

**Contributions to the nutritional ecology of the
endangered grasshopper *Chorthippus pullus*
(Philippi 1830) (Orthoptera: Acrididae)**



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Annik Steiner

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Leiter der Arbeit:

Prof. Dr. Jürg Zettel

Zoologisches Institut, Abteilung Synökologie, Bern

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Abstract

The nutritional ecology of the endangered grasshopper *Chorthippus pullus* (Philippi 1830) (Orthoptera: Acrididae) was investigated at Pfynwald (VS, Switzerland). The aim of this study was to gain more insight into the species' biology and habitat use. The diet composition of *C. pullus* was determined in two different habitats by faecal analysis. The grasshoppers turned out to have a rather wide food spectrum, including dicotyledons, monocotyledons as well as bryophytes. *Astragalus onobrychis* (Fabaceae) was the main food plant at all plots. Spatial and seasonal variation in diet composition was primarily present with regard to the amounts of moss consumed. A comparison of the diet composition and the vegetation cover showed that neither grasses nor forbs were clearly more preferred. The dietary niches of *C. pullus* and *C. vagans*, two syntopic species, overlapped to a great extent but due to an ample food supply, competition is rather unlikely. This study suggests that *C. pullus* is a polyphagous grasshopper species, in spite of the mandibular morphology that indicates a graminivorous diet.

Keywords: *Chorthippus pullus*, Acrididae, Orthoptera, diet composition, food preference, nutritional ecology, spatial variation, seasonal variation, faecal analysis

Zusammenfassung

Die Nahrungsökologie des Kiesbankgrashüpfers *Chorthippus pullus* (Philippi 1830) (Orthoptera: Acrididae), einer bedrohten Heuschreckenart, wurde im Pfynwald (VS, Schweiz) untersucht. Das Ziel dieser Studie war es, die Kenntnisse über Biologie und Habitatnutzung dieser Art zu vertiefen. Die Nahrungszusammensetzung von *C. pullus* wurde in zwei verschiedenen Habitaten mittels Kotanalyse bestimmt. Das Nahrungsspektrum der Heuschrecken erwies sich als sehr breit, sowohl Dikotyle, Monokotyle als auch Bryophyten wurden gefressen. *Astragalus onobrychis* (Fabaceae) machte an allen Standorten den Hauptteil der Nahrung aus. Räumliche und zeitliche Variation in der Nahrungszusammensetzung waren vor allem in Bezug auf die gefressenen Mengen an Moos vorhanden. Beim Vergleich der Nahrungszusammensetzung mit dem Nahrungsangebot wurde keine deutliche Präferenz für Gräser oder Kräuter gefunden. Die Nahrungsnischen von *C. pullus* und *C. vagans*, zwei syntopen Arten, überlappten weitgehend. Aufgrund eines genügend grossen Nahrungsangebots ist eine Konkurrenz aber eher unwahrscheinlich. Aus dieser Studie geht hervor, dass *C. pullus* eine polyphage Heuschreckenart ist. Dies steht im Gegensatz zur Morphologie der Mandibeln, welche auf eine graminivore Ernährung hindeutet.

Keywords: *Chorthippus pullus*, Kiesbankgrashüpfer, Acrididae, Orthoptera, Nahrungszusammensetzung, Nahrungspräferenz, Nahrungsökologie, räumliche Variation, zeitliche Variation, Kotanalyse

1 Introduction

The European grasshopper *Chorthippus pullus* occurs only in small populations in the alpine regions of Central Europe (MAAS ET AL. 2002). Its original habitats are the gravel banks of alpine rivers and sandy heath lands, from which it has disappeared to a great extent (BELL-MANN 1993). Natural habitats of *C. pullus* on the alpine rivers are characterized by periodical floods and the subsequent establishment of pioneer plant species (FOURNIER & MARCHESI 1995). Due to river regulation and the building of hydroelectric stations, such habitats are also becoming rare and therefore this species is critically endangered in Switzerland (THORENS & NADIG 1994), Germany (MAAS ET AL. 2002) and other parts of its range of distribution (SCHÄDLER & STADLER 2000). In Switzerland, today only five regions are known where *C. pullus* occurs (THORENS & NADIG 1997). Thus, more insight into the species' biology would be of great interest in order to conserve the remaining populations and their habitats. One important aspect is certainly nutrition, as nutrition has a huge impact on many processes and dimensions in the life cycle of grasshoppers, such as duration of development and life, body mass or fecundity (YANG & JOERN 1994, INGRISCH & KÖHLER 1998). In this context it is important to know whether a species is monophagous or polyphagous, i.e. how specialized it is in a certain diet. Only few data currently exist about *C. pullus*, according to which it is a mainly graminivorous and therefore oligophagous species like most of the Gomphocerinae (SCHWARZ-WAUBKE 1997b).

This thesis constitutes a part of a research project dealing with succession phenomena in one of the last dynamic flood plains of an alpine river, the Rhone, in Switzerland. This flood plain is located at Pfywald (VS), where the largest pine forest in Middle Europe is situated, which is listed in the Swiss national inventory of alluvions. Until recently, only two populations of *C. pullus* have been known to exist there. Unfortunately, their habitats are suboptimal, as they are threatened by the consequences of the Rhone regulation and increased spreading of the forest (CARRON 1999). One of these two populations exists at Rottensand in a dry side channel separated from the dynamics of the main river through embankments and spreading pine forest. The other population lives on the other side of the Rhone in a forest clearing, the site being called Russenbrunnen (FREIVOGEL 2003). This habitat cannot be reached any more by the river either. At Russenbrunnen experimental habitat management measures were carried out in 2004: the shrubs were cut down and all the moss was removed from two plots of 20 x 15 m each, in order to restore the site to a state closer to that of pioneer succession stages. However, in 2004, a new population of *C. pullus* was discovered nearby that is

thought to have been founded by individuals emigrated from Russenbrunnen. This population lives on a peninsula (here called Pullus-Island) of the river bank that is still influenced by the river dynamics; thus it can be seen as a more natural habitat for *C. pullus* than Russenbrunnen.

In order to assess the quality of these two habitats, two studies were carried out in 2005. One was concerned with aspects of the population ecology like habitat preference and population structure (WALTHER 2006), while the present study investigated aspects of the nutritional ecology. In particular, we asked the question how the diet of *C. pullus* was composed in terms of spatial and seasonal variation. We were interested in knowing whether diet composition was influenced by the partial removal of moss at Russenbrunnen, and whether it was influenced by a different food supply in different succession stages of the vegetation at Pullus-Island.

Moreover, we wanted to know how the available food was used, as this is an important aspect in assessing habitat quality. If plants are just consumed according to their availability, the diet composition should vary considerably between habitats with a different vegetation cover. However, the acceptance and avoidance of certain plant species has been shown many times (MULKERN 1967, BERNAYS & CHAPMAN 1970a, ROWELL 1985a, CHERRILL 1989, SWORD & DOPMAN 1999, LE GALL ET AL. 2003). Those plants should be preferred, which lead to the highest fitness gain by having either a high nutrient content or a low content of repellents. Besides, also physical and chemical characteristics of the plants influence the food selection (BERNAYS & CHAPMAN 1970b). Further we supposed water content to be an important factor, especially with regard to the xerothermic climate at Pfywald. Grasshoppers are generally thought to take up water by feeding (BERNAYS 1990, HOLDEREGGER 1999). Therefore, we investigated if the high moisture content of moss from dew in the morning enhanced its consumption by the grasshoppers. Comparison of the water contents of the most abundant plant species should show whether species with higher water content were preferred.

Another aspect of habitat use is the presence of possible competitors for food, especially of closely related species, which might have similar dietary niches. Therefore we aimed to compare the diet of *C. pullus* at Russenbrunnen with that of *Chorthippus vagans*. The vegetation cover and the microclimate conditions at Russenbrunnen are actually more suitable for *C. vagans* (FREIVOGEL 2003), as it prefers older succession stages of the vegetation than *C. pullus*. As *C. vagans* might also be able to utilize a wider food spectrum, this species is expected to have a broader niche.

2 Material and Methods

2.1 Study area

Study plots

The study area at Pfywald is situated between Leuk and Sierre (VS, Switzerland), inside of a nature preserve. Therefore, the flood plain of the Rhone is to a great extent still in a natural state. Russenbrunnen (site R, 611325/128390, 552 m asl) is located below Salgesch on the right side of the Rhone downstream. Pullus-Island (site I, 611792/128532, 552 m asl) is located ca. 500 m upstream of Russenbrunnen, on the same side of the river. At both sites, two study plots of 100 m² were chosen (Appendix, Fig. 7). The clearing of the forest at Russenbrunnen covers an area of 4500 m². In this habitat one plot was chosen randomly at the site with the normal thick moss layer (RM) and one at the site from which the moss had experimentally been removed (RR). Pullus-Island was created during a flood in 1993 and was restructured during another flood in 2000. The eastern part of the peninsula consists of a mosaic of zones with different soil substrates and unequally advanced succession stages of the vegetation, formed by the water dynamics; it covers an area of 14'336 m². In 2004, the succession stages were classified in six different zones (Appendix, Fig. 8) according to their vegetation cover and soil surface (WALTHER 2005). Zone one is nearly vegetationless while zone six is covered by broadleaf thickets of up to ca. 4 m high. For this study one plot was chosen at zone four (IZ4) and one at zone three (IZ3), which represent intermediate succession stages. They were chosen because they had contained the highest densities of *C. pullus* in 2004.

Grasshopper community

The following grasshopper species occurred together with *Chorthippus pullus* at Russenbrunnen as well as at Pullus-Island: *Chorthippus vagans*, *Oedipoda caerulescens* (Acrididae) and *Calliptamus italicus* (Catantopidae) were the most abundant species, whereas *Chorthippus brunneus*, *Chorthippus mollis* and *Oedipoda germanica* (Acrididae) were less abundant. At Russenbrunnen, also *Stauroderus scalaris* (Acrididae) and *Platycleis albopunctata* (Tettigoniidae) occurred, and at Pullus-Island *Sphingonotus caeruleus* (Acrididae).

2.2 Survey of vegetation and ground cover

At each plot, the vegetation was mapped once at the beginning of June. For this purpose, the plots were divided into 25 subplots of 4 m². At each subplot the following parameters were recorded: vegetation cover (grasses and forbs), shrub cover, cover of moss, sand, fine gravel

(0-5 cm), gross gravel (5-50 cm), blocks (>50 cm), litter and dead wood. For the estimation of the vegetation and shrub cover, only vegetation structures below 30 cm were considered, as *C. pullus* does normally not occur above 30 cm (SCHWARZ-WAUBKE 1997a). In this way, the average cover of the different parameters could be calculated for the whole plot. All plant species were identified (LAUBER & WAGNER 2001) and their cover in cm² within one subplot was visually estimated with the help of templates. The resulting numbers were added up to get the total cover for each plant species within one plot.

2.3 Faeces collection

Faeces collection at Pfywald

Faeces were collected once per month from the middle of May through August. In May, most of the grasshoppers were in the third nymphal stage, in the following months they had reached the adult stage. At each of the four plots 20 grasshoppers were caught with a sweep-net on two to three consecutive days at noon, i.e. from 11 am to 13.30 pm. Thus, grasshoppers could be captured at one or two sites per day. For each grasshopper the subplot in which it had been caught was recorded. Those subplots were the same as for vegetation sampling, being marked with flags. The grasshoppers were kept for three to four hours in plastic tubes with a moist plaster bottom in the shade. Subsequently, they were individually marked on the pronotum using a 5-digit colour code applied with Edding 780 paint markers; thus it could be avoided that twice data from the same animal were used. For this treatment the grasshoppers were anaesthetized with CO₂. The nymphs were not marked, as the markings would have disappeared with the next moulting anyway. Afterwards the grasshoppers were released in the same subplots where they had been caught. The faeces were removed from the plastic tubes, dried, and stored in Eppendorf tubes until being analysed. In the same way, faeces of 20 individuals of *C. vagans* were collected at RM in July and August.

Daily course of feeding

On June 23rd of 2005, the daily course of feeding was investigated, to see whether differences existed between the amounts of moss consumed at five different times of day. Therefore, ten grasshoppers were caught every two and a half hours starting at 7 am at a plot at Russenbrunnen that was not used for the other studies. The animals were also kept for ca. three hours in plastic tubes and then marked.

Faeces collection at Val Ferret

On August 12th of 2005, we collected faeces from 38 individuals of a population of *C. pullus* on the Dranse de Ferret at Val Ferret (VS, Switzerland, 573690/88220, 1520 m asl). This population lives on the banks of a natural and highly dynamic river. The grasshoppers were captured between 10 and 11 o'clock and kept for ca. one hour in plastic tubes. Afterwards, they were released at the site of capture.

2.4 Faecal analysis

Preparation of the epiderms

To identify the plant species eaten, the plant epiderms had to be gained from the faeces. All faecal pellets from each animal were processed. Thus, a total of 410 preparations resulted. Preparation of the epiderms largely followed the method developed by ZETTEL (1974). The time intervals were slightly shortened and the whole method was adapted to delicate grasses and forbs and the intensity of digestion by the grasshoppers:

1. The faecal pellets were heated with some distilled water in a glass tube so that they could be desintegrated with a glass stirrer.
2. After removing the water, ca. 5 ml of a 1:1 mixture of 10% nitric acid (HNO₃) and 10% chromate acid (H₃CrO₃) was added. The glass tube was put into boiling water for ca. 20 seconds until the solution became brownish and bubbles formed on the epiderms. This procedure served to bleach the epiderms.
3. After that, the acid was immediately removed and distilled water was added for cleaning. Parts of the mesophyll could be loosened from the epiderms by strong pipetting. Then the plant fragments were allowed to settle for at least ten minutes.
4. The water was removed again and 5 ml of an alcoholic solution of Sudan III (96%) was added. Sudan III is a lipophilic dye that can be used, e.g. for dyeing the cuticle. Colouration lasted at least one hour.
5. Again, the solution was rinsed with distilled water. Through sedimentation, the epidermis and the mesophyll could be separated. The fragments were then embedded in glycerol gelatine on microscopic slides. In order to get permanent preparations, the cover slip was sealed with wax.

Reference slides from the available plant species at the four study sites were made by the same procedure as described above but involving two more steps at the beginning: first, plant items had to be softened by heating them in a 1:1 mixture of glycerol and H₂O. Secondly,

they were macerated by cooking them in a 10% solution of caustic potash (KOH) for ca. seven minutes.

Analysis

Large cover slips (24 x 60 mm) were used to obtain only one to three preparations per grasshopper. These were analysed under the microscope at 100 x magnification. The fragments were identified by means of the reference slides and some photographs (ZETTEL 1974, NELSON & GANGWERE 1981). All fragments of one plant species were counted. In order to take into account the different size of the fragments, their cover on the slide was estimated in units. For this purpose and for better orientation a grid of 0.04 mm² printed on a transparent foil was laid over each slide. From the number of fragment units the relative abundance of each plant species in the faeces of one grasshopper could be calculated.

2.5 Feeding experiments

Duration of the gut passage and feeding activity

On June 9th of 2005, 21 individuals of *C. pullus* were brought to the Zoological Institute at the University of Bern and kept in a climatic chamber in plastic boxes (33.5 x 22.5 x 9 cm) with wet sand as substrate. The temperature was held at 25°C during the day and 15°C during the night and the light regime was adapted to natural conditions. The grasshoppers were fed with a standard lawn mixture and fish food according to SCHWARZ-WAUBKE (2001). They also got a glass tube with a wet cotton-wool swab as water supply. The experiment took place on June 16th. Between 7 and 8 am all grasshoppers were placed individually in a plastic box (19 x 9.5 x 8 cm) with a wet plaster bottom. The animals were allowed to adapt to the new conditions for ca. one hour. Then each grasshopper was fed a fresh leaf of *Astragalus onobrychis*. This plant was chosen because it seemed to be the main food source of *C. pullus* at Pfywald according to a previous study (STEINER 2005). Moreover it can easily be distinguished from grass under the microscope. All the boxes were placed next to each other, so that they could be observed at the same time. Each feeding event was recorded until 7 pm. At intervals of 30 minutes the boxes were checked for faecal pellets; these were removed and stored in separate Eppendorf tubes. In this way, 116 samples of faeces were gained. They were analysed by squashing a sample between a slide and a cover slip in a droplet of water. The time of the first appearance of *A. onobrychis* in the faeces was recorded, and by this a minimum duration of the gut passage could be calculated.

Food selection

In order to test the food selection in the laboratory, 30 grasshoppers were again brought to Bern on July 27th. They were held under the same conditions as described above. Fresh plant material was collected the same day and stored wrapped in wet paper towel in polythene bags in the refrigerator. The following day, the grasshoppers were placed in the same experimental boxes as described before. In order to test whether *C. pullus* prefers grasses or forbs, its main dicotyledonous and monocotyledonous food plants in the field, *A. onobrychis* (Fabaceae) and *Calamagrostis epigejos* (Poaceae) were offered. Of each plant species, five pieces of roughly equal size (about 1 x 2 cm) were distributed randomly in each box. Findings from the gut passage experiment suggested this to be enough for an oversupply. The animals were kept in the boxes from 7 am to 7 pm. After that, the remaining plant material was collected and for each piece one of the following consumption categories was noted (as suggested by SMITH & CAPINERA 2005a): 1 = 0-20 % consumed, 2 = 21-40 % consumed, 3 = 41-60 % consumed, 4 = 61-80 % consumed and 5 = 81-100 % consumed. The numbers of the five pieces of one plant species were added up.

2.6 Mandibular morphology

In order to investigate the structure of the mandibles of *C. pullus* four animals were used which had died during their stay in the laboratory. Their mandibles were dissected out and compared to descriptions in the literature of the three mandible types that can be distinguished in grasshoppers: the graminivorous, forbivorous and herbivorous type (ISLEY 1944, SMITH & CAPINERA 2005b).

2.7 Plant water content

The water content of the two most abundant forbs *A. onobrychis* and *Artemisia campestris*, the most abundant grass *C. epigejos*, and the most abundant moss species *Dicranoweisia crispula*, was determined in the laboratory. Fresh plant material was collected on September 7th of 2005 at noon in the study area and stored with wet paper towel in polythene bags in a cold box. Per plant species, 20 leaves were weighed on a Mettler Toledo scale with an accuracy of 0.1 mg and then dried for 36 hours at 60°C. From *C. epigejos*, only leaf parts of ca. 10 cm in length could be used, as whole leaves were too heavy for the scale. The dry material was weighed again allowing the percentage of water loss to be calculated from the weight difference to the fresh material.

2.8 Statistics

Non-parametric tests were used for all analyses. The program JMP was used to analyse the spatial and seasonal differences between the amounts of different plant species eaten. The Mann-Whitney-U-test was used for analysing the pairwise differences between the sites at Russenbrunnen and those at Pullus-Island. Accordingly, the Kruskal-Wallis test was used for analysing the seasonal differences. The pairwise differences between the diet composition in June, July and August were analysed with the Dunn-test. The same procedure was used for the comparison of the different times of day and the water content of the four plant species. To see whether a preference existed for a given plant species, Manly's α index of preference for constant prey populations was calculated from data of the vegetation survey and the diet composition. If $\alpha = (1/m)$ (m = total number of prey species), no selective feeding occurs. If $\alpha_i > (1/m)$ prey species i is preferred. Conversely, if $\alpha_i < (1/m)$, prey species i is avoided (KREBS 1999). In order to get the niche breadths and the niche overlap of *C. vagans* and *C. pullus*, Levin's standardized index of niche breadth and Horn's index of niche overlap were calculated. Both indices range from 0 to 1; for Levin's standardized niche index 1 means that an animal has the broadest possible niche, whereas for Horn's index of niche overlap it means that overlap is complete (KREBS 1999). For those as well as for Manly's α index of preference, the statistical program Ecological Methodology was applied. The amounts of the two plant species eaten in the food selection experiment were compared by a Sign-test.

3 Results

3.1 Vegetation and ground cover

Vegetation cover

Vegetation sampling resulted in a total of 30 different plant species (Tab. 1). The three most abundant plant species over all sites were the forbs *Astragalus onobrychis* and *Artemisia campestris* and the moss *Dicranoweisia crispula* (Fig. 1). IZ4 and RR proved to be similar with respect to the composition of their plant cover. They had rather balanced proportions of the three main species, each covering ca. 20% of the space. At RM, *D. crispula* was the dominating plant species (67%), whereas the proportion of *A. onobrychis* was much smaller (9%). In contrast, *A. onobrychis* constituted the largest part of the ground vegetation at IZ3 (40%). Beside it *Calamagrostis epigejos* (4%) and *Bryum klinggraeffii* (6%) were quite frequent. At this site, the amount of shrubs was highest (44%). All the sites showed similar numbers of present plant species (16-19).

Ground cover

The biggest difference in ground cover between RM and RR was the presence of moss and consequently the amount of gravel, which was higher at RR (Tab. 2). Like the moss, the vegetation cover (grasses and forbs) also proved to be higher at RM than at RR. At Pullus-Island, the older succession stage IZ4 had a higher cover of ground vegetation, including moss, but the shrub cover was almost equal at both sites. The mineral soil surface was very different between the two sites with IZ3 having much more sand but fewer stones than IZ4.

3.2 Plant epiderms

Overall, the epiderms of 12 different plant species could be identified in the grasshoppers' faeces (Tab. 1); six were dicotyledons, four monocotyledons and two bryophytes. Characteristics for distinguishing the plant species were the trichomes, the stomata with their guard and subsidiary cells and the structure of the epidermal cells (Appendix, Fig. 9 - Fig. 11). Tab. 3 shows the main characteristics, by which the different plant species could be identified. The microscopic differentiation of the moss species was rather difficult; therefore they were mainly identified according to their appearance at the different sites. Beside the plant epiderms, small chitin particles were found in some preparations, which implied that the grasshoppers sometimes also ingest animal food.

3.3 Diet composition

Diet composition

Astragalus onobrychis proved to be the main food plant of *C. pullus* at Pfywald. At each investigated site and in each month it represented more than 50% of the diet; at IZ4 and RR it exceeded even 70%. Only a few other food items were found in the diet of the nymphs in May (Fig. 2), the most important ones being *D. crispula* at RM (16%) and RR (7%), and *Stipa pennata* (9%) at RR. The diet composition in June was rather similar (Fig. 3). At all sites the consumption of *A. onobrychis* exceeded 90%, except for IZ3, where they also fed some *C. epigejos* (13%) and *Festuca curvula* (6%). In contrast, the food spectrum was wider in July, as higher amounts of food types other than *A. onobrychis* were consumed at all sites (Fig. 4). At RM, *D. crispula* constituted nearly half of the diet (45%), but also at IZ4 (19%) and RR (15%) its proportion was rather high. However, at IZ3 *C. epigejos* constituted 25% of the diet. In August, the amount of *A. onobrychis* increased again and its proportions were over 90% at all sites but RM (Fig. 5), where *D. crispula* was still eaten quite frequently (26%). As it can be seen on Figs. 2-5, the number of samples was not always 20. Reasons were either that no faeces were produced or that data from an animal had to be excluded because it had been caught for a second time. In August, not enough grasshoppers could be found anymore at RM and IZ3.

Spatial variation

Generally, most of the spatial variation in the amounts eaten was found for *D. crispula* and the bryophytes in total. In May, no significant differences could be detected (Tab. 4). However, in the summer months the amount of *D. crispula* in the diet at RM was significantly higher than at RR. As *D. crispula* was the only moss species eaten, more bryophytes were also consumed in total. In contrast, in June and July significantly more *A. onobrychis* was consumed at RR compared to RM. No significant differences could be found between IZ3 and IZ4 except for July, where significantly higher amounts of *D. crispula* were eaten at the later succession stage, IZ4.

Seasonal variation

Most of the seasonal variation was found due to July as more plant species other than *A. onobrychis* were eaten. Therefore, the overall diet composition was most diverse in that month. At RR no significant differences could be found between the three months, in which faeces of the adults had been sampled. At IZ4 the grasshoppers ate significantly more *A. onobrychis* in

June than in July ($n = 58$, $0.01 < p < 0.05$). At IZ3 however, the amount of *A. onobrychis* in the diet was significantly higher in August than in July ($n = 45$, $0.01 < p < 0.05$). RM was the site with highest seasonal variation, but all significant differences were found between June and July. In July the grasshoppers ate less *A. onobrychis* ($n = 34$, $0.01 < p < 0.05$) and also less dicotyledons in general ($n = 34$, $0.01 < p < 0.05$). In contrast, they fed more on *D. crispula* ($n = 34$, $p < 0.01$) and therefore more on bryophytes ($n = 34$, $p < 0.01$). Excluding August from the analysis because of its low sample number did not influence the results.

Daily course of feeding

There were no significant differences in moss consumption in the course of one day ($n = 49$, $p = 0.0949$). However, due to only ten replicates per time the power was rather low (power = 0.34).

3.4 Food preference

No clear food preference pattern could be found. Although *A. onobrychis* was the most frequently eaten plant species, it was not always the most preferred when comparing the diet composition with the food supply (Tab. 5 - Tab. 8). At RM however, *A. onobrychis* was the preferred food item in all months. At RR, the grasshoppers had a preference for *A. onobrychis* in July and August but *S. pennata* was preferred even three times, in May, June and August. At IZ4, grasses were also selected quite often; *Agropyron pungens* was preferred in June, while *F. curvula* was the most preferred plant species in July and August, and *A. onobrychis* in May and June. At IZ3 both *A. onobrychis* and *C. epigejos* were twice the preferred food plant, the first one in May and June and the second one in June and July. At IZ3, no preference index could be calculated for *F. curvula*, since this plant species had not been recorded in the vegetation survey. On the whole, neither the monocotyledons nor the dicotyledons were primarily selected, as in total the monocotyledons were preferred eight and the dicotyledons ten times. No preference for bryophytes could be found at all.

3.5 Dietary overlap with *C. vagans*

The diet of *C. pullus* and *C. vagans* was compared in July at RM. In June adults of *C. vagans* were not yet available and in August not enough individuals of *C. pullus* could be found anymore. The diet composition of *C. vagans* proved to be rather similar to that of *C. pullus* (Fig. 4). The most important food item was again *A. onobrychis* (78%), followed by *D. crispula* (22%). By comparing the trophic niches of *C. pullus* and *C. vagans*, they both turned out to have rather broad niches. Levin's standardized niche breadth was 0.977 for

C. pullus and 0.515 for *C. vagans*; therefore the niche of *C. pullus* seemed even broader. The high niche index also indicates that the species is not very specialized. The niches were quite similar, as Horns's index of niche overlap was 0.957.

3.6 Diet composition at Val Ferret

The diet of the population of *C. pullus* at Val Ferret consisted up to 97% of grasses. Only little amounts of moss (3%) and forbs (0.1%) were consumed.

3.7 Feeding experiments

As not all grasshoppers ate during the gut passage experiment, only data from 13 animals were gained. The resulting average minimum duration of the gut passage was 2 hours 45 minutes. On average, two animals fed per half hour. The feeding activity was rather continuous and no specific peak could be found; however it decreased in the evening.

In the food selection experiment, no difference between the amounts of *C. epigejos* and *A. onobrychis* eaten could be observed ($\chi^2 = 0.9259$, FG = 1). Therefore, we could not detect a preference for either of the two plant species under laboratory conditions.

3.8 Mandibular morphology

The mandibles of *C. pullus* could be allocated to the graminivorous type (Appendix, Fig. 12a - d). They had the grinding molars and the incisors fused into a scythe-like cutting edge as described in SMITH & CAPINERA (2005b).

3.9 Plant water content

The water content of the four plant species was significantly different ($n = 80$, $p < 0.0001$). On average, *A. onobrychis* had the highest water content (79%), followed by *A. campestris* (75%), *C. epigejos* (62%) and *D. crispula* (20%) (Fig. 6). Also the pairwise differences proved to be significant for all pairs except *A. onobrychis* and *A. campestris* (Tab. 9). However, when comparing only those two plant species with the Mann-Whitney-U-test, this difference as well turned out to be significant ($n = 40$, $p < 0.0001$).

4 Discussion

4.1 Diet composition

The diet of *C. pullus* at Pfywald included various forbs, some grasses, moss and probably even small insects, as some chitin particles were found in the faeces preparations. From these findings we suggest that *C. pullus* is a polyphagous grasshopper species. A reason for this may be found in the benefits of a mixed diet, by which a better nutrient balance can be achieved (CHAMBERS ET AL. 1996, SWORD & DOPMAN 1999). However, it is in contrast to the results of SCHWARZ-WAUBKE (1997b) but also to most of the data published so far, in which the Gomphocerinae are designated as a mainly graminivorous subfamily (BERNAYS & CHAPMAN 1970a, CHAPMAN 1990, PICAUD ET AL. 2003, INGRISCH & KÖHLER 1998). Only few other descriptions of either polyphagous or forb-feeding Gomphocerinae can be found in the literature (e.g. PICAUD ET AL. 2002).

The diet composition was similar at all study sites, in spite of a different vegetation cover. Overall, *A. onobrychis* was the most commonly eaten plant species of *C. pullus* at Pfywald. As *A. onobrychis* was also the most widely available plant species and availability normally plays an important role for the diet composition of grasshoppers (BERNAYS & CHAPMAN 1970b), this is very likely to be one reason for its high consumption. We often saw the grasshoppers sitting in these bushy and procumbent plants, which provide an ideal hiding place from possible predators, as *C. pullus* is a flightless and cryptic species. *A. onobrychis* could also be important for providing shade especially at noon, when the soil surface temperatures can exceed 50°C in summer. The frequent stay in these plants could therefore be another reason for the high consumption by the grasshoppers.

Spatial variation could especially be found with regard to the amounts of *D. crispula* eaten. In every month but May significantly more of it was consumed at RM in comparison to RR. Again availability might be important; as most of the moss had been removed at RR, much more moss was available at RM. The only significant difference between IZ4 and IZ3 was also the higher consumption of *D. crispula* at IZ4 in July. However, no significant difference was found for the bryophytes in total, since another moss species, *B. klinggraeffii* was eaten at IZ3.

Seasonal variation was mainly present because higher amounts of plant species other than *A. onobrychis*, particularly *D. crispula*, were consumed at all sites in July. This finding was especially pronounced at RM. In general, moss is considered to be poor in nutrients and therefore rarely consumed by herbivorous insects. The water content could be an important factor in this case: according to weather data (meteorological station of Sion) the relative humidity of the air was rather high at that time since it had rained heavily two days before. An extended moss carpet like that at RM can keep rainwater for a considerably long time (AICHELE & SCHWEGLER 1984). The grasshoppers might have eaten moss just for water uptake as they normally ingest water through feeding (BERNAYS 1990).

No difference in moss consumption could be detected in the course of one day. In contrast to our expectation that moss would be consumed mainly in the morning due to its water content from dew, it was consumed throughout the whole day. As the power of our analysis was rather low and the investigation was carried out on a single day, more data are needed.

4.2 Food preference

The second important factor beside the availability of food plants is the acceptability (BERNAYS & CHAPMAN 1970b), which means that the grasshoppers either accept or avoid certain plants. Whether grasshoppers feed selectively in the field can only be revealed by comparing their diet composition with the availability of the plant species in the field (MÜHLENBERG 1993, BEGON ET AL. 1998). In the case of *C. pullus* no clear preference pattern was found in this comparison. Neither forbs nor grasses were noticeably more preferred. This also corresponds to the results from the food selection experiment in the laboratory: no difference could be detected for the amounts of *A. onobrychis* and *C. epigejos* eaten.

However, the fact that some quite abundant plant species such as *Artemisia campestris* or *Euphorbia seguieriana* were eaten in much lower proportions than present in the food supply or not eaten at all indicates that some kind of preference must exist. Consistently, many studies have shown that grasshoppers - although many of them are quite generalist feeders – do select certain plant species (GANGWERE 1965, MULKERN 1967, BERNAYS & CHAPMAN 1970a, SHELDON & ROGERS 1978, ROWELL 1985b, HOWARD 1995, ISERN-VALLVERDÚ 1995, LE GALL ET AL. 2003). The reason is obvious: basically, vegetable food is not very nutrient-rich but the amount of nutrients and secondary plant compounds can vary considerably among different tissues, individuals and species (NENTWIG ET AL. 2004). Animals can maximize their fitness

through optimal foraging (BEGON ET AL. 1998). To choose the optimal diet, grasshoppers must be able to recognize suitable food. For this purpose, acridids possess chemoreceptors on their maxillar and labial palps as well as mechanoreceptors (INGRISCH & KÖHLER 1998).

However, the question why singular plant species were accepted or totally avoided by *C. pullus* is not so easy to answer. Apart from the nutrient content, the chemical and physical properties may also play a role (BERNAYS & CHAPMAN 1970b). Physical properties that might influence food selection are, e.g., leaf thickness, trichomes, hardness and moisture content. Different reasons for the avoidance of *A. campestris* may be possible: the water content might again be important as it was lower than in *A. onobrychis*. Moreover *A. campestris* contains tannins, which are known to inhibit insect feeding (BERNAYS & CHAMBERLAIN 1982). In contrast, the cuticle did not seem to be extremely thick when considering the cross-section of a leaf. For *E. seguieriana* the chemical aspect might also be decisive, as Euphorbiaceae have a reputation for being toxic. They contain sticky, milky sap; therefore they are only eaten by food specialists. Bryophytes have been eaten, but they did not belong to the preferred plant species. This confirms the assumption that they were eaten for the purpose of water uptake.

The fact remains unusual that *C. pullus*, although belonging to the Gomphocerinae, mainly fed on forbs and not on grasses at Pfywald. This was not the case at Val Ferret, where the grasshoppers ate hardly anything but grasses. However, there were considerably more and softer grasses available. The mandibular morphology of *C. pullus* at Pfywald also indicates a graminivorous diet. There are studies about geographic variation of host plant specialization (ROWELL 1985a, SWORD & DOPMAN 1999) suggesting a genetic background for the adaptation to different host plants. The mandibles of *C. pullus* at Pfywald do not show such an adaptation. Therefore, it could be a further confirmation of the suggestion of SMITH & CAPINERA (2005b) that behavioural plasticity or ecological opportunism also exists in Orthoptera. This may even be important for a pioneer species like *C. pullus*, since it must be able to adapt to different food supplies.

4.3 Competition for food?

Our data show that the diet composition of *C. pullus* and *C. vagans* at RM overlaps to a great extent. In spring, *C. pullus* is one of the first grasshopper species appearing at Pfywald. The population reaches its peak in June. In contrast, *C. vagans* has a shifted phenology with a peak in July/August. The population size of *C. pullus* at RM seemed to decline after the ap-

pearance of the first adult *C. vagans*. This contrasts with the other sites, where the population size declined later in the season. The competition for food might be one reason for that. Not only *C. vagans* but also other grasshopper species are possible food competitors. Particularly *O. caerulescens* has also been shown to feed mainly on *A. onobrychis* at Rottensand (HOLDE-REGGER 1999). However, interspecific competition in grasshoppers for food resources is likely to occur only when the ratio of consumers to available resources is unusually high (ISERN-VALLVERDÚ ET AL. 1995). Data from the vegetation survey show that the vegetation cover at RM is rather high compared to the other sites. In contrast, the population density of the grasshoppers is not very high; for *C. pullus* it is only 0.25 ind./m² (WALTHER 2006). Therefore, another reason for the disappearance of *C. pullus* seems more likely, e.g. the lack of suitable places for oviposition (FREIVOGEL 2003), which may have the consequence that the grasshoppers leave suboptimal habitat patches.

4.4 The advantage of faecal analysis

Faecal analysis is only one of a variety of different methods that can be used to determine the diet composition of grasshoppers in the field. Grasshoppers can also be observed during feeding activity or the gut contents can be analysed (INGRISCH & KÖHLER 1998). Feeding observations have the great disadvantage that animals are disturbed very easily, which can lead to a change in their behaviour and eventually to a different diet composition. Apart from that, it is time consuming and data from different individuals cannot be collected at the same time. Analysis of gut contents has the advantage that the plant fragments are well conserved, but the animals must be killed. It is also probable that further breakdown of the epidermal characteristics of plant fragments from the gut are slight in other parts of the digestive tract, as indicated by MULKERN (1967). Therefore, faecal analysis is more appropriate, especially for an endangered species like *C. pullus*. It has a wide application field, as it is not only used for the analysis of the diet composition of grasshoppers (e.g. ROWELL 1985a, CHERRILL 1989, PICAUD ET AL. 2002, LE GALL ET AL. 2003) but also, e.g., of mammals (e.g. SHERLOCK & FAIRLEY 1993, WOLFE ET AL. 1996, DINGERKUS & MONTGOMERY 2001).

Faecal analysis also has some disadvantages. Some plants are more easily digested than others, which can lead to a different representation in the faeces (PUTMAN 1984). Moreover the record represents only a limited time span. If the gut passage lasts very long, it is probable that an animal has covered a great distance between the events of feeding and defecation. In that case, the comparison of plant availability and diet composition would not be very repre-

sentative. As laboratory experiments have shown that the minimum duration of the gut passage of *C. pullus* is rather short and that the feeding activity is rather constant during the day, we suppose that the plant material found in the faeces had been eaten within a few hours before the sampling. Apart from that, *C. pullus* is a rather sedentary species with activity ranges of about 40-50 m² (SCHWARZ-WAUBKE 1998). Therefore, we can assume that the grasshoppers are very likely to have fed inside our study plots or at least not far away.

4.5 Implications for conservation

Our findings on the nutritional ecology of *C. pullus* suggest that this species can adapt to habitats with different food supply. Although the grasshoppers preferred certain plant species, they turned out to have a rather wide food spectrum including such different plants as monocotyledons, dicotyledons and bryophytes. The fact that their most commonly eaten food item is also the most widely available is in agreement with the statement of ROWELL (1985a) that the principal food plant of a grasshopper population is always a relatively common one. Therefore, the survival of *C. pullus* does not depend on the presence of singular plant species but primarily on the habitat structure and the microclimate conditions (WALTHER 2006). Nevertheless, suitable food must be available in a grasshopper's habitat. If plant succession proceeds, the ground vegetation is thinning out. At the moment, this phenomenon can be observed at Russenbrunnen but will also occur at Pullus-Island. If the shrub cover becomes too high, the grasshoppers can find neither suitable food nor suitable microclimate conditions. As long as the Rhone does not have the possibility of creating new gravel bars and setting the succession back to earlier stages, habitat management measures are necessary to conserve the populations of *C. pullus*. In order to give the grasshoppers the possibility to colonize new habitats, migration corridors to the active river bed should be kept free from shrubs and very dense ground vegetation.

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6 Figures

- Fig. 1** Vegetation cover at the four study sites. (Others = all plant species with a proportion of < 2%. RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 2** Diet composition of *C. pullus* nymphs in May 2005. (Others = all plant species with a proportion of < 2%. RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 3** Diet composition of *C. pullus* in June 2005. (Others = all plant species with a proportion of < 2%. RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 4** Diet composition of *C. pullus* in July 2005 and comparison with *C. vagans*. (Others = all plant species with a proportion of < 2%. RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 5** Diet composition of *C. pullus* in August 2005 and comparison with *C. vagans*. (Others = all plant species with a proportion of < 2%. RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 6** Water content of the most abundant plant species [% fresh weight].

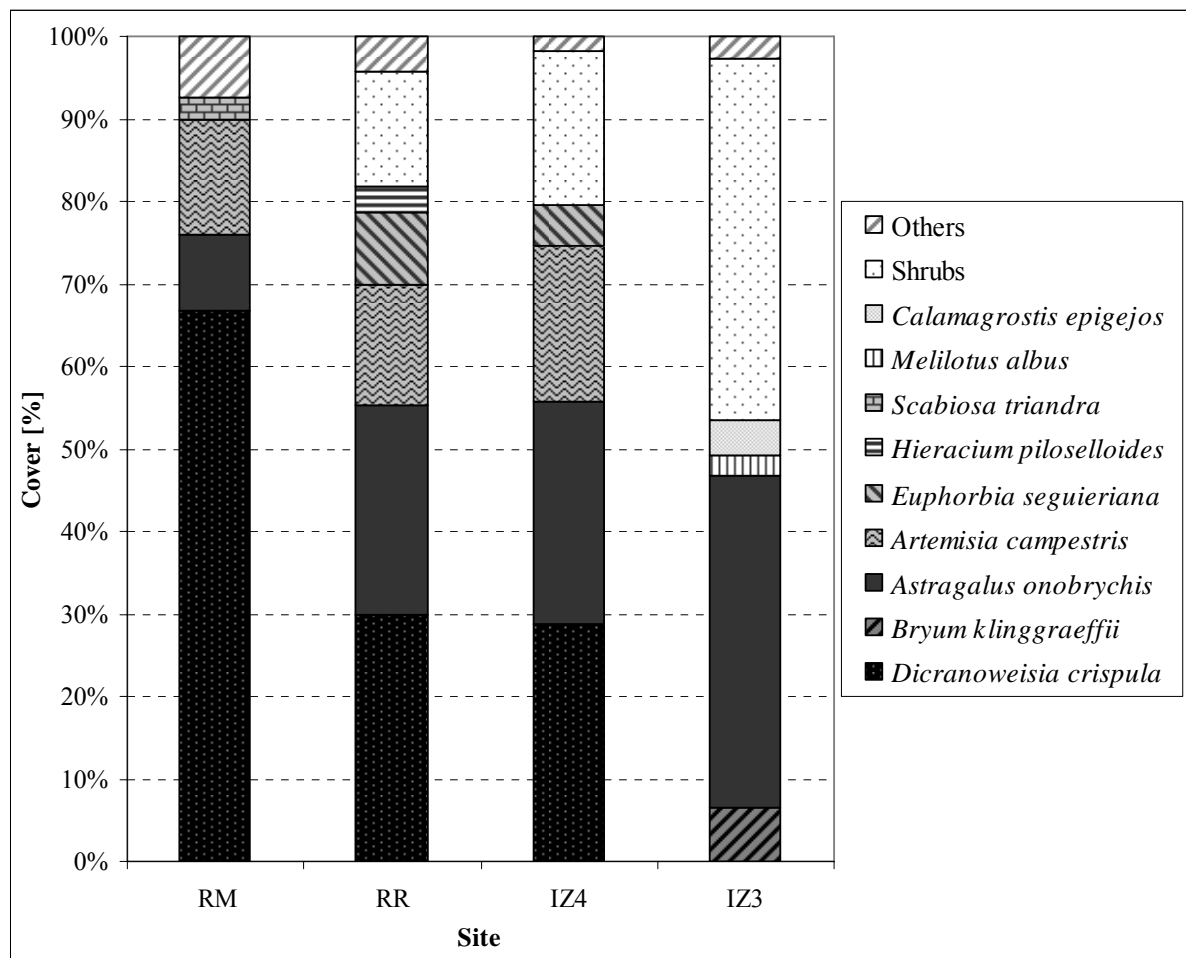


Fig. 1

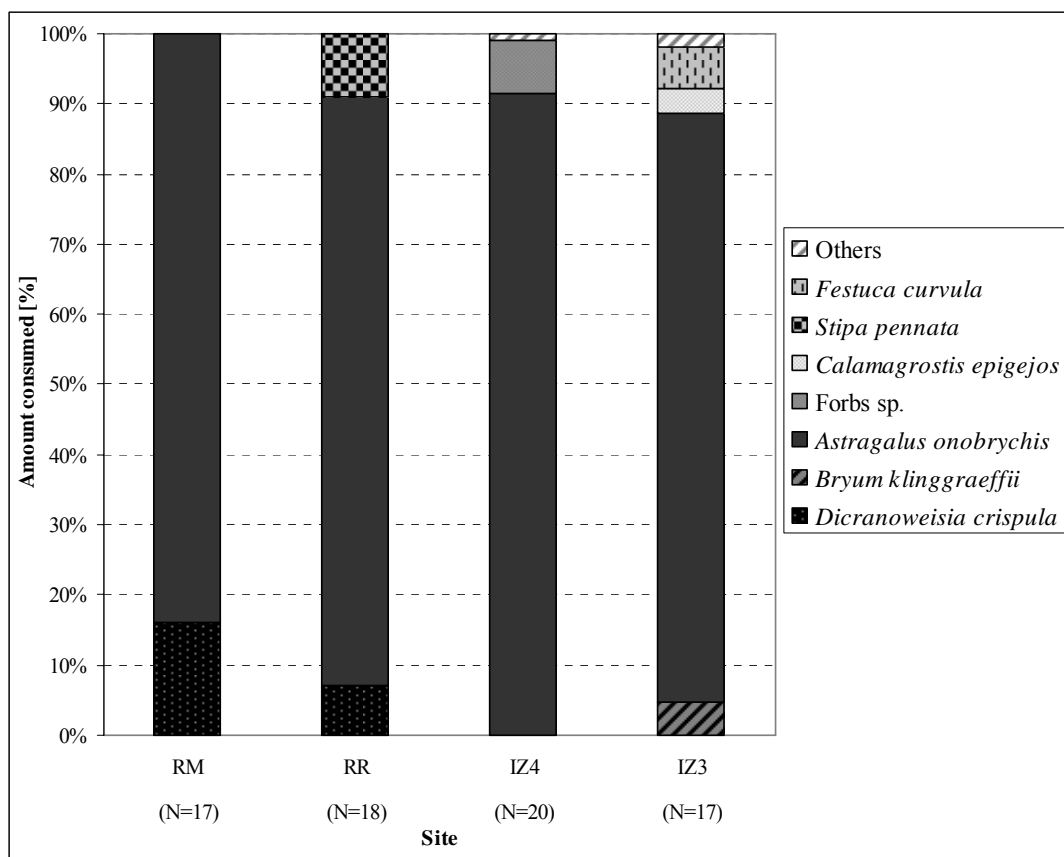


Fig. 2

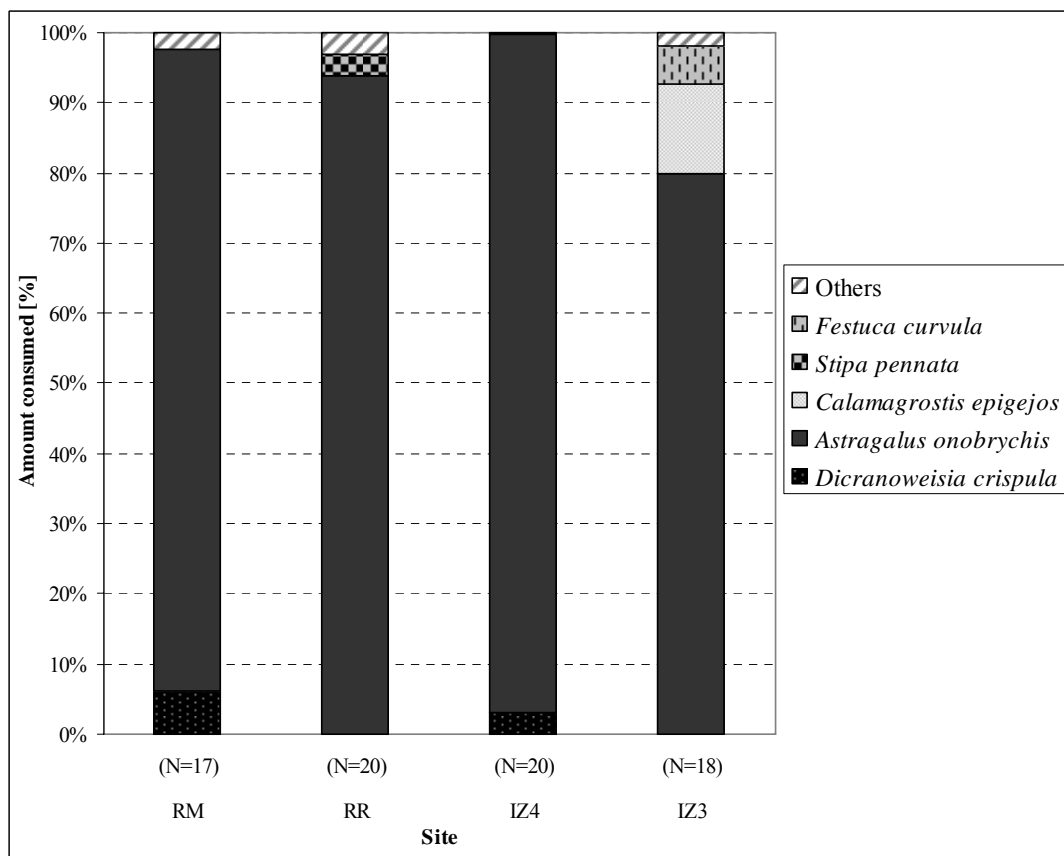


Fig. 3

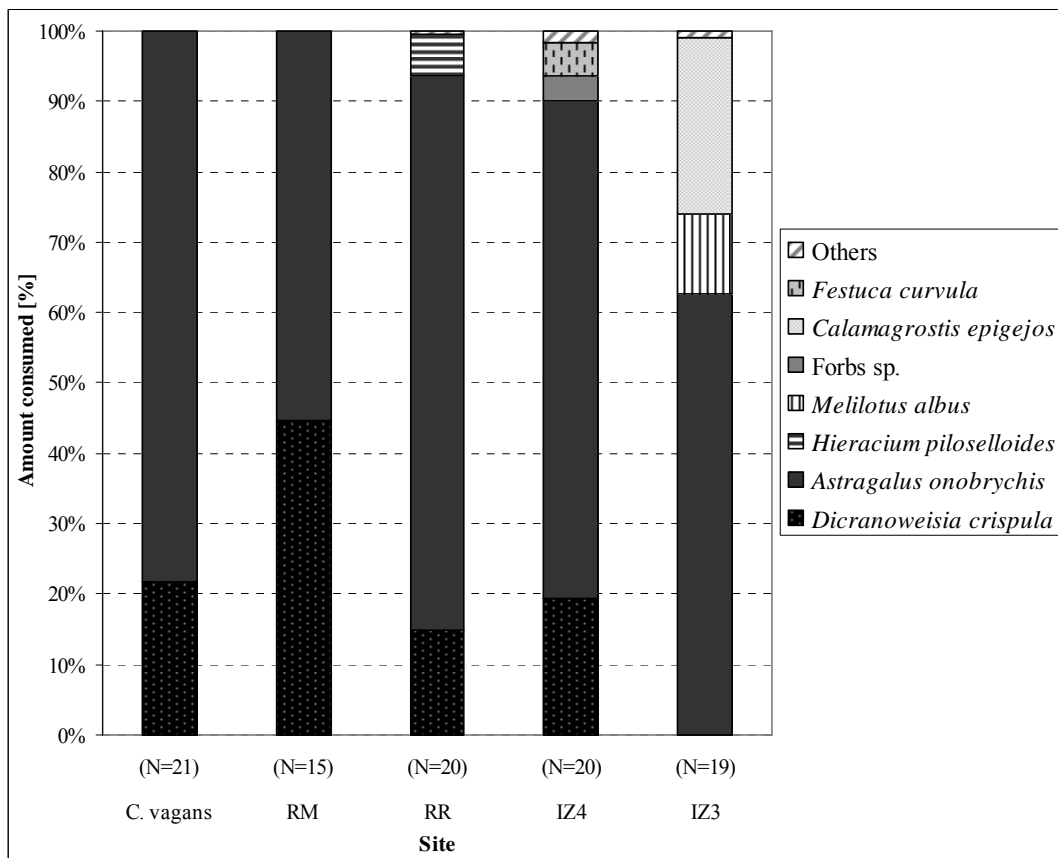


Fig. 4

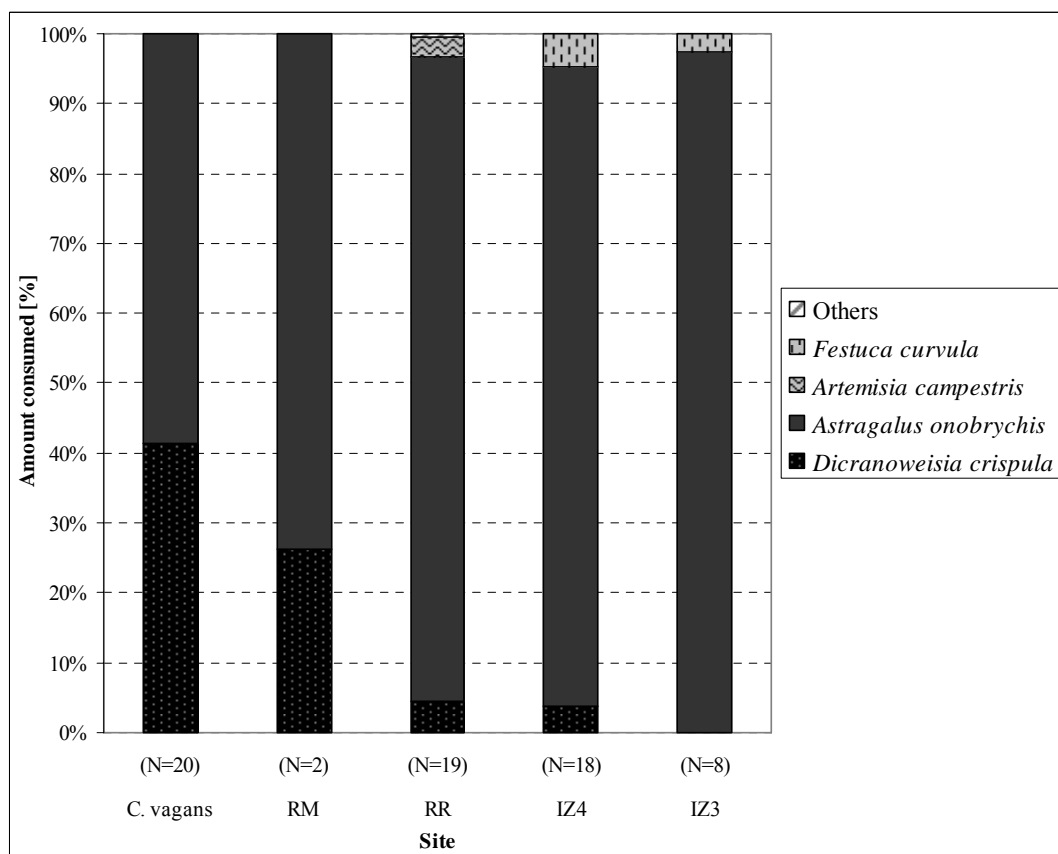


Fig. 5

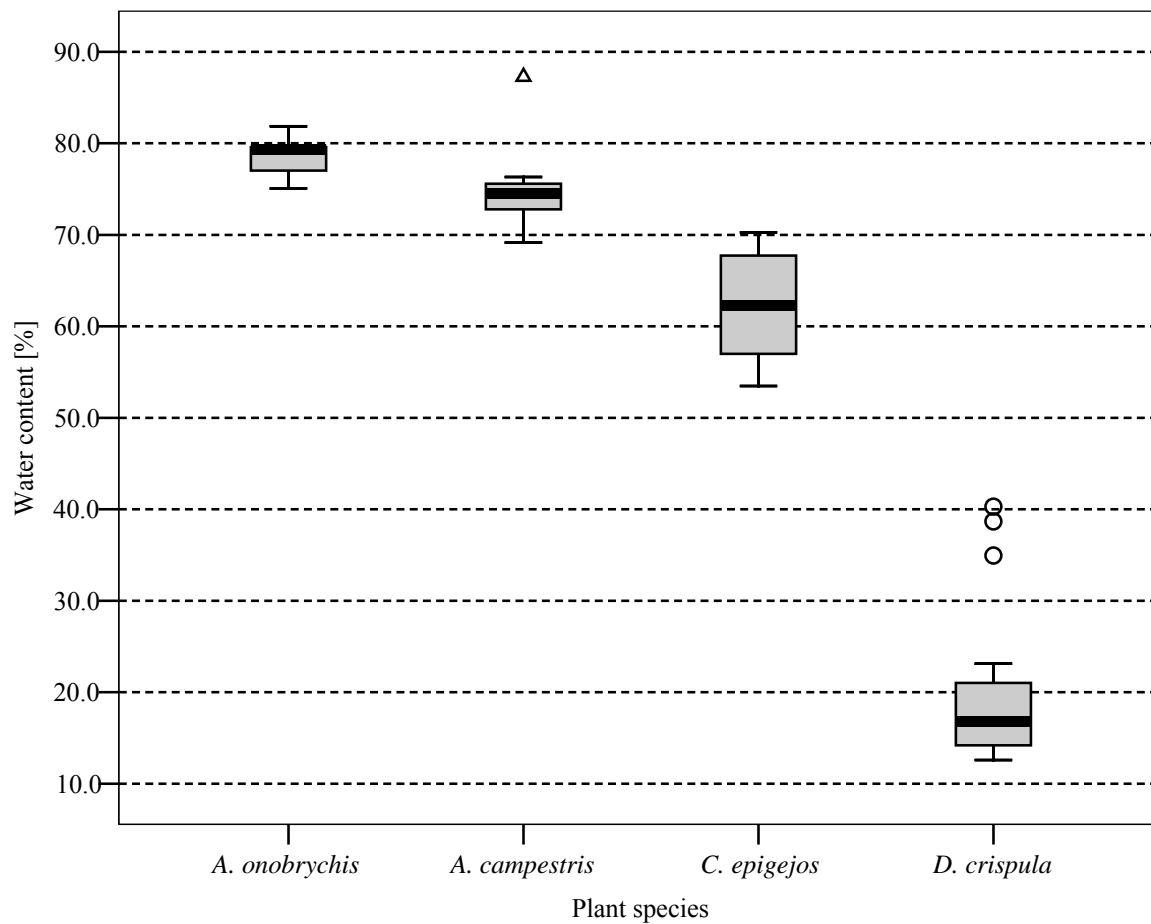


Fig. 6

7 Tables

- Tab. 1** Plant species found in the vegetation survey. Species found in the faeces are shaded.
- Tab. 2** Ground cover at the four study sites [% of surface] (RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Tab. 3** Main characteristics of the epiderms of the plant species found in the faeces of *C. pullus*.
- Tab. 4** Differences between the amounts of *A. onobrychis*, *C. epigejos* and *D. crispula* consumed at the four study sites. They represent the most commonly eaten forb, grass and moss species. Comparisons are also presented for the dicotyledons, the monocotyledons and the bryophytes in total (RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Tab. 5 - Tab. 8** Manly's α indices of preference for plant species for all study sites and months. Nb preferred = number of times a plant species was the most preferred in a month (RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Tab. 9** Pairwise comparisons of the water contents of the four plant species. *A. onobrychis* was the plant with the highest water content, followed by *A. campestris*, *C. epigejos* and *D. crispula*.

Tab. 1

Order	Family	Species
Dicotyledons	Asteraceae	<i>Artemisia campestris</i>
		<i>Centaurea valesiaca</i>
		<i>Hieracium piloselloides</i>
		<i>Scabiosa triandra</i>
	Brassicaceae	<i>Erucastrum nasturtiifolium</i>
		<i>Erysimum rhaeticum</i>
	Caryophyllaceae	<i>Gypsophila repens</i>
		<i>Silene otites</i>
	Euphorbiaceae	<i>Euphorbia seguieriana</i>
	Fabaceae	<i>Anthyllis vulneraria</i>
		<i>Astragalus onobrychis</i>
		<i>Melilotus albus</i>
	Lamiaceae	<i>Acinos arvensis</i>
	Onagraceae	<i>Epilobium dodonaei</i>
		<i>Epilobium fleischeri</i>
Scrophulariaceae	<i>Melampyrum pratense</i>	
	<i>Odontites luteus</i>	
Monocotyledons	Poaceae	<i>Agropyron pungens</i>
		<i>Calamagrostis epigejos</i>
		<i>Festuca curvula</i>
		<i>Koeleria vallesiana</i>
		<i>Stipa pennata</i>
	Elaeagnaceae	<i>Hippophae rhamnoides</i>
	Pinaceae	<i>Pinus sylvestris</i>
	Salicaceae	<i>Populus nigra</i>
		<i>Salix alba</i>
		<i>Salix elaeagnos</i>
		<i>Salix purpurea</i>
Bryophytes	Bryaceae	<i>Bryum klinggraeffii</i>
	Dicranaceae	<i>Dicranoweisia crispula</i>

Tab. 2

	RM	RR	IZ4	IZ3
Vegetation (grasses + forbs)	18	12.6	18.6	5.6
Moss	37.4	6.6	10	0.8
Sand	0	1.8	39.2	80.6
Fine gravel (0-5 cm)	0.6	39	0.8	0
Gross gravel (5-50 cm)	22.6	32.2	9.4	1.6
Blocks (> 50 cm)	0	0	5	0
Litter	17.6	4.4	9.6	5.2
Dead wood	3.4	0.2	0.8	0.8
Shrubs	0.4	3.2	6.6	5.4

Tab. 3

Taxon	trichomes	stomata	other characteristics
Dicotyledons		kidney-shaped	stained cuticle
Asteraceae		roundish, ± parallelly orientated	four subsidiary cells, two of them adjoining with a smaller part of their walls
<i>Artemisia campestris</i>	unicellular, elongated		
<i>Centaurea valesiaca</i>	multicellular, composed of one cell row		
<i>Hieracium piloselloides</i>	pappus bristles		
Brassicaceae			
<i>Erysimum rhaeticum</i>	unicellular, compass-needle shaped		two subsidiary cells
Fabaceae	heavily dyed base	triangular	
<i>Astragalus onobrychis</i>	unicellular trichomes with two horizontal branches		
<i>Melilotus albus</i>	unicellular, tapered trichomes		
Monocotyledons			
Poaceae		dumbbell-shaped	cell walls undulated
<i>Agropyron repens</i>	teeth in singular rows, elongated trichomes		cork cells rectangular, heavily stained
<i>Calamagrostis epigejos</i>	two rows of teeth along the veins		conspicuous veins
<i>Festuca curvula</i>			cork cells kidney-shaped, epidermis with strong colouration and structure
<i>Stipa pennata</i>	elongated, tapered		delicate structure, silica-cork couples well visible
Bryophytes		no stomata	no colouration

Tab. 4

Month	Sites	<i>A. onobrychis</i>		<i>D. crispula</i>		<i>C. epigejos</i>		Dicotyledons		Monocotyledons		Bryophytes		N
		p		p		p		p		p		p		
May	RM x RR	n.s.		n.s.		-		n.s.		n.s.		n.s.		35
	IZ4 x IZ3	n.s.		n.s.		-		n.s.		n.s.		n.s.		37
June	RM x RR	0.042		0.048		-		n.s.		n.s.		0.048		37
	IZ4 x IZ3	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		40
July	RM x RR	0.036		0.003		-		0.003		-		0.003		35
	IZ4 x IZ3	n.s.		0.030		n.s.		n.s.		n.s.		n.s.		39
August	RM x RR	n.s.		0.038		-		0.038		n.s.		0.038		21
	IZ4 x IZ3	n.s.		n.s.		-		n.s.		n.s.		n.s.		26

Tab. 5

RM	May 05	June 05	July 05	Aug 05	Nb preferred
<i>Artemisia campestris</i>		0.010			
<i>Astragalus onobrychis</i>	0.974	0.910	0.901	0.954	4
<i>Erysimum rhaeticum</i>		0.005			
<i>Hieracium piloselloides</i>		0.036			
<i>Stipa pennata</i>		0.030			
<i>Dicranoweisia crispula</i>	0.026	0.008	0.099	0.046	
Nb of food types	2	6	2	2	
α if non-selective feeding	0.500	0.167	0.500	0.500	
Dicotyledons	0.918	0.876	0.728	0.858	4
Monocotyledons		0.097			
Bryophytes	0.082	0.027	0.272	0.142	
α if non-selective feeding	0.500	0.333	0.500	0.500	

Tab. 6

RR	May 05	June 05	July 05	Aug 05	Nb preferred
<i>Artemisia campestris</i>		0.001	0.003	0.025	
<i>Astragalus onobrychis</i>	0.035	0.109	0.534	0.455	2
<i>Centaurea valesiaca</i>			0.057		
<i>Hieracium piloselloides</i>		0.011	0.320		1
<i>Stipa pennata</i>	0.962	0.878		0.500	3
<i>Dicranoweisia crispula</i>	0.003	0.001	0.085	0.019	
Nb of food types	3	5	5	4	
α if non-selective feeding	0.333	0.200	0.200	0.250	
Dicotyledons	0.032	0.080	0.752	0.440	2
Monocotyledons	0.963	0.919		0.520	3
Bryophytes	0.005	0.001	0.248	0.040	
α if non-selective feeding	0.333	0.333	0.500	0.333	

Tab. 7

IZ4	May 05	June 05	July 05	Aug 05	Nb preferred
<i>Agropyron pungens</i>		0.447			1
<i>Artemisia campestris</i>			0.006		
<i>Astragalus onobrychis</i>	0.993	0.537	0.174	0.223	2
<i>Festuca curvula</i>			0.775	0.768	2
<i>Dicranoweisia crispula</i>	0.007	0.016	0.044	0.008	
Nb of food types	2	3	4	3	
α if non-selective feeding	0.500	0.333	0.250	0.333	
Dicotyledons	0.784	0.754	0.146	0.181	2
Monocotyledons	0.206	0.203	0.786	0.806	2
Bryophytes	0.010	0.044	0.068	0.013	
α if non-selective feeding	0.333	0.333	0.333	0.333	

Tab. 8

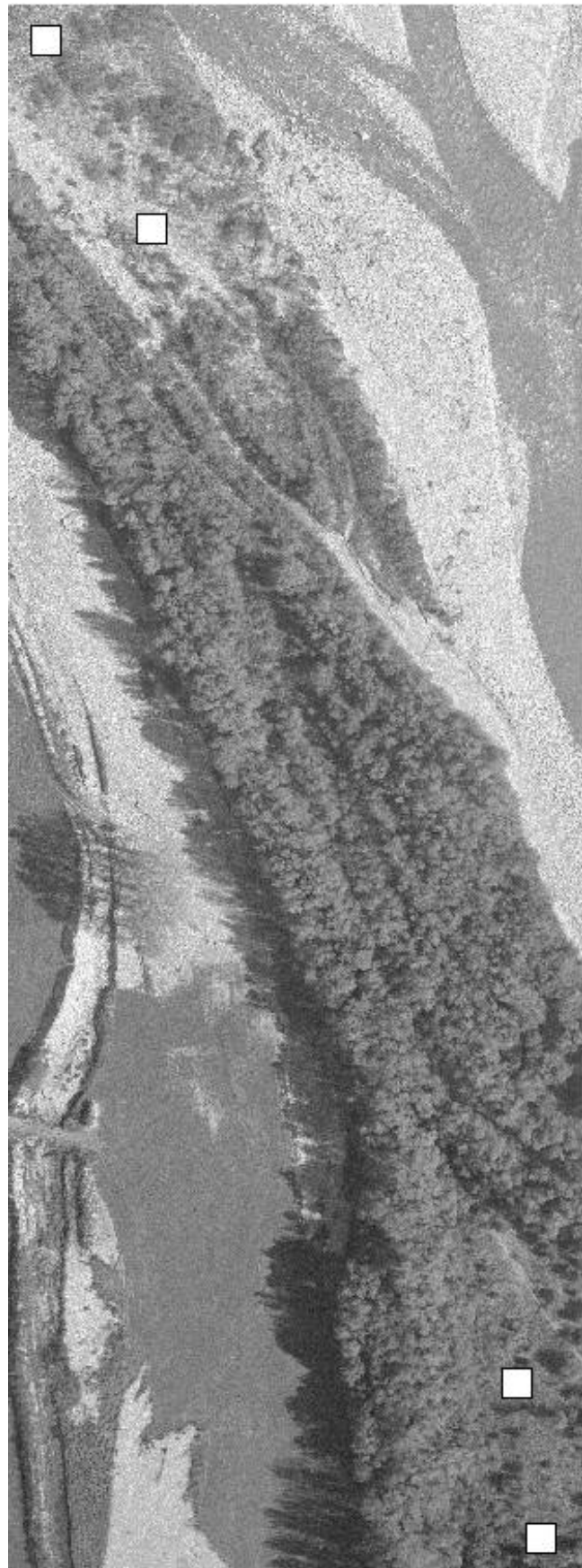
IZ3	May 05	June 05	July 05	Aug 05	Nb preferred
<i>Astragalus onobrychis</i>	0.540	0.394	0.130		2
<i>Calamagrostis epigejos</i>	0.217	0.585	0.486		2
<i>Melilotus officinalis</i>			0.376		1
<i>Bryum klinggraeffii</i>	0.243	0.022	0.008		
Nb of food types	3	3	4	1	
α if non-selective feeding	0.333	0.333	0.250		
Dicotyledons	0.404	0.330	0.250	0.811	2
Monocotyledons	0.396	0.650	0.736	0.189	3
Bryophytes	0.200	0.020	0.014		
α if non-selective feeding	0.333	0.333	0.333	0.500	

Tab. 9

Plant species	<i>A. onobrychis</i>	<i>A. campestris</i>	<i>C. epigejos</i>	<i>D. crispula</i>
<i>D. crispula</i>	p<0.01	p<0.01	0.01<p<0.05	
<i>C. epigejos</i>	p<0.01	0.01<p<0.05		
<i>A. campestris</i>	n.s.			
<i>A. onobrychis</i>				

8 Appendix

- Fig. 7** Location of the four study plots at Russenbrunnen and Pullus-Island. Each plot covers an area of 100 m² (RM = Russenbrunnen, site with moss; RR = Russenbrunnen, site with moss removed; IZ4 = Pullus-Island, zone four; IZ3 = Pullus-Island, zone three).
- Fig. 8** Classification of the different succession stages of the vegetation at Pullus-Island. The older the succession stage, the darker is the shading.
- Fig. 9** Epidermis of *A. onobrychis* from faeces of *C. pullus* (Compare also to Tab. 3). The scale represents 0.5 µm.
- Fig. 10** Epidermis of *C. epigejos* from faeces of *C. pullus* (Compare also to Tab. 3). The scale represents 0.5 µm.
- Fig. 11** Epidermis of *D. crispula* from faeces of *C. pullus* (Compare also to Tab. 3). The scale represents 0.5 µm.
- Fig. 12a - d** Left and right mandible of a female (a,b) and a male (c,d) *C. pullus*. The scale applies for all figures.



IZ4

IZ3

Fig. 7

RR

RM

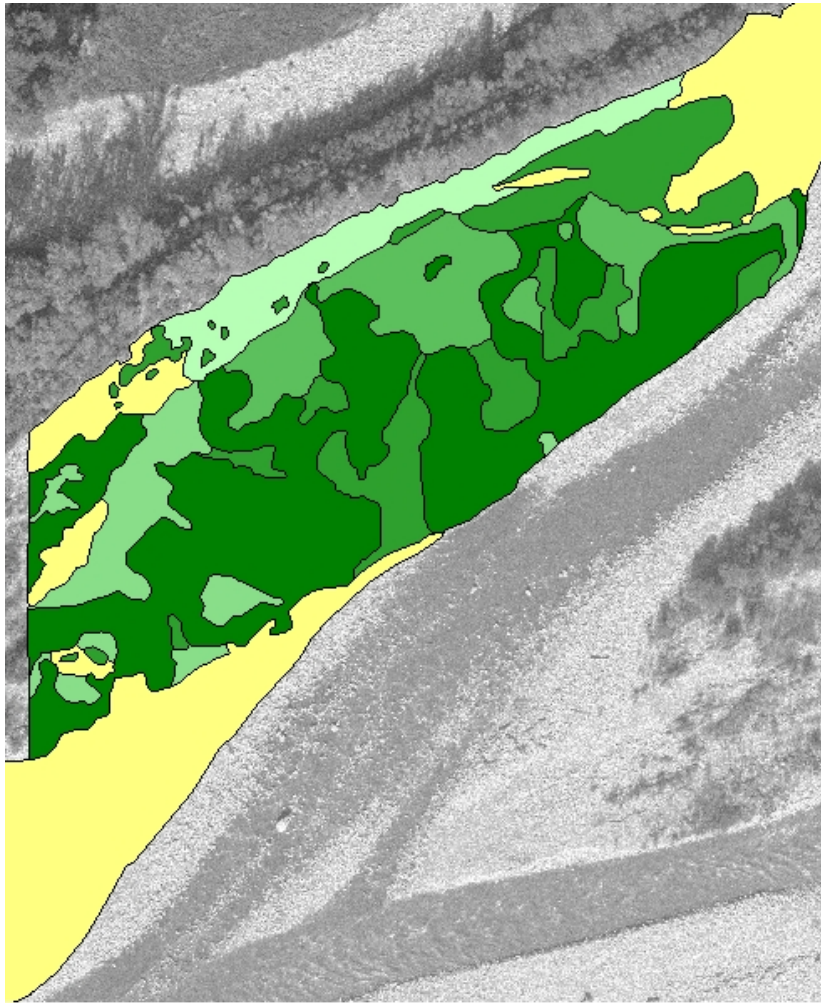


Fig. 8

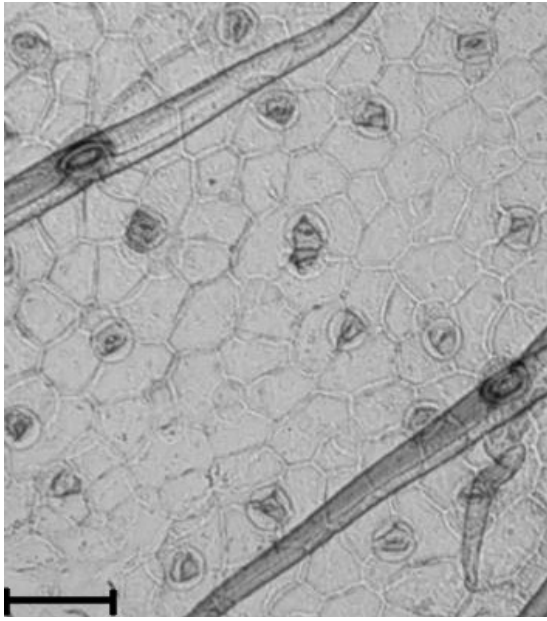


Fig. 9

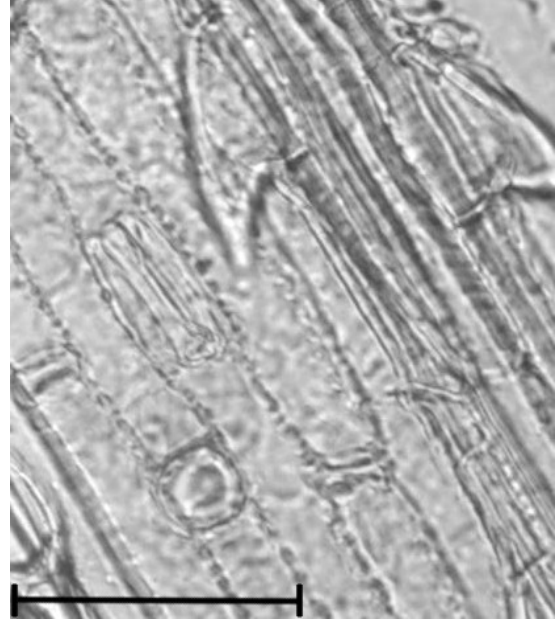


Fig. 10

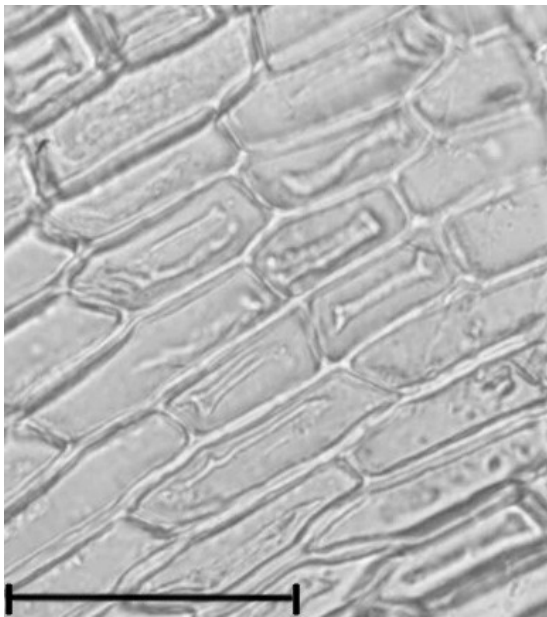


Fig. 11



0.5 mm

Fig. 12a



Fig. 12b



Fig. 12c



Fig. 12d