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ECOLOGICAL REQUIREMENTS AND FEATURES ADAPTING THE KARINTHIAN MOUNTAIN GRASSHOPPER *MIRAMELLA CARINTHIACA* TO LIVE IN MEADOWS AT THE ALPINE TREELINE

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Abstract – The Karinthian Mountain Grasshopper, *Miramella carinthiaca* (Obenberger, 1926) (Orthoptera: Catantopidae), was investigated at the alpine treeline in the Seckau Alps (Styria, Austria). Field studies show that because they are flightless, these grasshoppers cannot easily move to a new habitat to escape harmful environmental influences. The readiness to feed on non-preferred plants in addition to preferred plants seems to be an adaptation in this case. Feeding experiments showed that the fresh leaves of more than thirty grass, wildflower and woody plant species in the habitat can serve as food sources. It is critical for *M. carinthiaca* females to find oviposition sites in open patches of earth surrounded by the fresh leaves of evergreen plants that provide a food source for early nymphs. At the treeline, *M. carinthiaca* shares the habitat with *Chorthippus* species, *Omocestus viridulus*, *Euthystira brachyptera* and *Gomphocerus sibiricus*. The ecological niche of the latter seems similar to that of *M. carinthiaca*.

Key words: *Miramella carinthiaca*, alpine treeline, habitat, oviposition site, food plants

Izvleček – EKOLOŠKE ZAHTEVE IN ZNAČILNOSTI ALPSKE KOBILICE *MIRAMELLA CARINTHIACA* NA TRAVNIKIH OB DREVESNI MEJI

Raziskovali smo alpsko kobilico vrste *Miramella carinthiaca* (Obenberger, 1926) (Orthoptera: Catantopidae) ob drevesni meji na območju Seckauskih Alp (Štajerska, Avstrija). Ker je kobilica brez kril, se ne more enostavno preseliti v nov habitat, da bi ubežala pred neugodnimi okoljskimi razmerami. Na osnovi terenskih opazovanj sklepamo, da je pripravljenost, da se kobilica hrani z rastlinami, ki jih po navadi ne izbira, adaptacija na omenjene razmere. V prehranjevalnih poskusih smo ugotovili,

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da vir njene hrane predstavljajo listi več kot trideset rastlinskih vrst – od trav do lesnatih rastlin. Za kobilico *M. carinthiaca* je odločilno, da izbira mesta za leženje jajčec na zaplatah zemlje, ki jih obdajajo listi zimzelenih rastlin, ki predstavljajo vir hrane za izlegle nimfe. Ob drevesni meji si kobilica *M. carinthiaca* deli habitat še z vrstami *Chorthippus* sp., *Omocestus viridulus*, *Euthystira brachyptera* in *Gomphocerus sibiricus*. Videti je, da je ekološka niša slednje vrste podobna kot za *M. carinthiaca*.

KLJUČNE BESEDE: *Miramella carinthiaca*, alpska drevesna meja, habitat, lokacija ovipozicije, hranilne rastline

Introduction

Species and subspecies of the genus *Miramella* (Catantopidae; see BELLMANN, 2006) are found in the Pyrenees, Western and Eastern Alps, Julian and Karavanke Alps, Slavonian Mountains, Carpathians, Balkan Mountains and other European mountainous regions such as the higher altitudes of the Black Forest, Bavarian Forest and Bohemian Forest (HARZ, 1957, 1975, 1982; NADIG, 1989; PILS, 1992; DETZEL, 1995, 1998; KÖHLER & INGRISCH, 1998; KÖHLER & al., 1999; ILLICH & WINDING, 1999; ILLICH, 2003; NAGY, 2003; ZECHNER & al., 2005; BELLMANN, 2006; IORGU & al., 2008; HELFERT & KREHAN, 2009; SZÖVÉNYI & PUSKÁS, 2012; IMIELA & al., 2016; KENYERES & al., 2017; ZUNA-KRATKY & al., 2017). These grasshoppers occur in submontane, montane, subalpine and alpine habitats in large contiguous areas as well as in fragmented and even completely isolated small areas. *Miramella* habitats are located at altitudes up to a maximum of 2800 m (in the Swiss Alps). During excursions over a number of years at and above the alpine treeline in the Seckau Alps (Styria, Austria) (Figure 1), I have observed *Miramella* grasshoppers in pastures and meadows between 1600 and 2100 m (K. KRAL, unpubl. obs.). It should be noted that in the Seckau Alps, in addition to *M. alpina*, *M. carinthiaca* can also be present, and both can be overlapping, with possible intergrades (FORSTHUBER & ZACHERL, 2005; ZUNA-KRATKY & al., 2017; T. ZUNA-KRATKY, pers. comm.). This mountain range, with a maximum altitude of 2417 m, is located south of the Liesing and Palten valleys and

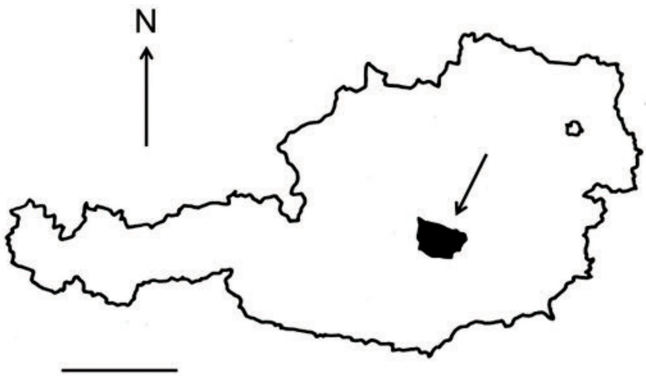

Fig. 1: Map of Austria showing the location of the Seckau Alps (arrow). Scale bar: 100 km.

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Fig. 2: Photograph illustrating alpine meadows in the Seckau Alps as a typical habitat of *M. carinthiaca*. Note that the alpine meadows are separated from one another by areas of mountain pine and scree. The picture was taken in mid-July.

north of the Upper Mur valley. It consists mainly of granite and granite gneisses surrounded by para-gneisses and biotite gneisses (Metz, 1976). Toward the Upper Mur valley, the climate is characterised by continental influences, with cold winters, relatively warm summers and lower precipitation (~800 mm per year) than in the western part of the Niedere Tauern. The *Miramella* grasshoppers observed seemed to prefer open areas that had rather wet soils with distinctive wildflowers and/or low woody plants, stones and patches of bare earth. The grasshoppers often occurred in sites that were separated by areas of mountain pine and scree (see Figure 2). The aim of the present study was to obtain more detailed information about such habitat conditions and how *Miramella carinthiaca* adapts to them in light of its restricted mobility due to flightlessness.

Material and methods

The grasshoppers investigated here were clearly determined to be *Miramella carinthiaca*, on the basis of a morphological analysis of the male genitals. The study was carried out in the most easterly part of the Seckau Alps (47° 19' 18" N / 14° 48' 11" E) in the year 2017. The study site was located on a slope facing southeast at about 1710 m, at the treeline formed by mountain spruce (*Picea abies*), larch trees

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(*Larix decidua*), mountain pine (*Pinus mugo*) and juniper bushes (*Juniperus communis* subsp. *nana*). The study site was monitored from the beginning of May to the middle of September. The plant species were identified with the aid of morphological keys and the advice of botanists (e.g., Schauer & Caspari, 1975; Angerer & Muer, 2004; I. Paušič, pers. comm.). Plant flowers and fruits facilitated species determination. As a measure of *M. carinthiaca* population density, the number of adult females was calculated by direct observation, or by netting within an area of 20 x 15 m. In addition, the presence of other grasshopper species was considered. Species identification was performed with the aid of sonograms, and structural and optical features of the body (Bellmann, 2004, 2006).

For *M. carinthiaca*, the site and time of emergence, development and maturity were recorded. Particular attention was focused on the external appearance and body size. Body weight was measured with a touch screen pocket scale (G&G GmbH, Neuss, Germany). Photographs of nymphs and adults in their natural environment were taken with a Nikon D90 digital camera equipped with the macro lenses AF Micro Nikkor 60 mm, 1:2.8 D (Chiyoda, Tokyo, Japan).

Feeding experiments were carried out. Direct observations in the field were used to record how many early instar *M. carinthiaca* nymphs were found on what plant species. Fresh leaves of the preferred plants were then placed in a plastic tube (4.6 x 10 cm) together with a specimen of an early instar nymph in order to study the feeding behaviour. Each plant species was tested with three specimens.

The acceptability of plants in the habitat as food was systematically investigated for adult females in the years 2017 and 2018. For this purpose, freshly caught *M. carinthiaca* females were kept in a laboratory room (at 16 to 20°C) in the nearby village of Seckau. During the first two days no food was provided. In this starvation phase, a lack of further defecation indicated that the gut was empty. This was always the case after two days. The *M. carinthiaca* females were then placed singly in aerated transparent plastic feeding chambers (18 x 12 x 7 cm) with absorbent paper on the bottom. In each case, one plant species from the study site was provided. Each feeding experiment lasted two days, to give the grasshoppers the opportunity to adjust to the plants offered. All of the plants used for the feeding experiments were potted, so that fresh leaves could be provided for the duration of the trials. Due to the limited number of females, each specimen was tested with three different plant species selected at random (with the exception of one specimen that was tested with two plant species). As far as possible, grasses, wildflowers and woody plants were mixed, and the plants were offered in random order. For each plant species, three specimens were tested. After each trial the females were kept for another two days without food, for fitness control, and to prepare for subsequent trials if necessary. It was recorded only whether the plants or parts of them were ingested within two days. This was indicated by a reduction in or damage to the plant material, as well as by the production of fecal pellets. The amount of food consumed by the grasshoppers was not assessed, because previous feeding behaviour in the field could not be taken into account (Freeland, 1975).

Results

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At the study site the meadow was rich in wildflowers, low woody plants and grasses, which often formed tussocks (Table 1). There were pebbles, small exposed rocks, traces of juniper roots, and patches of bare earth on flat or uneven ground surrounded mainly by *Vaccinium* species and *Geum montanum* (see Figure 3). At the end of July, the estimated density of adult females was 0.13/m².

M. carinthiaca females used patches of moist bare earth as oviposition sites. The pH values measured at various possible oviposition sites ranged from 4.8 to 6.6. Following overwintering of the egg pods, early instar nymphs could be observed in May. The first adult females and males appeared toward the end of June and in the first half of July. Postembryonic development comprised five nymph instars in both genders. Adults could be distinguished from nymphs in the last instar via the complete overlap of the very short brownish wings (absolutely unsuited to flight). This is illustrated in images (d) and (e) in Figure 4. During postembryonic development, female nymphs were already larger and heavier than male nymphs (e.g. in mid-instar, female: body weight 0.20 g, body length 16.5 mm; male: body weight 0.08 g, body length 12 mm).

Fig. 3: View of part of the meadow at the study site in the second half of July. The study site provides patches of bare earth for oviposition and exposed stones for basking, as well as wildflowers and woody plants. The green colour of their leaves ensures camouflage for *M. carinthiaca* throughout the season.

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Table 1: Plant species from the study site at the alpine treeline accepted as food by female *M. carinthiaca* adults in the feeding experiments

Scientific name	Common name
Poaceae	**Sweet grasses**
Agrostis sp.	Bent grass
Agrostis stolonifera L.	Creeping bent grass
Festuca sp.	Fescues
Phleum rhaeticum (Humphries) Rauschert	Alpine timothy grass
Phleum sp.	Timothy grass
Sesleria sp.	Blue grass
Cyperaceae	**Sedges**
Carex caryophyllea Latourr.	Spring sedge
Carex curvula All.	Curved sedge
Juncaceae	**Rushes**
Luzula sp.	Woodrush
Luzula multiflora L.	Common woodrush
Asteraceae	**Composite plant family**
Achillea millefolium agg.	Common yarrow
Antennaria dioica (L.) Gaertn.	Mountain everlasting
Arnica montana L.	Mountain arnica
Crepsis pontana (L.) Dalla Torre	Mountain hawksbeard
Homogyne alpina (L.) Cass.	Alpine coltsfoot
Ericaceae	**Heather plant family**
Calluna vulgaris (L.) Hull	Common heather
Loiseleuria procumbens (L.) Desv.	Trailing azalea
Vaccinium myrtillus L.	European blueberry
Vaccinium uliginosum L.	Bog bilberry
Vaccinium vitis-idaea L.	Lingonberry, cowberry
Campanulaceae	**Bellflower family**
Campanula scheuchzeri Vill.	Bellflower
Phyteuma sp.	Rampion
Caryophyllaceae	**Pink family**
Cerastium sp.	Mouse-ear chickweed
Rubiaceae	**Bedstraw family**
Galium anisophyllon L.	Bedstraw, gaillet
Gentianaceae	**Gentian family**
Gentiana acaulis L.	Stemless gentian
Rosaceae	**Rose family**
Geum montanum L.	Alpine avens
Potentilla aurea L.	Dwarf cinquefoil
Orchidaceae	**Orchid family**
Gymnadenia conopsea (L.) R.Br.	Fragrant orchid, marsh fragrant orchid
Orobanchaceae	**Broomrape family**
Pedicularis sp.	Lousewort
Primulaceae	**Primrose family**
Primula villosa Wulfen	Mountain primrose
Ranunculaceae	**Buttercup family**
Pulsatilla alpina (L.) Delarbre	Alpine anemone
Ranunculus montanus Willd.	Buttercup
Lamiaceae	**Labiate family**
Thymus pulegioides agg.	Broad-leaved thyme
Plantaginaceae	**Plantain family**
Veronica chamaedrys L.	Germander speedwell

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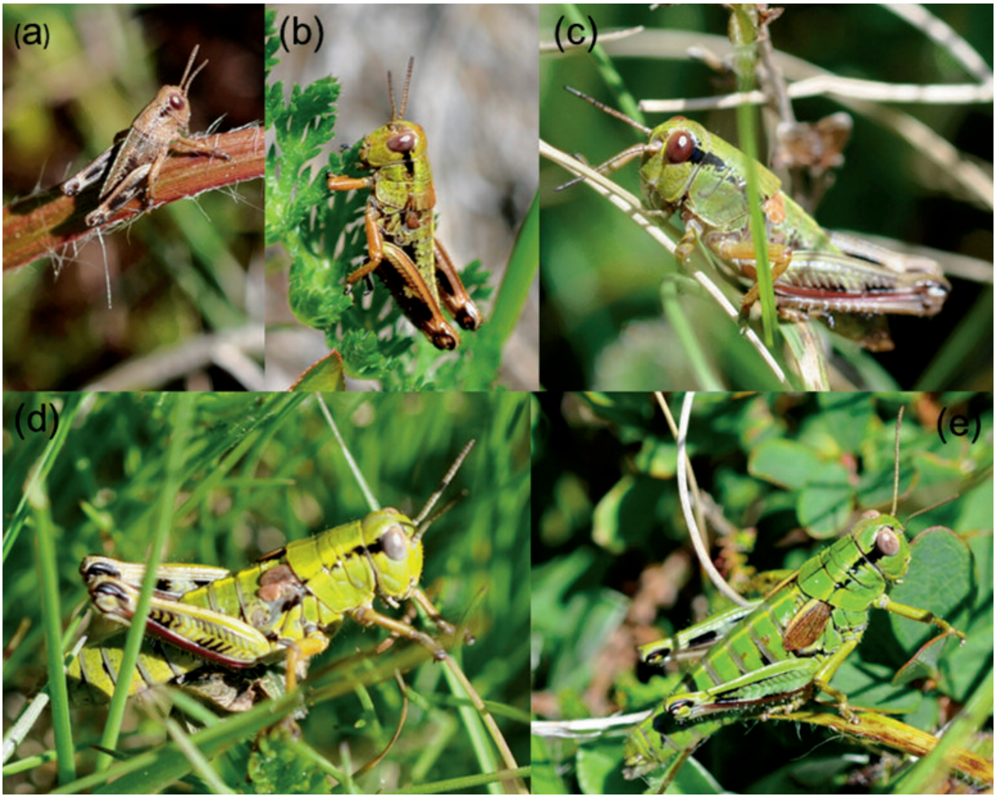

Fig. 4: Body colour and patterns in *M. carinthiaca* females during postembryonic development. Different individuals were photographed under similar lighting conditions. Images (a, b) early instar nymphs: body length 5 mm and 10 mm; (c) mid-instar nymph: body length 16 mm; (d) late instar nymph: body length 21 mm; and (e) adult stage: body length 24 mm.

In the first instar, *M. carinthiaca* nymphs appeared brown and dark grey, and in the case of males often almost black. In the next instar, the nymphs were usually yellow-green, however with parts of the body such as the legs still light to dark brown. The middle instar nymphs were green, and this was also the case in the later stages, including the adult stage. However, the shade of green of the body colour varied between specimens of the same stage and between specimens of different stages. The early instars had a distinct brown to black body pattern (Figure 4). According to the literature, this is caused by melanisation of the exocuticle (e.g., Sugumaran & Barek, 2016). However, in male nymphs the pattern was more extensive and more evident, with the result that the male nymphs generally appeared darker than the female nymphs. This was also the case with later nymph instars and the adult stage. In Figure 5, melanin pigment can be seen in the last exuviae of a *M. carinthiaca* female and male.

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Observation records of forty-four early instar *M. carinthiaca* nymphs in the field (see Figure 4) show that 45% of them were located on leaves of *G. montanum*. These leaves often had recognisable traces of feeding. The second most frequent location of early instar nymphs was on leaves of *Vaccinium vitis-idaea* (see Table 2). Feeding experiments performed with nymphs in the field during the day showed that in addition to *G. montanum* and *V. vitis-idaea*, the less frequently occupied plants *Potentilla aurea*, *Homogyne alpina* and *Achillea millefolium* were also accepted as food. It was noticeable that the leaves of *G. montanum* and *H. alpina* in particular were consumed readily by the nymphs. Grass leaves were eaten only sparingly, after the nymphs had been kept in a feeding tube for a further day. Systematic feeding experiments with adult *M. carinthiaca* females in the laboratory showed that the fresh leaves of thirty-four of the thirty-five plant species from the habitat that were offered were accepted as a food source if alternatives were not available (see Table 1). Only the pyramidal bugle *Ajuga pyramidalis* (Lamiaceae) was not eaten. Potential long-term health impacts on the grasshoppers resulting from the use of these different plant species as food could not be addressed here. Since the range of available plant species becomes more extensive later in the spring, the adults may feed on a greater variety of plant species than the nymphs do.

Five other grasshopper species (Acrididae) were found at the study site: the flying *Chorthippus biguttulus* L.; *C. dorsatus* Zett.; *Omocestus viridulus* L.; *C. parallelus* Zett., with shortened wings in females; and the emerald green *Euthystira brachyptera* Ocsk., with shortened wings in males and females. Of these, the most frequent species were *O. viridulus* and *C. parallelus*. All of these species were found mostly in grass up to 50 cm in height. *Gomphocerus sibiricus* L., capable of flight, was observed mostly in low vegetation and on patches of bare earth. In addition, *Metrioptera brachyptera* L., a member of the Tettigonioidea, was occasionally found near dwarf shrubs of *J. communis* subsp. *nana*, although only at the end of August and in September. In the case of the different *Chorthippus* species and *O. viridulus*, early instar nymphs could be observed at the end of May. *G. sibiricus* appeared later and was present at the study site only until early August.

Table 2: Plants on which early instar *M. carinthiaca* nymphs were located

Plant species	Number of early instar nymphs
Geum montanum	20
Vaccinium vitis-idaea	12
Potentilla aurea	6
Homogyne alpina	3
Achillea millefolium	1
Luzula multiflora	1
Sesleria sp.	1

Discussion

The meadow at the alpine treeline provides *M. carinthiaca* with a suitable environment for oviposition and foraging purposes. *G. montanum* and *V. vitis-idaea* appear to be among the most important food sources. These plants are usually found

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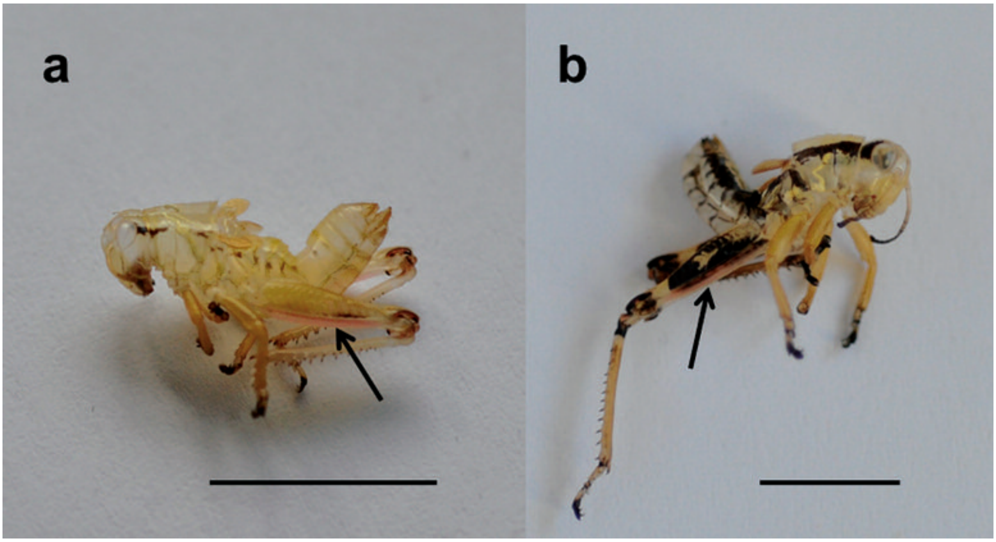

Fig. 5: Last exuviae of (a) female and (b) male *M. carinthiaca*. Scale bars: 12 mm and 6 mm, respectively. Moulting took place within one day after the nymphs had been caught in their natural environment. Note brown to black melanisation on the head, body and legs, as well as reddish melanisation on the underside of the hind femurs (indicated by arrows).

where *M. carinthiaca* is present, and the grasshoppers were frequently found on their leaves and could be observed feeding. It should be noted that this is also the case in alpine meadows with poor vegetation at higher elevations, 1900 to 2100 m above sea level. The reliability of *G. montanum* and *V. vitis-idaea* as food sources is aided by the fact that these plants are particularly stress-resistant, as shown by various studies (Manuel & al., 1999; Aubert & al., 2004; Glass & al., 2005; Saarinen & Lundell, 2010). These plants can tolerate the low temperatures and high levels of irradiation (including UV irradiation) that occur when the snow melts. They are also very robust with regard to drought conditions that can occur during summer heat waves on terrain that is exposed to the sun. Further evidence that *Vaccinium* species may be an important food source has been found by Asshoff & Hättenschwiler (2005), in the case of *M. alpina* living at the alpine treeline in the Swiss Alps. These authors clearly show that atmospheric changes such as increased carbon dioxide can have a negative effect on the nutritional quality of *V. myrtillus* and *V. uliginosum* leaves, and hence on the growth rate of *M. alpina*. In this connection, the willingness of early nymphs to eat the leaves of the alpine coltsfoot *H. alpina*, a robust plant with overwintering green leaves that is well adapted to alpine environments (Streb & al., 1998; Lütz & al., 2005), should also be mentioned. In addition, the importance of the role of evergreen plants in providing camouflage for the green grasshoppers is not to be underestimated. However, after snowmelt, when the whole habitat appears more brown than green the brown early nymphs may be better protected from predators.

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The feeding experiments in the laboratory show that, if necessary, female *M. carinthiaca* adults can accept the leaves of a relatively large number of plant species of various families growing in the habitat as food sources (see Table 1). The leaves consumed in the experiments have a wide range of tissue hardness and toughness, from needle-like to thick and fleshy. The grasshoppers are clearly able to use their strong mandibles to overcome the physical defences of the plants (Kuřavová, 2015). This robust feeding behaviour may be a necessary adaptation in cases where the preferred plants lose their nutritional quality (see above, Asshoff & Hättenschwiler, 2005) or are unavailable. Plants which are rejected as a food source may be inedible or harmful (Bernays & Chapman, 2000). Thus, it may be that *Ajuga pyramidalis* is avoided because this plant contains phytoecdysones which can disturb the hormone-controlled moulting of insect larvae (Anufrieva & al., 1995; Chaubey, 2018). It was interesting to observe that the *M. carinthiaca* females touched the leaf surface of *A. pyramidalis* with their mouthparts without biting it, presumably to evaluate the quality of the food via external mechanical and/or chemical sensory information. However, the female *M. carinthiaca* adults did not reject the leaves of *Thymus pulegioides* as food, although in the case of the herbivorous bush cricket *Leptophyes punctatissima* it has been found that monoterpenes of the common thyme plant *Thymus vulgaris* can deter feeding (Linhart & Thompson, 1999). In *M. carinthiaca*, a possible reason for terpene tolerance could be good body condition, perhaps even with detoxification capability (see Reid & Purcell, 2011). However, in this study it was not possible to determine the long-term health effects on the grasshoppers that might result from feeding on such plants with secondary compounds as well as other non-preferred plants. Polyphagous behaviour similar to that of *M. carinthiaca*, with a preference for certain plant species, is also described in the case of *M. alpina* by Hägele & Rowell-Rahier (1999; see also Ibanez & al., 2013). Food selection experiments with the grass-feeding grasshopper *O. viridulus* conducted by Berner & al. (2005) suggest that *O. viridulus* can compensate for the low protein content of grass via selective feeding on grasses with contrasting protein content. In this way, the grasshoppers can balance their intake of protein and energy. It was not possible to investigate individual feeding behaviour in the field within the *M. carinthiaca* population. What remains to be addressed is the specific basis upon which the grasshoppers recognize a plant as suitable food.

Finally, the question arises concerning the role played by competition with other grasshopper species that share the habitat of *M. carinthiaca*. My initial impression was that *G. sibiricus* occupies an ecological niche similar to that of *M. carinthiaca*. *G. sibiricus* females also prefer low plants, and in the literature it has been reported that they require open patches of earth for oviposition. However, *M. carinthiaca* eggs seem to need higher humidity levels for successful development, and appear to be more sensitive to dehydration than is the case with *G. sibiricus* eggs (see also Illich & Winding, 1999). This is supported by the fact that I found more *M. carinthiaca* oviposition sites in wetter areas. Nevertheless, it is possible that *M. carinthiaca* may be more xerophilic than *M. alpina* (T. Zuny-Kratky, pers. comm.). I observed that *G. sibiricus* had disappeared from the study site by early August. It should also be noted

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that I was not able to observe *G. sibiricus* at the study site in the years prior to 2017, when the study took place. According to Thomas Zuny-Kratky (pers. comm.), *G. sibiricus* does not often occur together with *M. alpina* or *M. carinthiaca*. Illich & Winding (1999) found that *G. sibiricus* can exhibit wide population fluctuations in the case of unfavourable changes in the environment. Although in this study it was not possible to observe the choice of oviposition site of the three *Chorthippus* species, I know from my experience with *C. parallelus* and *C. brunneus* that they will accept a variety of soil conditions (K. Kral, unpubl. obs.). According to Choudhuri (1958), *C. parallelus* may prefer loose sandy soil. In the case of *O. viridulus* and *E. brachyptera*, which prefer to live in grasses, the females usually oviposit at the base of grass stems (e.g. *Festuca* sp.) and between the leaves of grasses (Reinhardt, 1998; Bellmann, 2006). Overall, it seems that the three *Chorthippus* species, *O. viridulus*, and *E. brachyptera* do not impact *M. carinthiaca* population dynamics significantly with respect to competition for food or oviposition sites. Due to their eurytopic character (K. Kral, unpubl. obs.), these five species can clearly also switch to other areas that are less suitable for *M. carinthiaca*. Throughout the season, I could find only *Miramella* grasshoppers in alpine meadows on ridges exposed to the wind in the eastern part of the Seckau Alps at approximately 1900 to 2000 m above sea level. These meadows were mainly covered with lichens, mosses and carpet-like *Loiseleuria procumbens*, as well as with *P. aurea, G. montanum*, short *Carex curvula* and sparse low *Sesleria* sp., interspersed with open patches of earth (K. Kral, unpubl. obs.). On the windswept ridges, it is evident that the flightlessness of these grasshoppers may be an important morphological adaptation, which prevents flight during strong winds that could cause the grasshoppers to be carried away to unsuitable or even dangerous habitats such as extensive scree areas.

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