrösi et al. 2008, van Dyck & Regniers 2010). Eggs are mostly laid on the closed flower buds or in their immediate vicinity (Czekes et al. 2014).

In order to protect the clearly visible exposed eggs from predation, they are relatively thick-walled with exception of their base. After about seven days, the caterpillars hatch through the thin underside of their egg (Thomas et al. 1991, Bos et al. 2006, Wynhoff et al. 2015). They live for three larval stages in the flower buds of this plant, before they drop to the ground and get adopted by ants of the genus *Myrmica* (Elmes et al. 1991b, Akino et al. 1999, Thomas & Settele 2004).

Some studies reported a clumped or uneven distribution of *P. alcon* eggs across the entirety of the foodplant shoots present (Vilbas et al. 2016, Nowicki et al. 2019). A few plants with a large number of eggs contrast with many plants with no or very few eggs in the same habitat (Vilbas et al. 2016). Clearly pronounced distribution patterns indicate that there are clear preferences among females for shoots with certain characteristics. The criteria by which females select a shoot for oviposition and the mechanisms involved are much-studied questions (Czekes et al. 2014, Thomas & Elmes 2001, van Dyck & Regniers 2010).

To complete the preimaginal development, the larvae are not only dependent on plants, but also on ants of certain *Myrmica* species. Therefore, it is expected that ovipositing females take into account not only characteristics of the foodplant, but also indications of the presence of host ants. While some studies found a positive correlation between oviposition and the presence of host ants (van Dyck & Regniers 2010, Wynhoff et al. 2015, Carleial et al. 2018), others did not (Thomas & Elmes 2001, Nowicki et al. 2005, Fürst & Nash 2010). On the other hand, many studies have shown a correlation between plant characteristics and oviposition.

The following characteristics of the foodplants appear to have a positive effect:

- The number of flower buds per gentian branch (Dolek et al. 1998, Küer & Fartmann 2005, Nowicki et al. 2005, van Dyck & Regniers 2010, Arnaldo et al. 2014, Wynhoff et al. 2015, Carleial et al. 2018).
- The size of the plant for the length of its shoots (Dolek et al. 1998, Nowicki et al. 2005, Wynhoff et al. 2015, Osváth-Ferencz et al. 2016).
- The prominence of their shoots, in example the height difference to the surrounding vegetation (Küer & Fartmann 2005, Nowicki et al. 2005, Arnyas et al. 2006, Vilbas et al. 2016).
- The size/length of the buds (Fürst & Nash 2010, Wynhoff et al. 2015).

In addition to these plant characteristics, a crucial criterion for the choice of a foodplant is the degree of maturity of its buds, because the young larvae need to feed on the still soft ovaries (Bräu et al. 2006). Laying eggs on buds with too few or too developed ovaries would therefore reduce the larvae's chances of survival (Arnaldo et al. 2014).

Patricelli at al. (2011) and Thomas & Elmes (2001) showed that all four European species of *Phengaris* are dependent on buds at a certain phenological stage for oviposition. According to Thomas & Elmes (2001), *P. alcon* H and *P. alcon* X both favour the earliest of the investigated stages "tight young buds with sepals apparent" (Thomas & Elmes 2001) which agrees with results of Arnaldo et al. (2014) and Bräu et al. (2006). Even late-flying females, which have all bud stages available, preferred to lay their eggs on the green buds. As only few buds of the suitable stage are available, "clumped oviposition" can be observed at the beginning of the flight period, while a greater dispersion takes place, as the flight period progresses (Bräu et al. 2006). According to Thomas & Elmes (2001), individual plant parts are in a suitable stage for oviposition for only two to five days, a complete plant for 5 to 15 days. Hence, during the imagines flight period of 30 to 40 days, there is necessarily a change in oviposition from rather early to rather late flowering plants (Thomas & Elmes 2001).

The current study

Only the xerophilous form of *P. alcon* is known in Styria. The eggs are mainly laid on *Gentiana cruciata* (Habeler 2008, Tartally et al. 2014), but two more possible foodplants occur in the investigated habitats: *G. asclepiadea* and *Gentianella germanica* agg. *Gentiana cruciata* forms buds and flowers earlier than *G. asclepiadea* and *Gl. germanica* agg., but these times overlap (which they do typically not in lowland habitats such as in the pre-Alpine foothills of Bavaria). In this study, two Styrian populations were analysed using the capture-mark-recapture method (CMR or mark-release-recapture, MRR, Cini et al. 2020, Maes et al. 2004, Neve et al. 1996). Extensive fieldwork was conducted to evaluate whether females use all three gentian species for oviposition and if so, which species is preferred, and if this changes with time. The chosen habitats are ideal for this kind of investigation, because they comprise *G. cruciata* and *G. asclepiadea* in good numbers and in close proximity, because these species show overlapping budding and flowering times, and because they can be easily reached for fieldwork.

Materials and methods

Study locations

Fieldwork was conducted at two study sites in the mountainous region Grazer Bergland north of the city of Graz, Styria, Austria, in June and July 2023.

Locality Wolfsattel

The first area of initerest was on the mountain Wolfsattel next to the village Gschaid bei Weiz. The mean annual temperature is 6.0°C, the mean annual amount of precipitation is 1251 mm, the rock in the study area is Schöckelkalk, a Palaeozoic limestone (GIS-Steiermark 2023). The top of the Wolfsattel is a pasture extensively grazed by cattle. It is a rather nutrient-rich, fresh grassland and part of the Natura 2000 nature protection area "Weizklamm mit Wolfsattel". The pasture is bordered on all sides by spruce forests. The habitat investigated in detail is a cow pasture of about 4.8 ha in the far east of the mountain ridge between 1020 and 1070 m above sea level (N 47.266°, E 15.571°).

In contrast to the rest of the mountain top, this is a lean pasture (Fig. 1), dominated by *Festuca rupicola* and *Festuca rubra agg.*, *Avenula pubescens*, *Agrostis capillaris*, *Briza media*, *Phleum* sp. are frequently mixed in (grünes handwerk Kammerer & Ressel OG 2022). The proportion of herbs is very high, comprising *Achillea millefolium agg.*, *Centaurea jacea, Thymus pulegioides, Anthyllis vulneraria, Taraxacum* sect. *Ruderalia* as well as occasionally *Carlina acaulis* or *Hypericum perforatum* (grünes handwerk Kammerer & Ressel OG 2022). The mapped plants indicate lean, fresh, slightly alkaline to slightly acidic conditions, according to Ellenberg et al. (2001).

Locality Pleschkogel

The Pleschkogel is a mountain near the town Gratwein-Straßengel. The mean annual temperature is 6.7°C, the mean annual amount of precipitation is 1361 mm, the rocks are predominantly Palaeozoic dolomitic and occasionally also dark, fossil-rich limestones (Schönlaub 1979, GIS-Steiermark 2023). The slopes of the Pleschkogel are steep and for the most part covered by spruce monocultures, partially thinned out by extensive clearcutting. On the mountain ridge, there are a few meadows and pastures. They are part of the nature reserve NSG-c 03 Pleschkogel, Walzkogel, Mühlbachgraben (GIS-Steiermark 2023).

The investigated habitat (N 47.135°, E 15.223°) of 1.1 ha size is, however, outside this nature reserve in an approximately 20 m wide, steeply sloping aisle through the spruce forest, underneath a power line, with a hiking trail along and extends over a length of 300 m between 910 and 960 m a.s.l. (Fig. 2). It is overgrown with young spruce trees and bushes of *Rosa* spec., *Viburnum lantana, Rubus idaeus* and *Rubus* sect. *Rubus* and grass and herbs in between. Both typical meadow species (*Galium mollugo* agg.) and forest species (*Clematis vitalba*) grow here. The indicator plants according to Ellenberg et al. (2001) indicate fresh to slightly dry, moderately nitrogen rich and slightly alkaline to slightly acidic conditions (*Buphthalmum salicifolium, Euphorbia amygdaloides, Epipactis helleborine* agg.).

Field methods

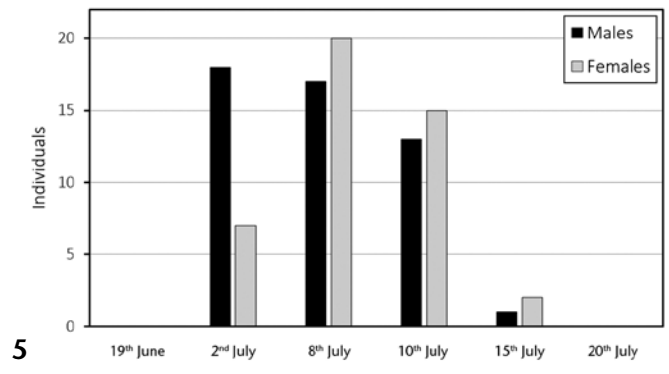
Habitat characterization

The habitats were inspected for the first time at the beginning of June 2023, and the locations of *G. cruciata* and *G. asclepiadea* were localised in GIS. At the end of July 2023, a representative area of around 10 × 10 m was selected in both habitats and a list of all plant species observed in this area was compiled. The "Flora incognita" smartphone app was used for plant identification and later checked using various textbooks for confirmation (e.g., Jäger 2017). A list of important plant species is given (Table 1).

Table 1: List of plant species in the habitat at study sites.

Study site Wolfsattel	
Achillea millefolium agg.	*Leucanthemum vulgare* agg.
Ajuga reptans	*Lotus corniculatus* agg.
Anthyllis vulneraria	*Origanum vulgare*
Bellis perennis	*Pimpinella saxifraga* agg.
Centaurea jacea agg.	*Plantago lanceolata*
Cirsium arvense	*Plantago media*
Euphorbia cyparissias	*Ranunculus acris* agg.
Galium mollugo agg.	*Rhinanthus aristatus* agg.
Gentiana asclepiadea	*Stellaria graminea*
Gentiana cruciata	*Thymus pulegioides*
Hypericum maculatum agg.	*Trifolium montanum*
Hypericum perforatum	*Trifolium pratense*
Leontodon hispidus	*Trifolium repens*
Study site Pleschkogel	
Achillea millefolium agg.	*Knautia dipsacifolia*
Anthyllis vulneraria	*Leontodon hispidus*
Bellis perennis	*Lotus corniculatus* agg.
Buphthalmum salicifolium	*Medicago lupulina*
Campanula rapunculoides	*Melampyrum pratense*
Centaurea jacea agg.	*Picea abies*
Clematis vitalba	*Pimpinella saxifraga* agg.
Cytisus hirsutus	*Rhinanthus aristatus* agg.
Dianthus carthusianorum agg.	Rosa spec.
Epipactis helleborine agg.	*Rubus* sect. *Rubus*
Euphorbia amygdaloides	*Rubus idaeus*
Euphorbia cyparissias	*Solidago virgaurea*
Galium mollugo agg.	*Teucrium chamaedrys*
Genista germanica	*Thymus pulegioides*
Gentiana asclepiadea	*Verbascum nigrum*
Gentiana cruciata	*Viburnum lantana*
Hieracium spec.	

Figs. 1–4: The sites of the field study. **Fig. 1:** Study site Wolfsattel. **Fig. 2:** Study site Pleschkogel. **Fig 3:** *G. cruciata* close to *G. asclepiadea* at study site Pleschkogel. **Fig 4:** Horse pasture at the north end of the Pleschkogel site with *G. cruciata, G. asclepiadea, Gl. germanica* agg. and *P. alcon*.



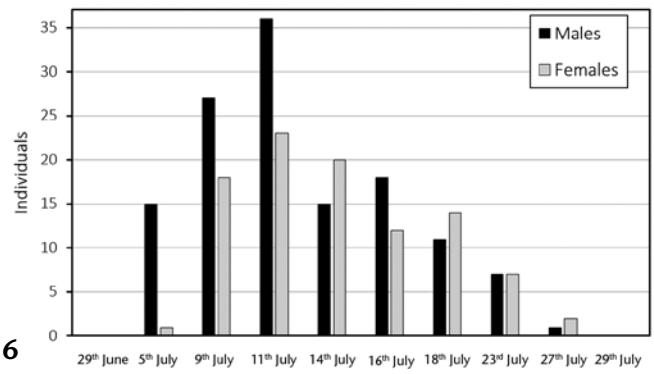
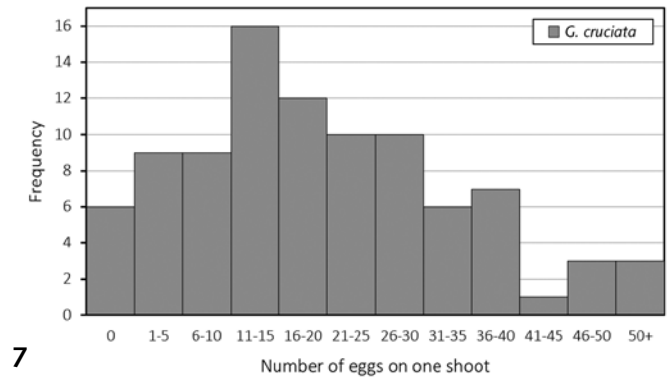
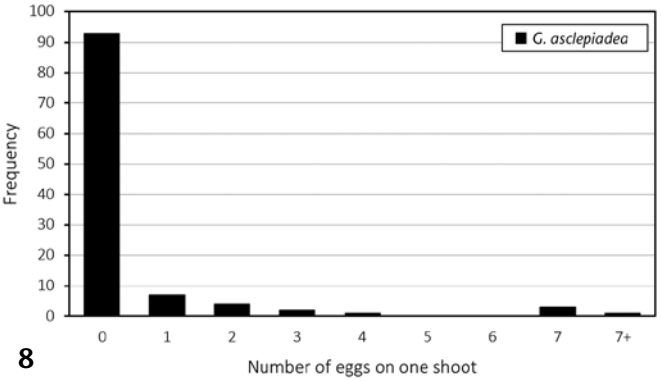
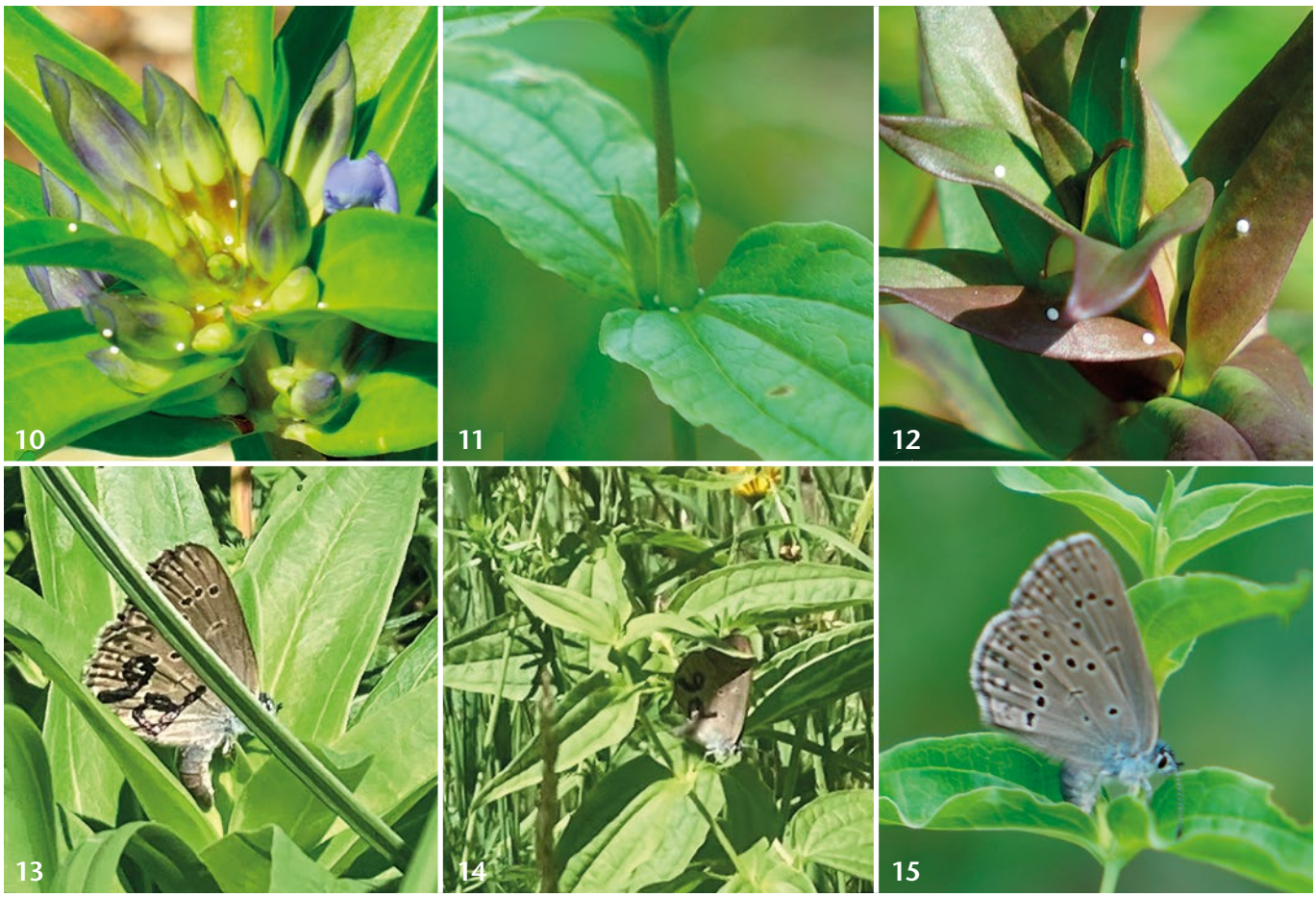


Fig. 5. Captured imagines of *P. alcon* at study site **Wolfsattel**. — **Fig. 6.** Captured imagines of *P. alcon* at study site **Pleschkogel**.





Figs. 7–8: Egg countings at Pleschkogel. **Fig. 7:** Frequency of egg numbers on shoots of *G. cruciata* (July 23rd; N = 92). **Fig. 8:** Frequency of egg numbers on shoots of *G. asclepiadea* (July 23rd; N = 111).



Figs. 10–12: P. alcon eggs on *G. cruciata* (**10**), *G. asclepiadea* (**11**) and *Gl. germanica* agg. (**12**). — **Figs. 13–14:** Marked female deposits egg on *G. cruciata* (**13**). Shortly afterwards, the same female investigates *G. asclepiadea* (**14**). — **Fig. 15:** Unmarked female lays egg on *G. asclepiadea*.

Capture-mark-recapture method

From the beginning of June, both sites were visited at intervals of several days to look for *P. alcon* adults. During the flight period from the beginning to the end of July, a capture-mark-recapture study with *P. alcon* adults was carried out at both sites every two to five days between 10 a.m. and 5 p.m., weather permitting.

Imagines were caught with a net (prior permission was granted by Steirische Landesregierung, Abt. 13-696098/2022-13). Using a thin fineliner pen, a number was written on the underside of each of the hindwings and the marked butterfly was photographed from both sides with its wings closed. The butterfly was then released on the spot. For each capture, the date, time, sex, and the number assigned were recorded and the GPS position entered into a GIS app. The start of the flight period, presumably in the last week of June, was missed at Wolfsattel due to difficult weather conditions at this time.

Egg countings

On July 15th, about 25 shoots of *G. asclepiadea* and 25 shoots of *G. cruciata* were marked in the habitat on the Wolfsattel on two areas of about 15 × 15 m each. A string was attached to the selected shoots as a marker. On these plants, all eggs were counted. On July 20th, shortly after the end of the flight period, the eggs were counted on the marked plants again.

On July 14th and 16th, around 100 shoots each of *G. cruciata* and *G. asclepiadea* were marked in the Pleschkogel habitat along the hiking trail through the habitat. The eggs on the marked shoots were counted on several days until July 31st.

Data collection and statistical analysis

To facilitate fieldwork and data collection, a cloud-based feature class was set up with all relevant information about species, foodplants and stage of development. By using ArcGIS Field Maps, data could be collected easily using a tablet or mobile phone and was synchronized to our GIS database for later statistical and spatial analysis and mapping.

To enable comparison, despite less surveyed shoots, the egg count on *G. cruciata* from July 14th at Pleschkogel was extrapolated. The gathered average of eggs per shoot was multiplied with the mean shoot number of the other five counting events (88.6).

Results

Plant mapping

At **Wolfsattel,** occurrences of *G. cruciata* were concentrated in the rather sparse cow pasture in the north-east of the area. *G. asclepiadea,* in contrast, was found all over the area at forest margins as well as along paths and on

Table 2: Summary of the capture-mark-recapture study implemented at two sites in Styria, Austria, in July 2023. — *Individuals captured at least once at another day before.

Date	Study sites	Marked individuals			Recaptured individuals*		
		Total	Males	Females	Total	Males	Females
2. VII.	Wolfsattel	25	18	7	0	0	0
8. VII.		36	16	20	1	1	0
10. VII.		18	7	11	10	6	4
15. VII.		3	1	2	0	0	0
5. VII.	Pleschkogel	16	15	1	0	0	0
9. VII.		43	25	18	2	2	0
11. VII.		35	17	18	24	19	5
14. VII.		16	6	10	19	9	10
16. VII.		18	10	8	12	8	4
18. VII.		14	5	9	11	6	5
23. VII.		8	4	4	6	3	3
27. VII.		2	0	2	1	1	0
Totals	Wolfsattel	**82**	**42**	**40**	**11**	**7**	**4**
	Pleschkogel	**152**	**82**	**70**	**58**	**35**	**23**

Table 3: Summary of the eggs counted on *G. cruciata* and *G. asclepiadea*.

Gentiana cruciata	Pleschkogel						Wolfsattel	
Date	**14th July**	**16th July**	**18th July**	**23rd July**	**27th July**	**31st July**	**15th July**	**20th July**
Shoots	75	90	86	92	88	87	50	44
N with eggs	68	84	81	86	80	80	37	30
Sum of eggs	915	1379	1517	1820	1655	1591	351	286
Mean	12.2	15.3	17.6	19.8	18.8	18.3	7.0	6.5
Standarddeviation	14.2	15.5	16.1	15.4	16.2	14.3	6.9	7.6
Mean	13.5	16.4	18.7	21.2	20.7	19.9	9.5	9.5
Standarddeviation	14.3	15.5	15.9	15.0	15.8	13.8	6.3	7.5
Minimum	1	1	1	1	1	1	1	1
Median	11	13	16	19	18	16.5	8	7.5
Maximum	97	103	101	81	81	67	28	34
Interquartile range	14	17	16.5	18	19	20.5	7	7
Gentiana asclepiadea								
Shoots	114	109	99	111	104	99	53	50
N with eggs	14	12	21	18	17	21	6	8
Sum of eggs	15	29	56	66	64	69	8	8
Mean	0.13	0.27	0.57	0.59	0.62	0.7	0.15	0.16
Standarddeviation	0.36	1.1	1.5	2.3	2.3	2.5	0.46	0.37
Mean	1.1	2.4	2.7	3.7	3.8	3.3	1.3	1.0
Standarddeviation	0.3	2.6	2.3	4.6	4.6	4.6	0.5	0.0
Minimum	1	1	1	1	1	1	1	1
Median	1	2	2	2	2	1	1	1
Maximum	2	9	7	20	20	21	2	1
Interquartile range	0	3.25	3	3.75	4.5	2.5	1	0

clearcuts between young spruce trees, often in stands of several plants (Map 1). Plants of both *Gentiana* species could be found within several meters of each other. The third species, *Gl. germanica* agg., was found as rare clusters of a few plants only few meters away from the next plants of *G. cruciata*.

At **Pleschkogel,** *G. cruciata* plants were concentrated in three places. A medium-sized stand in a horse pasture near the summit, a large stand along the power line in the south of the area and a small stand next to a gravel road, west of the power line. In contrast, *G. asclepiadea* was found all over the area on forest margins and roadsides, on clearcuts between young spruce trees and only rarely exposed to the sun (Map 2). It typically formed stands of several plants. Plants of *G. asclepiadea* were also found at the three *G. cruciata* sites, within a few meters distance. Along the power line, plants of both species grew less than one meter apart in several places (Fig. 3). At the horse pasture in the north of the investigated area (Fig. 4), a stand of around 20 plants of *Gl. germanica* agg. grew at around 10 m distance to groups of *G. cruciata* and *G. asclepiadea*.

Capture-mark-recapture study

The first *P. alcon* imagines at **Wolfsattel** were tagged on July 2nd, the last ones on July 15th (Fig. 5). However, the beginning of the flight period was probably a few days earlier (see above). The sex ratio of 18 ♂♂ to 7 ♀♀ on

the first survey date (Table 2) indicates protandry, as was also described for *P. alcon* by Dziekańska et al. (2020), Meyer-Hozak (2000), Nowicki et al. (2019) and Osváth-Ferencz et al. (2016). In total, 82 butterflies were caught and marked, including 42 (51.2%) ♂♂ and 40 (48.8%) ♀♀ (Table 2). On July 10th, 10 butterflies were recaptured. All of them had been caught for the first time on July 8th, 6 out of 17 (=35%) ♂♂ and 4 out of 20 (=20%) ♀♀. 1 ♂ was recaptured on July 8th, after a first catch on July 2nd. No other recaptures succeeded, rendering an overall recapture rate of 13% (♂♂: 17%, ♀♀: 10%) for this site.

The first imagines of *P. alcon* at **Pleschkogel** were tagged on July 5th, but the first *P. alcon* imagines were already observed at Pleschkogel on July 2nd (S. Gasparitz, pers. comm.). The last butterflies were tagged on July 27th (Fig. 6). A total of 152 butterflies were caught and marked, including 82 (53.9%) ♂♂ and 70 (46.1%) ♀♀. 58 butterflies were recaptured at least once (Table 2). This corresponds to a recapture rate of 38%, includes 35 ♂♂ (43%) and 23 ♀♀ (33%). The average lifespan (simply expressed as difference between captures) was 3.9 days (median: 3.0) for ♂♂ and ♀♀. 1 ♂ was recaptured after 14 days, 1 ♂ was and 2 ♀♀ after 9 days.

Egg deposition systematics

At both sites, eggs were observed on *G. cruciata, G. asclepiadea* and *Gl. germanica* agg. The eggs were laid predominantly between the buds and basally on the leaves, very close to the buds.

At **Wolfsattel,** 351 eggs were counted on 50 shoots of *G. cruciata* on July 15th (arithmetic mean: 7.0 eggs per shoot, standard deviation: 6.9, median = 6.0, Table 3) and only 13 (26.0%) of the shoots were unoccupied. If these are excluded, the arithmetic mean is 9.5 eggs per shoot (standard deviation: 6.3, median = 8.0). One shoot carried 28 eggs.

On July 20th, 44 of these shoots caried a total of 286 eggs (arithmetic mean: 6.5 eggs per shoot, standard deviation: 7.6, median = 5.0), 14 (31.8%) of the shoots were unoccupied. If these are excluded, the arithmetic mean is 9.5 eggs per shoot (standard deviation: 7.5, median = 7.5). One shoot carried 34 eggs.

At the same dates, 8 eggs were counted on 6 shoots (out of 53 in total) of *G. asclepiadea* on July 15th (arithmetic mean: 0.15 eggs per shoot, standard deviation: 0.46, Table 3), 47 shoots were unoccupied. If the unoccupied shoots are excluded, the arithmetic mean is 1.3 eggs per shoot (standard deviation: 0.5, median = 1.0). Two shoots carried 2 eggs each.

On July 20th, a total of 8 eggs were again counted on 50 of these shoots (arithmetic mean: 0.16 eggs per shoot, standard deviation: 0.37, median = 0.0), 42 (84.0%) of the shoots were unoccupied.

Eggs on shoots of *Gl. germanica* could be found towards the end of the flight period. Only a few relatively tall and mature shoots were occupied with 1 to 10 eggs.

At **Pleschkogel,** egg counting took place on July 14th, 16th, 18th, 23rd, 27th and 31st on about 90 marked shoots of *G. cruciata* and 114 marked shoots of *G. asclepiadea*.

On *G. cruciata,* 1379 eggs on 90 shoots (15.3 eggs per shoot, median = 11.5) were counted on July 16th, 6 (6.7%) of the shoots were unoccupied (Table 3). Excluding these, the average was 16.4 eggs per shoot (median = 13.0). 1 shoot was crowded with 97 eggs.

On July 23rd, on 92 of these shoots a total of 1820 eggs were counted (19.8 eggs per shoot, median = 18.0), 6 (6.5%) of the shoots were unoccupied (Fig. 7). Excluding these, an average of 21.2 eggs per shoot (median = 19.0) is resulting. 1 shoot carried 81 eggs.

On July 14th, 15 eggs were found on 114 shoots of *G. asclepiadea* (arithmetic mean: 0.13 eggs per shoot, standard deviation: 0.36, median = 0.0, Table 3), 100 (87.7%) of the shoots were unoccupied (Fig. 8). If these are excluded, the arithmetic mean is 1.1 eggs per shoot (standard deviation: 0.3, median = 1.0). 1 shoot carried two eggs.

After the end of the flight phase, on July 31st, 99 of these shoots carried a total of 69 eggs (arithmetic mean: 0.70 eggs per shoot, standard deviation: 2.47, median = 0.0), 78 (78.8%) of the shoots were empty. If these are excluded, an arithmetic mean of 3.3 eggs per shoot is obtained (standard deviation: 4.6, median = 1.0). 1 shoot carried 21 eggs.

Eggs on shoots of *Gl. germanica* could be found towards the end of the flight period. Approximately every third shoot was occupied with 1–5 eggs.

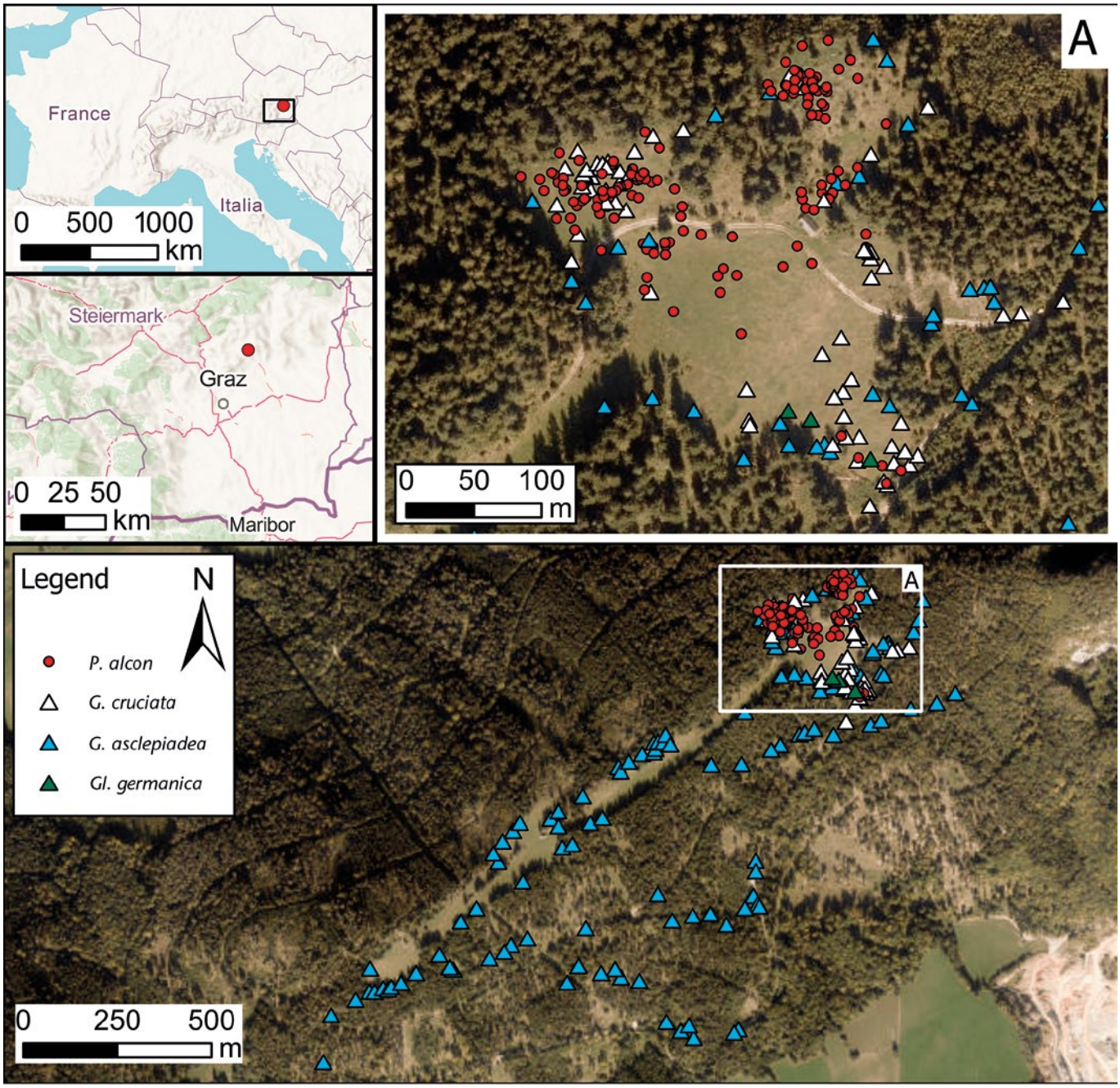
Discussion

Capture-mark-recapture study

The observed flight period of the population at **Pleschkogel** ranged from the beginning to the end of July and lasted 26 days (Fig. 6). Flight periods of around 4 weeks have also been reported for other populations of *P. alcon* X (Meyer-Hozak 2000, Kőrösi et al. 2008).

At **Wolfsattel,** the flight period documented was shorter, because the start of the flight period was missed. Importantly, the flight periods of the two populations described in this paper were synchronised with the bud stages of *G. cruciata* suitable for oviposition.

The sex distribution among the captured imagines was roughly balanced, with a slight preponderance of male imagines. This effect has also been documented in other capture-mark-recapture studies with *P. alcon* adults, because ♂ imagines fly higher in search of a mate, while ♀ butterflies fly lower over the vegetation to lay their eggs (Arnyas et al. 2006, Osváth-Ferencz et al. 2016). In addition, ♂♂ are more conspicuously coloured than ♀♀, stand out more from their surroundings and are better noticed (Meyer-Hozak 2000, Osváth-Ferencz et al. 2016, Nowicki et al. 2019, Dziekańska et al. 2020).

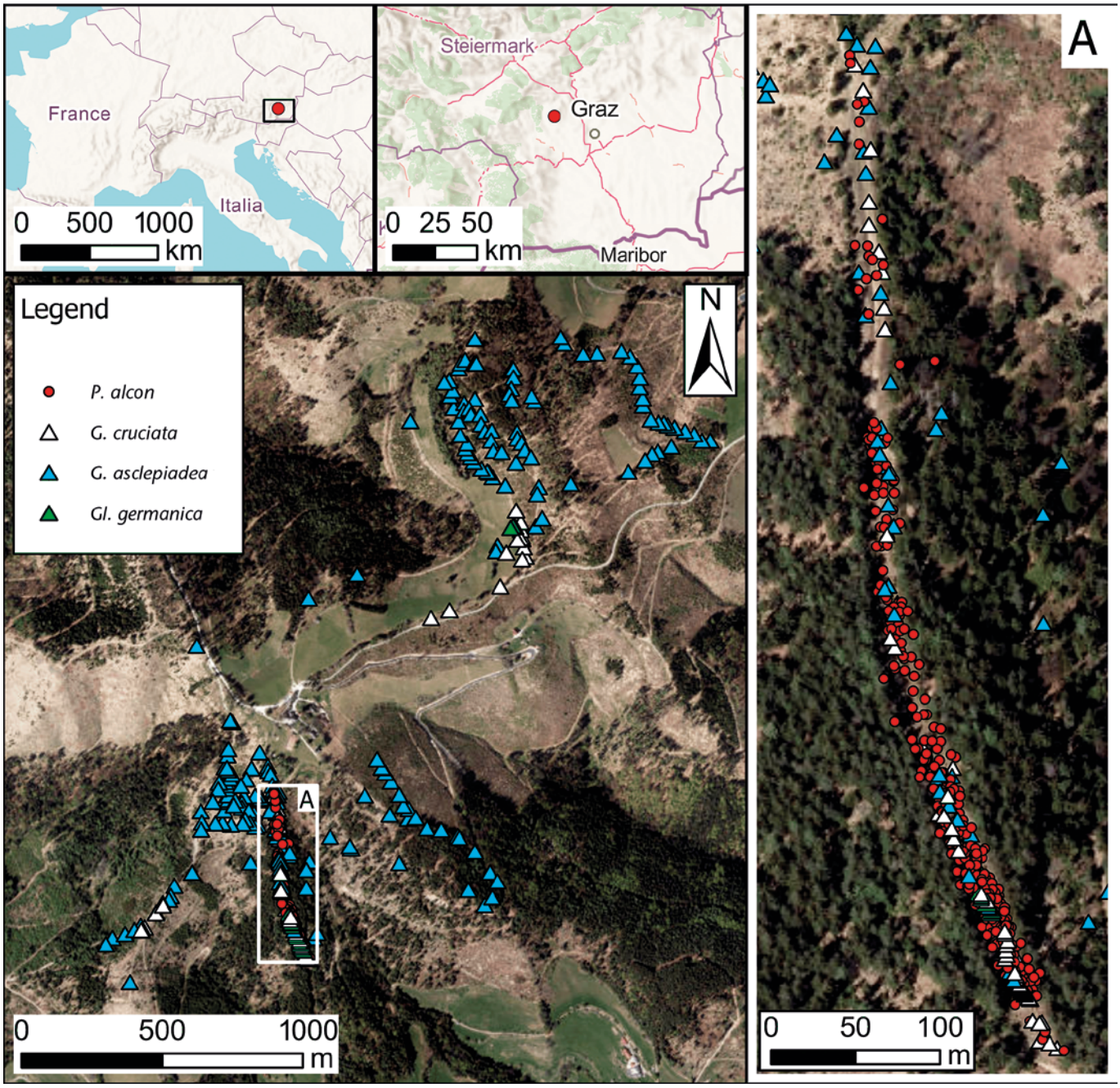


Map 1: Exact locations of foodplants and captured *P. alcon* imagines at locality **Wolfsattel.** (Sources: Esri, Maxar, Earthstar Geographics, Geoland, NASA, NGA, USGS, Map data ©OpenStreetMap contributors, Microsoft, Facebook, Inc. and its affiliates, Esri Community Maps contributors, Map layer by Esri, Geoland, Intermap, NASA, NGA, USGS, GIAR.)

At the **Pleschkogel** site, a maximum imaginal lifespan of 14 days (1 ♂) and 9 days (2 ♀♀) was documented. The average lifespan among the recaptured individuals (difference: day of last capture, day of first capture) was about 3.9 days for both sexes, but the majority of individuals (at this site: 62%) were not recaptured at all. Therefore, the lifespan of an average butterfly was probably lower than this value, but statistical modelling was – because of the quite low numbers and because it was not the prime research question of this work – not performed. A significantly lower proportion of ♀ adults were recaptured at all. This could be an effect of the CMR method ('observer bias', see previous section), but it could also indicate a shorter lifespan of the ♀♀. Timuş et al. (2013) estimated the lifespan of an imago of *P. alcon* X to be around 6 days and that of an imago of *P. alcon* H to be 2–3 days. Kőrösi et al. (2008) give a lifespan of around 2.6 days for *P. alcon* X.

Which foodplant species were used?

Outside bogs and wet meadows, *G. cruciata* is by far the most important larval foodplant of *P. alcon* (Czekes et al. 2014, Settele et al. 2015, Tartally et al. 2016, Bereczki et al. 2018). *G. asclepiadea* was previously known as a foodplant almost only for *P. alcon* H (Krismann 2000, Bräu et al. 2006, Bolt et al. 2010), in some cases even as the only one (Marktanner 1985, Bolt et al. 2010, Carleial et al. 2018), despite the fact that Bräu et al. (2006) found *G. asclepiadea* to be less suitable as a foodplant than the sympatrically occurring *G. pneumonanthe* (Bräu et al. 2006). Just Kolev (2002) described a population of *P. alcon* X with almost 700 eggs on 71 of the 96 *G.*



Map 2: Exact locations of foodplants and captured *P. alcon* imagines at locality **Pleschkogel.** (Sources: Esri, Maxar, Earthstar Geographics, Geoland, NASA, NGA, USGS, Map data ©OpenStreetMap contributors, Microsoft, Facebook, Inc. and its affiliates, Esri Community Maps contributors, Map layer by Esri, Geoland, Intermap, NASA, NGA, USGS, GIAR.)

asclepiadea found in a *G. cruciata*-free habitat at around 1000 m a.s.l. in Bulgaria. These grew on calcareous rocks and at forest margins.

P. alcon X seems to have adapted to oviposition on *G. asclepiadea* at this montane site, possibly due to the lack of available *G. cruciata*. Gros (2002) investigated *P. alcon* X in the province of Salzburg. Although *G. asclepiadea* and *Gl. germanica* agg. were more common than *G. cruciata* at the sites studied, eggs were only found on *G. cruciata*. Meyer-Hozak (2000) also found no signs of oviposition of *P. alcon* X on *Gl. germanica* agg. in North Rhine-Westphalia, Germany, in *G. cruciata*-bearing habitats, although Fartmann (2004) described such a behaviour in a population of *P. alcon* X in the same region. He counted 47 eggs on four particularly far developed and tall-growing *Gl. germanica* agg. plants (Fartmann 2004). In the Hochschwab area, which is part of the Styrian Limestone Alps, Tartally et al. (2014) documented the use of *Gl. germanica* subsp. *rhaetica* as larval foodplant of *P. alcon* '*rebeli*' above the tree line, but failed to find eggs on *G. asclepiadea*, despite its common presence. The latter was also described in the Swiss Alps as a foodplant of *P. alcon* '*rebeli*' (Jutzeler 1988, 1989).

Interestingly, eggs in the present study were not only found on *G. cruciata*, but also on *G. asclepiadea* and *Gl. germanica* agg. In the studied montane populations (situated between the "typical" low-level *P. alcon* X and the Alpine *P. alcon* '*rebeli*' habitats, eggs were also documented on *G. asclepiadea* and *Gl. germanica* agg. Hence, these low mountain-range populations around 1000 m

a.s.l. provide a link both to the Bavarian pre-Alpine populations which use *G. asclepiadea* (Bräu et al. 2006) and to the Alpine populations on *Gl. germanica* agg. in the Hochschwab region (Tartally et al. 2014). Hence, the montane populations investigated here could have been a stepping stone for *P. alcon* to colonise habitats above the tree line.

The reason for these populations at intermediate altitudes being able to use all three gentian species, is probably very simply related to the fact that only at these altitudes *G. cruciata, G. asclepiadea* and *Gl. germanica* agg. produce flower buds suitable for oviposition (see Introduction) at similar times, which allows even imagines synchronized with *G. cruciata* to oviposit on the other gentian species. In other words: if suitable buds are present during the "normal" flight time, all gentian species are used (however, in different intensity, *G. cruciata* still is the most important larval foodplant also in these habitats). This will be discussed in more detail in the following section.

Oviposition systematics

The results of the egg counts at **Wolfsattel** show no change in egg numbers between the two counting events (July 15th and 20th), which supports the observation that the flight period ended in mid-July. As in the studies of Arnyas et al. (2006) and Czekes et al. (2014), eggs were deposited mostly on and between the buds and basally on the leaves next to the buds (Fig. 10). The fact that the counted number of eggs on *G. cruciata* from Pleschkogel decreased during the last three counting events (Table 3) was probably related to the facts that it was more difficult to count all eggs due to the blossoming of the buds and that some of the eggs fell off the plant or were eaten by predators.

At the end of the flight period at **Pleschkogel,** the proportion of occupied *G. cruciata* shoots was about 4.5 times higher than the proportion of occupied shoots of *G. asclepiadea,* and the occupied *G. cruciata* shoots were covered with about 6 times more eggs than those of *G. asclepiadea*. At Wolfsattel, the sample of analysed shoots was considerably smaller, but the collected data show similar ratios. Towards the end of the flight period, between 18th and 23rd July, the number of eggs at Pleschkogel increased by 300 on the approximately 100 marked *G. cruciata,* while the number of eggs on the marked *G. asclepiadea* only increased by 10 (Table 3) The results of the study show that *G. cruciata* is the favoured foodplant for oviposition at the investigated sites. *G. asclepiadea* is used much less frequently and with significantly fewer eggs (Table 4 and Fig. 9).

Confirming the results of (Thomas & Elmes 2001, Arnaldo et al. 2014), the ♀♀ preferred the earliest stages of the buds for oviposition, when they were still green, completely closed and rather small, but already recognisable. The majority of ovipositions on *G. asclepiadea* occur towards the end of the flight period (Fig. 9) because *G. asclepiadea* has a later phenology than *G. cruciata:* the buds appear later, swell later and flower later.

The time of the flight period of *P. alcon* at both sites is adapted to the local phenology and bud stages of *G. cruciata* as an oviposition plant. The fact that more ♀♀ probably use *G. asclepiadea* for oviposition at the end of the flight period than at the beginning is an indication of the strong role played by the phenology of the foodplants in oviposition. Nevertheless, even at the end of the flight period, *G. cruciata* remains the gentian clearly favoured by the females for oviposition.

Is there a difference in foodplant occupancy between the females?

Studies that compared the size of populations with the number of eggs laid determined an average of around 35–150 eggs laid for a female of *P. alcon* (Meyer-Hozak 2000, Kőrösi et al. 2008, Nowicki et al. 2019).

In the **Pleschkogel** habitat, a total of only about 70 eggs on about 100 shoots of *G. asclepiadea* were counted, which appears too low to come from a few ♀♀ exclusively specialised in laying eggs on *G. asclepiadea*. Based on the later increase in egg-laying on *G. asclepiadea,* it can be assumed that ♀♀ that hatch later lay eggs more frequently on this gentian species. The reason for this is probably the preference for a certain bud stage and not a genetically defined foodplant preference. Due to the high availability of *G. asclepiadea* distributed over the entire area of the sites (Map 1 and Map 2), ♀♀ could potentially expand beyond the habitats dominated by *G. cruciata*. Such behaviour was not documented at either site. Neither deposited eggs nor flying imagines were found outside the *G. cruciata*-bearing habitats.

This agrees with studies documenting that imagines of *P. alcon* do not fly long distances out of the core zone of their habitat (Maes et al. 2004, Kőrösi et al. 2008, Timuş et al. 2013). Kőrösi et al. (2008) documented for the ♀♀ of *P. alcon* X a "home range" of only around 325 m² indicating that the ♀♀ do not move far away from the ant nest from which they hatched. This behaviour is typical of *Phengaris* Blues and could be due to their obligate myrmecophily (Hovestadt & Nowicki 2008, Skórka et al. 2013).

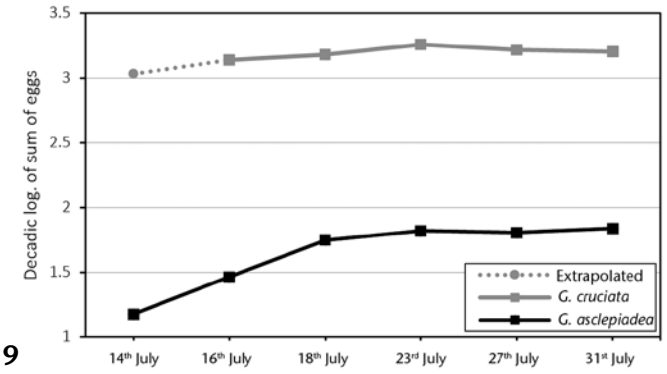
Conclusions

At two investigated low-mountain range sites in Styria, Austria, *P. alcon* uses three different larval foodplants: *G. cruciata, G. asclepiadea* and *Gl. germanica* agg.. Although the contribution of the two latter plants to the larval development of the population is probably negligible, considering the amount of the eggs laid, the present work shows that:

1. In Styria, *P. alcon* uses *G. cruciata* as well as *G. asclepiadea* and *Gl. germanica* agg. for oviposition.
2. *G. cruciata* is indisputably the most important of the three foodplants and the timing of the flight period of

Table 4: Absolute and relative distribution frequency of egg numbers on *G. cruciata* and *G. asclepiadea* shoots (relative values in rounded %).

Numbers of eggs on one shoot																						
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	≥ 20	Totals
Wolfsattel																							
G.c.	abs.	27	1	8	3	2	6	5	4	7	6	5	1	5	0	2	0	4	0	1	1	6	94
	%	–	1	12	4	3	9	7	6	10	9	7	1	7	0	3	0	6	0	1	1	9	–
G.a.	abs.	89	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	103
	%	–	86	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–
Pleschkogel																							
G.c.	abs.	39	18	22	21	17	17	9	12	15	12	14	26	17	14	19	14	12	8	12	13	187	518
	%	–	4	5	4	4	4	2	3	3	3	3	5	4	3	4	3	3	2	3	3	39	–
G.a.	abs.	533	54	19	7	2	4	4	8	1	1	0	0	0	0	0	0	0	0	0	0	3	636
	%	–	52	18	7	2	4	4	8	1	1	0	0	0	0	0	0	0	0	0	0	3	–



9

Fig. 9: The total amount of eggs with time on *G. cruciata* and *G. asclepiadea;* the egg count on *G. cruciata* at July 14th is extrapolated (see Statistics).

the imagines is synchronised with the phenology of the bud stages of *G. cruciata*.

3. The majority of ovipositions on *G. asclepiadea* occur towards the end of the flight period, which shows the strong role that the phenology of the foodplants plays in oviposition.
4. A sympatric separation of the ♀♀ according to different foodplant use could not be documented.

These results corroborate observations by Sielezniew (2004), who reported that a population of *P. alcon* H in Poland mainly ovipositing on *G. pneumonanthe* also laid some eggs on *G. cruciata* in nearby drier patches, but that the much earlier phenology of *G. cruciata* allowed only the very first emerging butterflies to oviposit on *G. cruciata*. Also here, various Gentianaceae are used, but plant phenology determines the most important one.

P. alcon is, therefore, not really specialised in one or two particular larval foodplants, but ♀♀ use those plants which show the optimally developed buds in their flight radius (which is small). Although *G. pneumonanthe* in wet and *G. cruciata* in dry habitats are most important, *G. asclepiadea, Gl. germanica* agg., *G. lutea* and probably even more Gentianaceae are also used by various populations, some also being specialised on them. This flexibility allows the populations to become much more resilient in cases of extreme weather conditions (when synchronization with the "normal" foodplant does not work) and even against climate change, as using different foodplants with slightly different phenologies eases the process of adaptation to the changing environmental conditions.

If, according to Als et al. (2004), *P. alcon* H was the "original" form of the various ecotypes existing today, the low-mountian habitats such as the ones investigated here may have played a crucial role in conquering new habitats at drier or higher Alpine sites. In this sense, the investigated habitats may have acted as stepping stones from *P. alcon* H to *P. alcon* X and *P. alcon* '*rebeli*'.

Acknowledgements

We are grateful to Sabine Gasparitz, Emanuel Trummer-Fink, Daniel Linzbauer and Johannes Schaffler for their help during field work, with permits and for information on the populations. The whole study was initiated based on observations by G. Hermann, Hildrizhausen, the friendly sharing of which is particularly gratefully acknowledged. The fieldwork of this study was carried out under permit of the Styrian state government (Steirische Landesregierung, Abt. 13-696098/ 2022-13).

References

Akino, T., Knapp, J. J., Thomas, J. A., & Elmes, G. W. (1999): Chemical mimicry and host specificity in the butterfly *Maculinea rebeli,* a social parasite of *Myrmica* ant colonies. — Proceedings of the Royal Society of London, Series B: Biological Sciences, London, **266:** 1419–1426.

Als, T. D., Vila, R., Kandul, N. P., Nash, D. R., Yen, S.-H., Hsu, Y.-F., Mignault, A. A., Boomsma, J. J., & Pierce, N. E. (2004): The evolution of alternative parasitic life histories in large blue butterflies. — Nature, London, **432** (7015): 386–390. — DOI: 10.1038/ nature03020.

Arnaldo, P. S., Gonzalez, D., Oliveira, I., van Langevelde, F., & Wynhoff, I. (2014): Influence of hostplant phenology and oviposition date on the oviposition pattern and offspring performance of the butterfly *Phengaris alcon.* — Journal of Insect Conservation, Basel, **18** (6): 1115–1122. — DOI: 10. 1007/s10841-014-9721-x.

Arnyas, E., Bereczki, J., Tóth, A., Pecsenye, K., & Varga, Z. (2006): Egg-laying preferences of the xerophilous ecotype of *Maculinea alcon* (Lepidoptera: Lycaenidae) in the Aggtelek National Park. — European Journal of Entomology, Branisovska, **103** (3): 587–595.

Bence, S., & Richaud, S. (eds.) (2020): Atlas des papillons de jour & zygènes. Provence-Alpes-Côte d'Azur. — Le Naturographe, Gap, 544 pp.

Bereczki, J., Pecsenye, K., Peregovits, L., & Varga, Z. (2005): Pattern of genetic differentiation in the *Maculinea alcon* species group (Lepidoptera, Lycaenidae) in Central Europe. — Journal of Zoological Systematics and Evolutionary Research, Berlin, **43** (2): 157–165. — DOI: 10.1111/j.1439-0469.2005.00305.x.

——, ——, Varga, Z., Tartally, A., & Tóth, J. P. (2018): *Maculinea rebeli* (Hirschke) — a phantom or reality? Novel contribution to a long-standing debate over the taxonomic status of an enigmatic Lycaenidae butterfly. — Systematic Entomology, St. Albans, **43** (1): 166–182. — DOI: 10.1111/ syen.12259.

——, Sielezniew, M., Verovnik, R., Beshkov, S., Kuznetsov, G., Bonelli, S., & Tóth, J. P. (2022): Phylogeography reveals the origin of the two phenological forms of large blue, *Phengaris arion* (Lepidoptera: Lycaenidae). — Biological Journal of the Linnean Society, Oxford, **137** (2): 359–373. — DOI: 10.1093/biolinnean/blac081.

——, Tóth, J. P., Sramkó, G., & Varga, Z. (2014): Multilevel studies on the two phenological forms of large blue (*Maculinea arion*) (Lepidoptera: Lycaenidae). — Journal of Zoological Systematics and Evolutionary Research, Berlin, **52** (1): 32–43. — DOI: 10.1111/jzs.12034.

Boe, A. M. B., Simonsen, T. J., Colding-Jørgensen, C. T., Folman, P. H., Jensen, T. T., Spencer, K. J., Thomsen, P. F., & Nash, D. R. (2022): Spatial and temporal patterns of genetic diversity and structure in Danish populations of the alcon Blue butterfly *Phengaris alcon* (Denis & Schiffermüller). — Diversity, Basel, **14** (12): 1098. — DOI: 10.3390/d14121098.

Bolt, D., Neumeyer, R., Rey, A., & Sohni, V. (2010): Kleiner Moorbläuling (Lepidoptera: Lycaenidae: *Phengaris alcon*) und Echte Knotenameisen (Hymenoptera: Formicidae: *Myrmica*) am Pfannenstiel (Kanton Zürich, Schweiz). — Entomohelvetica, Bern, **3:** 27–48.

Bos, F., Bosveld, M., Groenendijk, D., van Swaay, C., & Wynhoff, I. (2006): De dagvlinders van Nederland: Verspreiding en bescherming, (Lepidoptera: Hesperioidea, Papilionoidea). Vol. **7.** — Utrecht (KNNV Uitgeverij), 381 pp.

Bräu, M., Gros, P., Nunner, A., Stettmer, C., & Settele, J. (2006): Der verlustreiche Weg in die Sicherheit eines Wirtsameisen-Nestes — neue Daten zur Entwicklungsbiologie und zur Mortalität der Präimaginalstadien von *Maculinea alcon* sowie zum Einfluss der Mahd. — *In:* Fartmann, T., & Hermann, G. (eds.): Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa.: Abhandlungen aus dem Westfälischen Museum für Naturkunde, Münster, **68** (3/4): 197–219.

Carleial, S., Maurel, N., van Kleunen, M., & Stift, M. (2018): Oviposition by the mountain alcon blue butterfly increases with hostplant flower number and host ant abundance. — Basic and Applied Ecology, Berlin, **28:** 87–96. — DOI: 10.1016/j. baae.2018.02.008.

Cini, A., Barbero, F., Bonelli, S., Bruschini, C., Casacci, L. P., Piazzini, S., Scalercio, S., & Dapporto, L. (2020): The decline of the charismatic *Parnassius mnemosyne* (L.) (Lepidoptera: Papilionidae) in a Central Italy national park: a call for urgent actions. — Journal of Insect Biodiversity, Auckland (NZ), **16** (2): 47–54. — DOI: 10.12976/jib/2020.16.2.2.

Council of the European Union (1992): Council directive 92/43/ EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. — URL: eurlex.europa.eu/legal-content/ EN/TXT/?uri=CELEX%3A31992L0043.

Czekes, Z., Markó, B., Nash, D. R., Ferencz, M., Lázár, B., & Rákosy, L. (2014): Differences in oviposition strategies between two ecotypes of the endangered myrmecophilous butterfly *Maculinea alcon* (Lepidoptera: Lycaenidae) under unique syntopic conditions. — Insect Conservation and Diversity, St. Albans, **7** (2): 122–131. — DOI: 10.1111/icad. 12041.

Dolek, M., Geyer, A., & Bolz, R. (1998): Distribution of *Maculinea rebeli* and hostplant use on sites along the river Danube. — Journal of Insect Conservation, New York, **2** (1): 85–89.

Drès, M., & Mallet, J. (2002): Host races in plant-feeding insects and their importance in sympatric speciation. — Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, London, **357** (1420): 471–492. — DOI: 10.1098/ rstb.2002.1059.

Dziekańska, I., Nowicki, P., Pirożnikow, E., & Sielezniew, M. (2020): A unique population in a unique area: The alcon blue butterfly and its specific parasitoid in the Białowieża forest. — Insects, Basel, **11** (10): 687. — DOI: 10.3390/ insects11100687.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulissen, D. (2001): Zeigerwerte von Pflanzen in Mitteleuropa. Volume **18.** 3. Auflage. — Göttingen (Verlag Erich Goltze), 262 pp.

Elmes, G. W., & Thomas, J. A. (1987): Die Gattung *Maculinea*. — Pp. 354–368, *in:* Tagfalter und ihre Lebensräume: Arten, Gefährdung, Schutz, Schweiz und angrenzende Gebiete. Bd. **1,** 1. Aufl., Schmetterlinge und ihre Lebensräume. — Schweizerischer Bund für Naturschutz, Basel, 516 S.

——, ——, Clarke, R. T., & Hochberg, M. E. (1996): Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli,* a parasitic butterfly of red ant colonies. — Acta Oecologica, Paris, **17** (1): 61–80.

——, ——, & Wardlaw, J. C. (1991a): Larvae of *Maculinea rebeli,* a large-blue butterfly and their *Myrmica* host ants: patterns of caterpillar growth and survival. — Journal of Zoology, London, **224** (1): 79–92. — DOI: 10.1111/j.1469-7998.1991.tb04789.x.

——, ——, & —— (1991b): Larvae of *Maculinea rebeli,* a largeblue butterfly, and their *Myrmica* host ants: wild adoption and behaviour in ant-nests. — Journal of Zoology, London, **223** (3): 447–460. — DOI: 10.1111/j.1469-7998.1991. tb04775.x.

Fartmann, T. (2004): Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales: Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. — Abhandlungen aus dem Westfälischen Museum für Naturkunde, Münster, **66** (1): 1–256.

Fric, Z. F., Wahlberg, N., Pech, P., & Zrzavý, J. (2007): Phylogeny and classification of the *Phengaris-Maculinea* clade (Lepidoptera: Lycaenidae): total evidence and phylogenetic species concepts. — Systematic Entomology, London, **32** (3): 558–567. — DOI: 10.1111/j.1365-3113.2007.00387.x.

Fürst, M. A., & Nash, D. R. (2010): Hostant independent oviposition in the parasitic butterfly *Maculinea alcon*. — Biology letters, St. Albans, **6** (2): 174–176. — DOI: 10.1098/rsbl. 2009.0730.

GIS-Steiermark (2023): A17 Landes- und Regionalentwicklung, Referat Statistik und Geoinformation. — Basiskarte (URL: gis. stmk.gv.at/wgportal/atlasmobile/map/Basiskarten/Basiskarte), Download 30th September 2023.

Gros, P. (2002): Nachweis von *Maculinea rebeli* (Hirschke, 1904) aus dem Bundesland Salzburg (Lepidoptera: Lycaenidae). — Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen, Wien, **54:** 15–22.

Grünes Handwerk Kammerer & Ressel OG (2022): Managementplan für das ESG Nr. 48 Weizklamm. — Botanik. — Stattegg, 32 S.

Habeler, H. (2008): Die subalpin-alpinen Lebensräume des Bläulings *Maculinea rebeli* (Hirschke, 1904) in den Ostalpen (Lepidoptera, Lycaenidae). — Joannea Zoologie, Graz, **10:** 143–146.

Hinojosa, J. C., Montiel-Pantoja, C., Sanjurjo-Franch, M., Martínez-Pérez, I., Lee, K. M., Mutanen, M., & Vila, R. (2023): Diversification linked to larval hostplant in the butterfly *Eumedonia eumedon*. — Molecular Ecology, Hoboken (New Jersey), **32:** 182–197.

Hovestadt, T., & Nowicki, P. (2008): Investigating movement within irregularly shaped patches: Analysis of mark-release-recapture data using randomization procedures. — Israel Journal of Ecology & Evolution, Leiden, **54** (1): 137–154. — DOI: 10.1560/IJEE.54.1.137.

Jäger, E. J. (ed). (2017): Rothmaler — Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband. 21st ed. — Berlin, Heidelberg (Springer, Spektrum), 934.

Jutzeler, D. (1988): Fund von *Maculinea rebeli* (Hirschke, 1904) im Glarnerland (Lepidoptera, Lycaenidae). — Mitteilungen der Entomologischen Gesellschaft Basel, Basel, **38:** 124–125.

—— (1989): *Maculinea rebeli* (Hirschke). Ein Raupenfund im Glarnerland (Lepidoptera: Lycaenidae). — Mitteilungen der Entomologischen Gesellschaft Basel, Basel, **39:** 92–93.

Kolev, Z. (2002): The species of *Maculinea* van Eecke, 1915 in Bulgaria: Distribution, state of knowledge and conservation status (Lycaenidae). — Nota lepidopterologica, Halle/Saale, **25** (2/3): 177–190.

Kőrösi, A., Örvössy, N., Batáry, P., Kövér, S., & Peregovits, L. (2008): Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies. — Oecologia, Berlin, **156** (2): 455–464. — DOI: 10.1007/ s00442-008-0986-1.

Koubínová, D., Dincă, V., Dapporto, L., Vodă, R., Suchan, T., Vila, R., & Alvarez, N. (2017): Genomics of extreme ecological specialists: multiple convergent evolution but no genetic divergence between ecotypes of *Maculinea alcon* butterflies. — Scientific reports, London, **7** (1): 13752. — DOI: 10.1038/s41598-017-12938-8.

Krismann, A. (2000): Zum Eiablageverhalten von *Maculinea alcon* ((D. & S.), 1775) an *Gentiana pneumonanthe* und *Gentiana asclepiadea*. — Pp. 103–110 *in:* Settele, J., & Kleinewietfeld, S. (ed.): Populationsökologische Studien an Tagfaltern, Band **2,** 110 S. — Leipzig.

Kudrna, O., & Fric, Z. F. (2013): On the identity and taxonomic status of *Lycaena alcon rebeli* Hirschke, 1905 — a long story of confusion and ignorance resulting in the fabrication of a "ghost species" (Lepidoptera: Lycaenidae). — Nachrichten des Entomologischen Vereins Apollo, Frankfurt am Main, **34:** 117–124.

Küer, A., & Fartmann, T. (2005): Prominent shoots are preferred: microhabitat preferences of *Maculinea alcon*([Denis & Schiffermüller], 1775) in Northern Germany (Lycaenidae). — Nota lepidopterologica, Dresden, **27:** 309–319.

Maes, D., & van Dyck, H. (2005): Habitat quality and biodiversity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. — Biological Conservation, Amsterdam, **123** (2): 177–187. — DOI: 10.1016/j.biocon.2004.11.005.

——, Vanreusel, W., Talloen, W., & van Dyck, H. (2004): Functional conservation units for the endangered alcon blue butterfly *Maculinea alcon* in Belgium (Lepidoptera: Lycaenidae). — Biological Conservation, Amsterdam, **120** (2): 229–241. — DOI: 10.1016/j.biocon.2004.02.018.

Marktanner, T. (1985): Die Bedeutung des Schwalbenwurzenzians als Futterpflanze von *Maculinea alcon* (Lep.: Lycaenidae) im oberschwäbischen Alpenvorland und die Verbreitung der Lycaenide in diesem Raum. — Entomologische Zeitschrift, Stuttgart, **95:** 257–272.

Meyer-Hozak, C. (2000): Population biology of *Maculinea rebeli* (Lepidoptera: Lycaenidae) on the chalk grasslands of Eastern Westphalia (Germany) and implications for conservation. — Journal of Insect Conservation, Dordrecht, **4** (2): 63–72.

Nash, D. R., Als, T. D., Maile, R., Jones, G. R., & Boomsma, J. J. (2008): A mosaic of chemical coevolution in a large blue butterfly. — Science, Washington D.C., **319** (5859): 88–90. — DOI: 10.1126/science.1149180.

Neve, G., Barascud, B., Hughes, R., Aubert, J., Descimon, H., Lebrun, P., & Baguette, M. (1996): Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). — Journal of Applied Ecology, London, **33** (1): 14–22.

Nowicki, P., Deoniziak, K., Dziekańska, I., Kostro-Ambroziak, A., Plazio, E., Rutkowski, R., & Sielezniew, M. (2019): What keeps 'living dead' alive: demography of a small and isolated population of *Maculinea* (= *Phengaris*) *alcon*. — Journal of Insect Conservation, London, **23** (2): 201–210. — DOI: 10.1007/s10841-018-0078-4.

——, Witek, M., Skórka, P., & Woyciechowski, M. (2005): Oviposition patterns in the myrmecophilous butterfly *Maculinea alcon* Denis & Schiffermüller (Lepidoptera: Lycaenidae) in relation to characteristics of foodplants and presence of ant hosts. — Polish Journal of Ecology, Warszawa, **53** (3): 409–417.

Oberdorfer, E. (2001): Pflanzensoziologische Exkursionsflora: Für Deutschland und angrenzende Gebiete. 8. Auflage. —Stuttgart (Eugen Ulmer), 1056 pp.

Osváth-Ferencz, M., Czekes, Z., Molnár, G., Markó, B., Vizauer, T.-C., Rákosy, L., & Nowicki, P. (2016): Adult population ecology and egg laying strategy in the '*cruciata*' ecotype of the endangered butterfly *Maculinea alcon* (Lepidoptera: Lycaenidae). — Journal of Insect Conservation, Basel, **20** (2): 255–264. — DOI: 10.1007/s10841-016-9858-x.

Pech, P., Fric, Z. F., & Konvička, M. (2007): Species-specificity of the *Phengaris* (*Maculinea*)-*Myrmica* host system: Fact or myth? (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae). — Sociobiology, Chico (California), **50**: 983–1003.

——, ——, ——, & Zrzavý, J. (2004): Phylogeny of *Maculinea* blues (Lepidoptera: Lycaenidae) based on morphological and ecological characters: evolution of parasitic myrmecophily. — Cladistics: the International Journal of the Willi Hennig Society, New York, **20** (4): 362–375. — DOI: 10.1111/j.1096-0031.2004.00031.x.

Pecsenye, K., Bereczki, J., Varga, Z., Peregovits, L., Tóth, A., & Tihanyi, B. (2007): Genetic differentiation among the *Maculinea* species (Lepidoptera: Lycaenidae) in eastern Central Europe. — Biological Journal of the Linnean Society, London, **91:** 11–21.

Radchuk, V., WallisDeVries, M. F., & Schtickzelle, N. (2012): Spatially and financially explicit population viability analysis of *Maculinea alcon* in The Netherlands. — PloS one, San Francisco, **7** (6): e38684. — DOI: 10.1371/journal.pone. 0038684.

Rundle, H. D., & Nosil, P. (2005): Ecological speciation. — Ecology Letters, Oxford, **8** (3): 336–352. — DOI: 10.1111/j.1461-0248.2004.00715.x.

Sala, M., Casacci, L. P., Balletto, E., Bonelli, S., & Barbero, F. (2014): Variation in butterfly larval acoustics as a strategy to infiltrate and exploit host ant colony resources. — PloS one, **9** (4): e94341. — DOI: 10.1371/journal.pone.0094341.

Schönlaub, H. P. (with a contribution by S. Scharbert)(1979): Das Paläozoikum in Österreich: Verbreitung, Stratigraphie, Korrelation, Entwicklung und Paläogeographie nicht-metamorpher und metamorpher Abfolgen. Band **33.** — Geologische Bundesanstalt, Wien, 124 pp.

Schönrogge, K., Wardlaw, J. C., Thomas, J. A., & Elmes, G. W. (2000): Polymorphic growth rates in myrmecophilous insects. — Proceedings of the Royal Society of London. Series B: Biological Sciences, London, **267** (1445): 771–777. — DOI: 10.1098/rspb.2000.1070.

Settele, J., Kühn, E. & Thomas, J. A. (eds.). (2005): Studies on the ecology and conservation of butterflies in Europe.: Species ecology along a European gradient: *Maculinea* butterflies as a model. 2nd ed. — Sofia (Pensoft Publishing), 289 S.

——, Steiner, R., Reinhardt, R., Feldmann, R., & Hermann, G. (2015): Schmetterlinge: Die Tagfalter Deutschlands. 3., aktualisierte Aufl. – Stuttgart (Hohenheim) (Ulmer), 256 pp.

Sielezniew, M., Rutkowski, R., Ponikwicka-Tyszko, D., Ratkiewicz, M., Dziekańska, I., & Švitra, G. (2012): Differences in genetic variability between two ecotypes of the endangered myrmecophilous butterfly *Phengaris* (=*Maculinea*) *alcon* - the setting of conservation priorities. – Insect Conservation and Diversity, St. Albans, **5** (3): 223–236. – DOI: 10.1111/ j.1752-4598.2011.00163.x.

Skórka, P., Nowicki, P., Kudłek, J., Pepkowska, A., Śliwińska, E. B., Witek, M., Settele, J., & Woyciechowski, M. (2013): Movements and flight morphology in the endangered large blue butterflies. – Central European Journal of Biology, London, **8** (7): 662–669. – DOI: 10.2478/s11535-013-0190-5.

Tartally, A., Kelager, A., Fürst, M. A., & Nash, D. R. (2016): Host-plant use drives genetic differentiation in syntopic populations of *Maculinea alcon*. – PeerJ, London, **4:** e1865. – DOI: 10.7717/ peerj.1865.

——, Koschuh, A., & Varga, Z. (2014): The re-discovered *Maculinea rebeli* (Hirschke, 1904): Host ant usage, parasitoid and initial foodplant around the type locality with taxonomical aspects (Lepidoptera, Lycaenidae). – ZooKeys, Sofia, **406:** 25–40. – DOI: 10.3897/zookeys.406.7124.

——, Thomas, J. A., Anton, C., Balletto, E., Barbero, F., Bonelli, S., Bräu, M., Casacci, L. P., Csősz, S., Czekes, Z., Dolek, M., Dziekańska, I., Elmes, G. W., Fürst, M. A., Glinka, U., Hochberg, M. E., Höttinger, H., Hula, V., Maes, D., Munguira, M. L., Musche, M., Nielsen, P. S., Nowicki, P., Oliveira, P. S., Peregovits, L., Ritter, S., Schlick-Steiner, B. C., Settele, J., Sielezniew, M., Simcox, D. J., Stankiewicz, A. M., Steiner, F. M., Švitra, G., Ugelvig, L. V., van Dyck, H., Varga, Z., Witek, M., Woyciechowski, M., Wynhoff, I., & Nash, D. R. (2019): Patterns of host use by brood parasitic *Maculinea* butterflies across Europe. – Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, London, **374:** 20180202. – DOI: dx.doi. org/10.1098/rstb.2018.0202.

Tessier, M. (2015): Inventaire de l'Azuré des mouillères *Maculinea alcon* (Denis & Schiffermüller, 1775) (Lepidoptera Lycaenidae) en Ariège. I. Résultats préliminaires. – Les Bulletins de la Société Linnéenne de Bordeaux, Bordeaux, **43:** 205–212.

Thomas, J. A. (1980): Why did the large blue become extinct in Britain? – Oryx, Cambridge, **15** (3): 243–247. – DOI: 10.1017/ S0030605300024625.

—— (1995): The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. – Pp. 180–196 *in:* Pullin, A. S. (ed.): Ecology and conservation of butterflies. – Dordrecht (Springer Netherlands), 363 S.

——, & Elmes, G. W. (1998): Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through trophallaxis rather than by predation. – Ecological Entomology, Oxford, **23** (4): 457–464. – DOI: 10.1046/j.1365-2311.1998.00153.x.

——, & —— (2001): Food-plant niche selection rather than the presence of ant nests explains oviposition patterns in the myrmecophilous butterfly genus *Maculinea*. – Proceedings of the Royal Society of London. Series B: Biological Sciences, London, **268** (1466): 471–477. – DOI: 10.1098/ rspb.2000.1398.

——, ——, & Wardlaw, J. C. (1998): Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. – Proceedings of the Royal Society of London. Series B: Biological Sciences, London, **265** (1408): 1895–1901. – DOI: 10.1098/rspb.1998.0517.

——, ——, ——, & Woyciechowski, M. (1989): Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. – Oecologia, Berlin, **79:** 452–457.

——, Munguira, M. L., Martin, J., & Elmes, G. W. (1991): Basal hatching by *Maculinea* butterfly eggs: a consequence of advanced myrmecophily? – Biological Journal of the Linnean Society, London, **44** (2): 175–184. – DOI: 10.1111/ j.1095-8312.1991. tb00615.x.

——, & Settele, J. (2004): Butterfly mimics of ants. – Nature, London, **432** (7015): 283–284.

——, Simcox, D. J., & Clarke, R. T. (2009): Successful conservation of a threatened *Maculinea* butterfly. – Science, Washington D.C., **325:** 80–83. – DOI: 10.1126/science. 1175726.

——, & Wardlaw, J. C. (1992): The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. – Oecologia, Berlin, **91:** 101–109.

Tilmon, K. J. (2008): Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects. – Berkeley (Univ. of California Press), 341 pp.

Timuş, N., Craioveanu, C., Sitaru, C., Rus, A., & Rákosy, L. (2013): Differences in adult phenology, demography, mobility and distribution in two syntopic ecotypes of *Maculinea alcon* (*cruciata* vs. *pneumonanthe*)(Lepidoptera: Lycaenidae) from Transilvania (Romania). – Entomologica Romanica, Cluj, **18:** 21–30.

Ugelvig, L. V., Vila, R., Pierce, N. E., & Nash, D. R. (2011): A phylogenetic revision of the *Glaucopsyche* section (Lepidoptera: Lycaenidae), with special focus on the *Phengaris-Maculinea* clade. – Molecular phylogenetics and evolution, Amsterdam, **61** (1): 237–243. – DOI: 10.1016/j.ympev. 2011.05.016.

van Dyck, H., & Regniers, S. (2010): Egg spreading in the ant-parasitic butterfly, *Maculinea alcon:* from individual behaviour to egg distribution pattern. – Animal Behaviour, Amsterdam, **80** (4): 621–627. – DOI: 10.1016/j.anbehav. 2010.06.021.

van Swaay, C., Cuttelod, A., Collins, S., Maes, D., Munguira, M. L., Šašić, M., Settele, J., Verovnik, R., Verstrael, T., Warren, M., Wiemers, M., & Wynhoff, I. (2010): European Red List of Butterflies. – Publications Office of the European Union, Luxembourg, 47 pp.

——, Maes, D., Collins, S., Munguira, M. L., Šašić, M., Settele, J., Verovnik, R., Warren, M., Wiemers, M., Wynhoff, I., & Cuttelod, A. (2011): Applying IUCN criteria to invertebrates: How red is the Red List of European butterflies? – Biological Conservation, Amsterdam, **144** (1): 470–478. – DOI: 10.1016/j. biocon.2010.09.034.

Vilbas, M., Esperk, T., Edovald, T., Kaasik, A., & Teder, T. (2016): Oviposition site selection of the alcon blue butterfly at the northern range margin. – Journal of Insect Conservation, Basel, **20** (6): 1059–1067. – DOI: 10.1007/s10841-016-9939-x.

WallisDeVries, M. F. (2004): A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. – Conservation Biology, Washington D.C., **18** (2): 489–499. – DOI: 10.1111/j.1523-1739.2004.00336.x.

Witek, M., Śliwińska, E. B., Skórka, P., Nowicki, P., Wantuch, M., Vrabec, V., Settele, J., & Woyciechowski, M. (2008): Host ant specificity of large blue butterflies Phengaris (*Maculinea*) (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe. – European Journal of Entomology, Branisovska, **105** (5): 871–877.

Wynhoff, I. (1998): Lessons from the reintroduction of *Maculinea teleius* and *M. nausithous* in the Netherlands. – Journal of Insect Conservation, New York, **2** (1): 47–57. – DOI: 10.1023/A:1009692723056.

——, Bakker, R. B., Oteman, B., Arnaldo, P. S., & van Langevelde, F. (2015): *Phengaris* (*Maculinea*) *alcon* butterflies deposit their eggs on tall plants with many large buds in the vicinity of *Myrmica* ants. – Insect Conservation and Diversity, St. Albans, **8** (2): 177–188. – DOI: 10.1111/icad.12100.

Received: 18./22. ii. 2024

© Entomologischer Verein Apollo e. V., Frankfurt am Main, Oktober 2024 ISSN 0723-9912