

# Determinants of seasonal feeding of the generalist snail *Arianta arbustorum* at six sites dominated by Senecioneae

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**Abstract** We investigated the diet constituents of *Arianta arbustorum* by means of faecal analysis and regressed their quantity on the availability and quality of food plants. We studied six sites, all dominated by plants from the Asteraceae tribe Senecioneae, early and later in the growing season, predicting that the snail's food choice would be determined by the presence of the different secondary compounds found in the Senecioneae. The snails consumed less green plant material and more leaf litter in May than in July. Plant water and nitrogen content were higher in May. For the May samples, regressions were only significant at sites that excluded *Adenostyles alliariae* and *Adenostyles alpina*; in July, the regression fit was higher at all sites. Of the measured plant parameters, only quantity (availability) was a consistently significant variable in the regressions. Circumstantial evidence suggested that plant secondary compounds had a major influence on snail food choice: fresh-plant consumption increased over the season, as the concentration of many secondary compounds decreased; both plant availability and quality could only explain about half of the observed variation in snail feeding, which argues for other hidden factors influencing snail feeding; the dynamics of feeding of the various senecionean plants were such that *A. alliariae* and *Senecio* sp. had a seasonal acceptance whereas *Petasites albus* was always and *A. alpina* never accepted, and, finally, the detection of a number of snail-deterrent fractions in *A. alpina* leaves, a plant which was never found to be consumed in this study.

**Keywords** Snails · Secondary plant compounds · Food quality · Food availability · Senecioneae

## Introduction

Feeding by any animal will primarily serve to meet its basic needs for nutrition. While in carnivores this can usually be done without ingesting other unwanted diet constituents, herbivores face the problem that in addition to the low and mostly unbalanced nutrient content of their diet, it almost always comes with added feeding deterrents, digestibility reducers or even toxic components (Crawley 1983; Strong et al. 1984; Simpson and Simpson 1990; Bernays and Chapman 1994). While specialised herbivores have evolved effective countermeasures to deal with these added complications to their nutrition, and some may even use them to their own advantage against their predators (Rowell-Rahier and Pasteels 1992; Rowell-Rahier et al. 1995), generalist herbivores, although capable of efficient detoxification (Brattsten 1992), are thought to be more affected by constitutive or induced secondary plant compounds (van der Meijden 1996; Karban and Baldwin 1997). Specialisation in herbivores has been fundamental in the predictions for the evolution of levels of plant defensive compounds, their dynamics and their characteristics with regard to plant life history (Feeny 1976; Rhoades and Cates 1976; Bryant et al. 1983; Coley et al. 1985; Feeny 1990; van der Meijden 1996). In some cases, predictions of these types of hypotheses have been confirmed (e.g. Bryant et al. 1989), whereas in others, the evidence has been only partially supportive (e.g. Hägele and Rowell-Rahier 1999b).

Research on slugs and snails as generalist herbivores, although less extensive than in insects and vertebrates, has a long tradition in herbivore biology. In fact, one of the first comprehensive studies on the effect of plant secondary compounds on herbivore feeding was done with slugs and snails (Stahl 1888). However, except for some slugs, most snails have omnivorous feeding habits, in-

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**Table 1** Pattern of pyrrolizidine alkaloid (PA) and sesquiterpene (ST) content of asteracean plants, known feeding response of *Arianta arbustorum* to *Adenostyles alliariae* and some secondary compounds, leading to hypotheses about acceptance or avoidance of a plants during the season

Plant species	Early season	Late season	Hypotheses on snail feeding	References
<i>Adenostyles alliariae</i>	High concentrations of non-deterrent PAs; low concentrations of snail-deterrent STs; avoided by <i>A. arbustorum</i>	Low concentrations of non-deterrent PAs; low concentration of snail-deterrent STs; accepted by <i>A. arbustorum</i>	Seasonal avoidance (dependent on non-PA secondary compounds)	Speiser and Rowell-Rahier 1991; Hägele 1992; Hägele et al. 1996; Hägele and Rowell-Rahier 1999b
<i>Adenostyles alpina</i>	Low concentrations of non-deterrent PAs; low concentrations of additional deterrent STs	Unknown concentrations of non-deterrent PAs; increased concentrations of additional deterrent STs	General avoidance due to ST content	Hägele 1992; Hägele et al. 1996; Hägele and Rowell-Rahier 1999b
<i>Senecio</i> sp.	Low concentrations of non-deterrent PAs; unknown concentrations of STs with untested effects	Unknown concentrations of non-deterrent PAs; unknown concentrations of STs with untested effects	(Partial) avoidance?	Seaman 1982; Rowell-Rahier et al. 1991
<i>Petasites albus</i>	No PAs; unknown concentrations of non-deterrent STs	No PAs; unknown concentrations of non-deterrent STs	Acceptance	Rowell-Rahier et al. 1991; Hägele et al. 1996

cluding fungi, and senescent and decaying plant material into their diet (Frömming 1937, 1962; Chang 1991). Since the nutritional value of decaying plant material is impoverished (through bacterial and fungal decomposition), the benefits of feeding on decomposing material might lie in increased palatability as secondary plant chemicals are also broken down. Nevertheless, fresh plant material should be most nutritionally valuable for the herbivore. For the plant, only the loss of green productive leaf mass should have (fitness) consequences, and therefore fresh leaf mass should be protected as a valuable resource (McKey 1979; Mattson 1980; Herms and Mattson 1992).

The importance of snails as generalist herbivores can only be determined by field studies, measuring their impact on the existing plant community. However, direct observation of feeding in the field is complicated by the partially nocturnal activity of snails and their being easily disturbed by an approaching observer, causing them to withdraw into the shell and become inactive. Therefore faecal analysis of snails, sampled in a given area, is an appropriate way to investigate their diet, providing an indirect record of all feeding events throughout a given time period, determined by the speed that food items pass through the dietary system (Speiser and Rowell-Rahier 1991). An experimental approach using artificially created systems with a defined species composition is a very useful method to determine the importance of snail herbivory under specific circumstances, but it can never mimic the field situation with its interactions at all trophic levels (Fraser and Grime 1999).

In their field study, Speiser and Rowell-Rahier (1991) found that plant availability was the only significant factor explaining part of the variability in snail feeding. They also found evidence for a seasonal change in palatability of the major food plant, *Adenostyles alliariae*, which was interpreted as the consequence of a possible

deterrent effect of the plant alkaloid content. This interpretation had to be withdrawn, when alkaloids themselves were found to have no snail-deterrent effect (Speiser et al. 1992). However, the discovery that sesquiterpenes from *A. alliariae* were snail deterrent (Speiser et al. 1992; Hägele et al. 1996, 1998) prompted further investigation. By comparing sites dominated by different senecionean plant species, we wanted to test the hypothesis that qualitative constitutive defences determine snail food choice.

Based on our knowledge about the major secondary compounds of the Senecioneae, pyrrolizidine alkaloids (PAs) and sesquiterpenes (STs), we hypothesised that we could expect different feeding patterns according to the presence or absence of the plant compounds (see Table 1). We specifically asked whether (1) plant availability was the major predictor of snail feeding over the variety of habitats investigated, (2) there was seasonal variation in feeding as predicted by our knowledge of the occurrence of plant compounds, and (3) plant nutritious quality, measured as water, carbon, nitrogen, sugar and starch content, rather than secondary compounds, could predict a significant part of the variability in snail feeding.

## Materials and methods

We collected 22–30 adult snails of the species *Arianta arbustorum* (L.) (Gastropoda, Helicidae) at each of six field sites early and late in the growing season. We tried to sample exhaustively in the smallest possible area. *A. arbustorum* is the most common helioid snail in middle Europe (Kaestner 1982) and is common in humid habitats up to 2,700 m in altitude (Kerney et al. 1983). Each snail was placed into a small plastic container (4 cm diameter, 2.5 cm high) lined with moist white toilet paper. Snail faeces were regularly removed from the containers until the paper faeces appeared, which was usually after 1–2 days. This time period is therefore also representative of the sampled feeding period in the field. The faecal samples were stored frozen at  $-18^{\circ}\text{C}$  in Eppendorf cups.

A reference collection was established of the cuticles of all plants present at all sampling sites. The upper and lower leaf cuticles were embedded in glycerol-gelatine (Merck 9242) and examined microscopically for typical structures such as the form of single and multicellular hairs or crystalline vacuolar deposits. Structures were sketched and the microscopic slides were stored in a reference collection. To identify the faecal contents, we first placed the faecal strings on a microscopic slide and measured their total length. Contiguous areas of the same colour and texture were grouped and measured individually under the dissecting microscope. Three samples of each faecal string part with uniform characteristics were taken, at the beginning, the middle and the end of each string part. The samples were transferred to another microscopic slide and the tissue fragments were examined for typical structures. By comparison with the reference collection, most tissue fragments could be identified, and the faecal string length was regarded as a quantitative sample of a feeding event from the respective plant. Furthermore, the sample colour provided a clue as to whether the plant part had been consumed when fresh or in a stage of decay. Each typical faecal part was then quantified as a percentage of the total length of the faecal string.

Our field sites were Appenzell (patch of 20 m<sup>2</sup>, 9°27'28" E, 47°16'29" N; AI, Switzerland), Kandersteg (30 m<sup>2</sup>, 7°39'15" E, 46°28'32" N; BE, Switzerland), Lécherette 1 and Lécherette 2 (16 m<sup>2</sup>, 7°6'38" E, 46°27'4" N; 30 m<sup>2</sup>, 7°6'58" E, 46°26'56" N; VD, Switzerland), Weissenstein (30 m<sup>2</sup>, 7°31'55" E, 47°15'16" N; SO, Switzerland) and Zastler (30 m<sup>2</sup>, 8°20" E, 47°53'13" N; BW, Germany). At each field site, we identified all vascular plants and collected reference specimens for microscopic cuticle examination. Plant nomenclature follows Hess et al. (1984).

Twice, in May and July, the vegetation of a square metre, representative of the site-specific herbaceous plant cover, was removed, stored in closed plastic bags within a cooled container and transported to the laboratory. We determined the wet mass of each plant species, and after drying (at 50°C), each sample was weighed again to determine its dry mass. Plant water content was calculated as the difference between wet and dry mass and is expressed as a percentage of the wet mass. Leaves from a sample of the specimen of each dried plant species were homogenised with a mortar and pestle for carbon, nitrogen and sugar content analysis. Carbon and nitrogen content were determined spectroscopically from a powdered leaf sample of 2 mg with a CHN-900 analyser (Leco). Results are given as the percentage of carbon and nitrogen contained in each sample. For all plants collected in July, the starch and sugar content of a sample (5–10 mg) were measured with an enzyme-based assay, described in detail by Würth (1991) and based on the method of Wong (1990).

To identify the factors important to the snails' feeding choice, we conceptually divided the variables into a quantity factor (plant availability) and a quality factor (plant content of water, carbon, nitrogen, soluble sugars and starch). In a first step, a principal-component analysis with all quality factors was calculated and the first principal components were used together with the quantity factor as independent variables in a multiple regression, the

amount of green plant material found in the faeces being the dependent variable. Percentage values were arcsine-transformed and plant dry mass was log-transformed prior to analyses (Zar 1984). When appropriate, additional parametric and non-parametric methods, which are mentioned in the text, were used for data analysis. All analyses were computed using the software StatView and SuperAnova on a Macintosh computer.

## Results

Along with the well-defined stomach string enclosed in mucus and a fine liver string attached to the stomach string, most faecal samples contained a portion which was of a fine granular consistency and brownish in colour. Since no structure could be identified, we assumed that it represented additional excretion of the digestive gland and omitted it from analysis. There was no difference in the length of the digestive gland faeces between sampling dates but a tendency to differ among sampling sites (mean±SE: 5.4±0.48 mm and 6.8±0.66 mm in May and July, respectively; two-way random-effect ANOVA: month, MS=154.8,  $F_{1,5}=2.71$ ,  $P=0.16$ ; site, MS=275.2,  $F_{5,5}=4.81$ ,  $P=0.055$ ; interaction, MS=57.2,  $F_{5,297}=1.18$ ,  $P=0.31$ ).

Most plant tissue remains in the faecal strings could be identified. There was no difference in the total length of the faecal strings between dates and sites (mean±SE: 96.3±3.35 mm and 97.0±3.13 mm in May and July, respectively; two-way random-effect ANOVA: month, MS=209.9,  $F_{1,5}=0.093$ ,  $P=0.77$ ; site, MS=7,469.5,  $F_{5,5}=3.315$ ,  $P=0.11$ , interaction, MS=2,253.4,  $F_{5,297}=1.488$ ,  $P=0.19$ ).

The mean length of the faecal strings derived from feeding on green (fresh) plant parts differed between sampling dates and sites. The amount of fresh plant parts eaten in July was higher than in May, and at the Appenzell site, the snails ate more green plant parts than at Lécherette 2, Weissenstein and Zastler (Table 2; mean±SE: 25.2±1.6 and 40.1±2.32 mm in May and July, respectively; 44.4±3.85, 26.8±3.17, 27.2±3.86 and 26.5±3.43 mm for Appenzell, Lécherette 2, Weissenstein and Zastler, respectively; two-way random-effect ANOVA: month, MS=17,808,  $F_{1,5}=33.1$ ,  $P=0.002$ ; site, MS=2,786,  $F_{5,5}=5.2$ ,  $P=0.047$ ; interaction, MS=537,  $F_{5,297}=0.9$ ,  $P=0.480$ ). From the fresh (green) plant tissue

**Table 2** Mean proportion of green plant parts, brown plant parts, leaf litter, soil and other minor constituents of the snail faecal strings at six sites and on two sampling dates. Proportions are

	Appenzell		Weissenstein		Zastler		Kandersteg		Lécherette 1		Lécherette 2	
	May (n=26)	July (n=25)	May (n=25)	July (n=25)	May (n=22)	July (n=28)	May (n=27)	July (n=25)	May (n=25)	July (n=30)	May (n=25)	July (n=25)
Green plant parts	47.1	62.7	17.3	37.5	25.8	48.8	30.5	54.9	27.6	46.5	21.9	39.9
Brown plant parts	17.1	29.2	32.5	36.4	38	38	54.5	40	33.5	46.5	25.2	56.6
Leaf litter	35.4	5.7	29.1	2.6	24.9	5.8	11.5		21.1	4.1	40.6	3.1
Pollen scales			7		8.3							
Pappus hairs			7	4.7		2.5	1.2		17.6		2.9	
Arthropods	0.5	2.3	1.6	3.4	0.1	0.5	1.7	0.5	0.1	0.4	0.8	0.4
Soil			5.8	15.6	3	4.5	0.6	4.6	0.2	2.6	8.7	

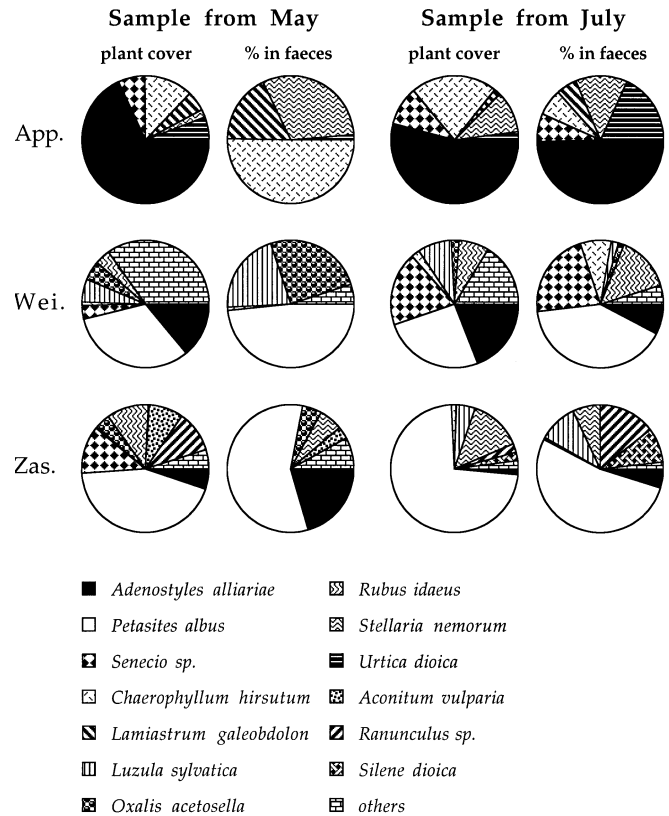
means of percentages of the total amount recovered from each individual snail. The number of snails examined (*n*) per site and collection date is shown

parts, which comprised 28% of the total faeces in May and 48% in July (Table 2), only 0–12% could not be identified (Appenzell 0%, 12%, Weissenstein 0.5%, 5%, Zastler 0%, 6%, Kandersteg 0%, 9%, Lécherette 1 0%, 8%, Lécherette 2 3%, 1%, in May and July, respectively).

There was no difference in the amount of decaying (brown) plant parts found in the faeces between sampling dates and sites (Table 2; means±SE: 45.9±3.06 and 41.1±2.73 mm in May and July, respectively; two-way random-effect ANOVA; month, MS=1,585,  $F_{1,5}=1.08$ ,  $P=0.345$ ; site, MS=6,759,  $F_{5,5}=4.62$ ,  $P=0.059$ ; interaction, MS=1462,  $F_{5,297}=1.22$ ,  $P=0.299$ ). However, the amount of leaf litter found in the faeces of the snails of all sites was always higher in May than in July (Table 2; mean±SE, 16.2±2.18 and 2.9±0.72 mm in May and July, respectively; two-way random-effect ANOVA: month, MS=13,256,  $F_{1,5}=9.43$ ,  $P=0.028$ ; site, MS=1,355,  $F_{5,5}=0.96$ ,  $P=0.515$ ; interaction, MS=1,405,  $F_{5,297}=3.95$ ,  $P=0.002$ ). The significant interaction term merely indicates that the mean values between sites are much more variable in May than in July and therefore the overall interpretation with regards to the seasonal effect is still valid. There was no difference in the amount of soil found in the faeces between the two sampling dates (Table 2; 3% in May and 5% in July, Wilcoxon test,  $df=5$ ,  $z=0.944$ ,  $P<0.35$ ).

In addition to the finding that plant dry mass was higher in July than in May (paired  $t$ -test,  $df=50$ ,  $t=5.85$ ,  $P<0.001$ ), we also found significant differences in plant quality between the two sampling dates. Plant water content was higher in May (83.9%) than in July (82.6%; paired  $t$ -test,  $df=45$ ,  $t=2.97$ ,  $P<0.005$ ). The nitrogen content of the plants was higher in May (3.7%) than in July (3.2%; paired  $t$ -test,  $df=47$ ,  $t=3.87$ ,  $P<0.001$ ). The nitrogen content of leaf litter was 1.5% (95% confidence interval: 1.2–1.9), which is much less than the above-noted nitrogen content of living plants. The overall carbon content of plants did not differ between sampling dates (May: 42.7%, July: 42.4%; paired  $t$ -test,  $df=48$ ,  $t=0.374$ ,  $P=0.71$ ), and the carbon content of leaf litter (41.4%) did not differ from that of living plants ( $t$ -test,  $df=8$ ,  $t=1.021$ ,  $P<0.33$ ). Total non-structural carbohydrate (sugars and starch) and soluble sugars were only measured in the July sample. Soluble sugars accounted for 1.2% (95% confidence interval: 1–1.5%) of total plant dry mass and starch accounted for 2.7% (95% confidence interval: 2.1–3.3%).

At two sites in May, Weissenstein and Zastler, we found pollen scales of *Picea abies* in the snail faeces (7% and 8%, respectively). At four sites in May, a proportion of the faeces comprised asteracean pappus hairs (Weissenstein 7%, Kandersteg 1.2%, Lécherette 1 17.6%, Lécherette 2 3% of faeces). Only *Petasites albus* is in flower at these sites and time. The snails are likely also consuming developing seeds along with the pappus hairs of *P. albus*, although no evidence for this could be detected in the faeces. In July, pappus hairs appeared in the faeces of snails from two sites (Weissen-



**Fig. 1** Plant mass availability and proportion of green plant parts in snail faeces in habitats which included *Adenostyles alliariae*. The number of snails sampled per site and month were: Appenzell (App.) 26 and 25, Weissenstein (Wei.) 25 and 25, Zastler (Zas.) 22 and 28 in May and July, respectively

stein 4.7% and Zastler 2.5%). At Weissenstein, we observed snails feeding from *Senecio nemorensis* flowers; at Zastler, no flower feeding was observed in the field, even though *S. fuchsii* and *A. alliariae* flowers were available at this time of the year. Arthropod remains were found in small quantities in the snail faeces from each site and date (Table 2).

In habitats which included *A. alliariae* as a prominent part of the plant cover, it was not found in the faeces in the May samples, but was found in those from July, as would be expected according to its proportion of the plant cover (Fig. 1). One exception seemed to be the sample from Zastler where a large proportion of *A. alliariae* was found in the faeces of the May sample. However, this observation originated from two snails which were found on an almost entirely defoliated plant of *A. alliariae*, whereas all other surrounding *A. alliariae* plants had not been touched by any other snail. Plant quality, measured as water, carbon, nitrogen, soluble sugars and starch content, was never a significant factor in snail food choice in *A. alliariae* habitats. In all cases, except at Appenzell in May, snail food choice can be explained largely by the available plant biomass (Table 3).

In habitats without *A. alliariae*, *P. albus* was the most prominent single plant species (Fig. 2). Here we could

**Table 3** Multiple regression of plant quantity (log plant dry weight) and quality on snail feeding in habitats including *Adenostyles alliariae*. The first principal component (*PC1*) produced by a principal-component analysis (PCA) on water, nitrogen and carbon content produced the “quality factor” for the multiple regression. In all analyses from July, the PCA was extended to include soluble sugars and starch content also. Log-transformed plant dry weight is used as the quantity variable. The estimated regression coefficients ( $\beta$  coefficient) and their SEs are shown (*n.a.* not available)

<sup>a</sup> PC1 accounted for a total of the variability in plant quality: Appenzell May 57.5%, July 54.6%; Weissenstein May 61.3%, July 60.2%; Zastler May 50.9%, July 50.4%

	$\beta$ coefficient	SE	<i>t</i>	<i>P</i> -value	Adjusted multiple <i>r</i> <sup>2</sup>	<i>F</i> -statistic <i>P</i> -value
Appenzell, May					n.a.	0.676
Intercept	3.975	2.305	1.725	0.119		
Log plant dry weight	0.720	4.549	0.158	0.878		
PC1 <sup>a</sup>	-1.888	2.681	0.704	0.499		
Appenzell, July					0.719	0.069
Intercept	-0.119	0.096	1.245	0.301		
Log plant dry weight	0.348	0.106	3.275	0.046		
PC1 <sup>a</sup>	-0.132	0.082	1.605	0.207		
Weissenstein, May					0.269	0.084
Intercept	0.332	0.671	0.495	0.632		
Log plant dry weight	2.359	0.954	2.473	0.033		
PC1 <sup>a</sup>	-0.406	0.587	0.691	0.505		
Weissenstein, July					0.534	0.064
Intercept	0.001	0.031	0.030	0.977		
Log plant dry weight	0.076	0.029	2.589	0.048		
PC1 <sup>a</sup>	-0.032	0.021	1.537	0.185		
Zastler, May					0.272	0.114
Intercept	-0.022	0.037	0.603	0.563		
Log plant dry weight	0.118	0.056	2.103	0.068		
PC1 <sup>a</sup>	-0.016	0.020	0.825	0.433		
Zastler, July					0.504	0.004
Intercept	0.010	0.024	0.410	0.689		
Log plant dry weight	0.099	0.027	3.631	0.004		
PC1 <sup>a</sup> (omitted)				(0.997)		

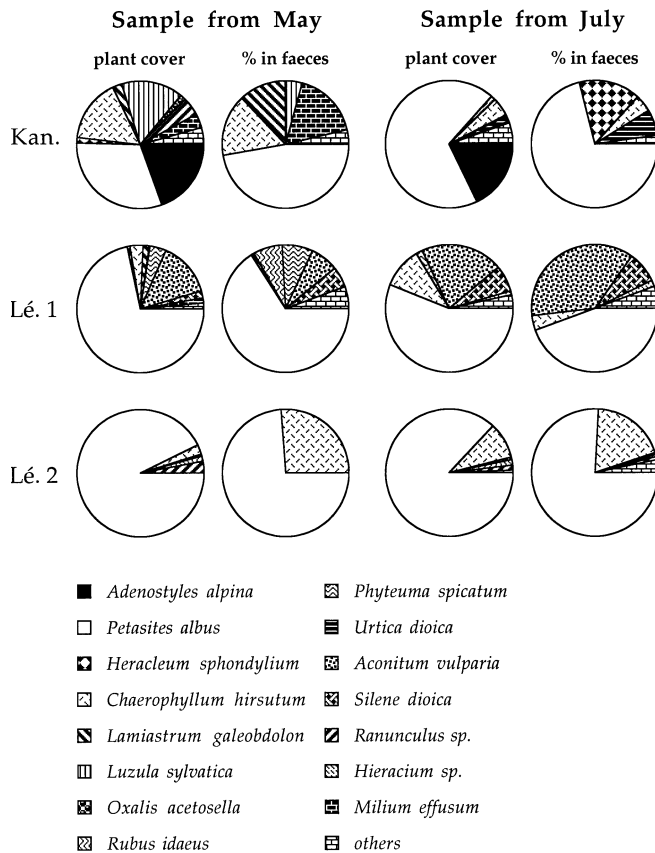
**Table 4** Multiple regression of plant quantity (log plant dry weight) and quality on snail feeding in habitats without *Adenostyles alliariae*. The first principal component (*PC1*) produced by a PCA on water, nitrogen and carbon content produced the “quality factor” for the multiple regression. In all analyses from July, the PCA was extended to include plant soluble sugars and starch content also. The second principal component (*PC2*) was included in the model from the data of Lécherette 2 in July. Log-transformed plant dry weight is used as the quantity variable. The estimated regression coefficients ( $\beta$  coefficient) and their SEs are shown

<sup>a</sup> PC1 accounted for a total of the variability in plant quality: Kandersteg May 48.2%, July 37.8%; Lécherette 1 May 40.7%, July 43.6%; Lécherette 2 May 60.0%, July 34%  
<sup>b</sup> PC2 accounted for 27.4% of the variability in plant quality

	$\beta$ coefficient	SE	<i>t</i>	<i>P</i> -value	Adjusted multiple <i>r</i> <sup>2</sup>	<i>F</i> -statistic <i>P</i> -value
Kandersteg, May					0.222	0.059
Intercept	0.038	0.014	2.641	0.018		
Log plant dry weight	0.061	0.023	2.614	0.019		
PC1 <sup>a</sup>	0.013	0.016	0.820	0.425		
Kandersteg, July					0.436	0.004
Intercept	0.039	0.028	1.411	0.182		
log plant dry weight	0.129	0.037	3.441	0.004		
PC1 <sup>a</sup> (omitted)				(0.985)		
Lécherette 1, May					0.635	<0.001
Intercept	0.111	0.019	5.900	<0.001		
Log plant dry weight	0.122	0.027	4.484	<0.001		
PC1 <sup>a</sup>	0.065	0.018	3.641	0.003		
Lécherette 1, July					0.787	<0.001
Intercept	0.051	0.024	2.146	0.064		
Log plant dry weight	0.206	0.033	6.201	<0.001		
PC1 <sup>a</sup>	-0.033	0.021	1.532	0.164		
Lécherette 2, May					0.631	0.008
Intercept	0.057	0.021	2.762	0.025		
Log plant dry weight	0.136	0.031	4.374	0.002		
PC1 <sup>a</sup>	-0.014	0.022	0.640	0.540		
Lécherette 2, July					0.903	<0.001
Intercept	0.016	0.017	0.922	0.383		
Log plant dry weight	0.258	0.027	9.637	<0.001		
PC1 <sup>a</sup>	0.012	0.017	0.692	0.509		
PC2 <sup>b</sup>	-0.029	0.017	1.740	0.120		

not observe a seasonal avoidance pattern: *P. albus* was readily consumed in May and July. Note that *Adenostyles alpina*, present at Kandersteg and closely related to *A. alliariae*, was consumed in neither May nor July. In these habitats also, plant biomass as a single variable

could explain most of the variation in snail feeding (Table 4). A notable extension to this statement is the sample from Lécherette 1 in May. Here, in addition to the significant contribution of plant mass (availability), the quality factor could also explain a significant propor-



**Fig. 2** Plant mass availability and proportion of green plant parts in snail faeces in habitats without *Adenostyles alliariae*. The number of snails sampled per site and month were: Kandersteg (*Kan.*) 27 and 25, Lécherette 1 (*Lé. 1*) 25 and 30, Lécherette 2 (*Lé. 2*) 25 and 25 in May and July, respectively

tion of the variation in snail feeding (Table 4). Plant water, carbon and nitrogen content correlated strongly with the principal component ( $H_2O$ : -0.69; C: 0.81; N: 0.28), which accounted for 41% of the original variation in plant quality.

## Discussion

The results from the faecal analyses confirm earlier findings that *A. arbustorum* along with other snails is an omnivorous feeder with a tendency to feed on fast-growing ephemerals and perennials (Frömming 1937, 1962; Grime and Blythe 1969; Chang 1991; Speiser and Rowell-Rahier 1991; Hägele 1992; Fraser and Grime 1999). However, for the first time, we can draw more general conclusions about feeding patterns of the species, since the sampling of various sites allows statistical comparison among them.

The appearance of minor opportunistic constituents in the faeces, such as arthropods, pollen scales or pappus hairs, further confirms the snail's omnivorous feeding habits. The ingestion of arthropods (soil insects and mites) is most probably an accidental by-product of soil

feeding, the significance of which is either in adding hard material to the stomach to facilitate tissue grinding or, more likely, to supply the calcium needed for shell formation (Fretter and Graham 1962). Whereas the pollen scales of *P. abies* seem to be a truly opportunistic food source which is ingested as soon as it is encountered, the case of the asteracean pappus hairs could be more complicated. If the whole tubular flower (including seed) is consumed together with the pappus hairs, which seems a plausible assumption, then they provide a very nutritious food source rich in protein (Richter 1988). However, seeds may be heavily protected by surrounding leaves, toxins and deterrents (Hartmann 1999) which, if effective against snails, might limit the window of opportunity for their consumption to periods when the concentration of protective compounds is still low. The fact that pappus hairs were only found in reasonable amounts in two out of the five sites where flowers of *P. albus* were available indicates that the window of opportunity for the consumption of this valuable food source must be small or the protective devices are difficult to overcome.

The function of litter feeding remains an enigma. If we accept that there is a functional connection between litter feeding and the quality of the green plant parts eaten at the same time of the year (May), litter feeding might somehow counteract the effects of high concentrations of secondary compounds by providing tannins. However, although tannins might interfere with the action of metal ions and alkaloids (Hagerman and Butler 1991), or with cyanogenic glycosides released through enzymatic action (Goldstein and Spencer 1985), both mechanisms require the harmful compound to be ingested together with the adsorbent, a condition which is not met in the case of the sequentially feeding snails (Speiser and Rowell-Rahier 1993). Therefore, we would expect the high tannin content to bind dietary proteins in the gut, an effect which is certainly counterproductive to food absorption (Hagerman and Butler 1991). Other possible benefits of litter feeding might include the ingestion of acidic components or litter-degrading microbes and their enzymes, which might be employed in lignin digestion. However, although we believe in a functional relationship between fresh plant and litter feeding early in the season, these suggestions remain highly speculative.

The most striking general pattern observed was the about twofold increase in the consumption of green plant material from May to July. Whereas the amount of consumed senescent plant material remained roughly the same, the amount of leaf litter consumed decreased drastically over the observation period (Table 2). In addition, food quality in terms of plant water and nitrogen content decreased from May to July; thus, if snails maximise nutrient quality at all times, they should have consumed much more fresh food early in the growing season.

We can think of two ecological processes which could bring about this pattern – predation and dietary unsuitability. Predation pressure might cause the snails to primarily hide in the leaf litter and only take advantage of

the herbaceous plant level when it is very dense and provides sufficient cover from predators later in the season. *A. arbustorum* does indeed hide in the leaf litter during the day, where it is hard to spot due to its brownish coloration (Kerney et al. 1983). This should provide good protection from visually hunting predators like birds. During the night, the snails are active, as are their insectivorous mammalian predators (Kerney et al. 1983). Climbing into the plant canopy should provide some protection from these predators and brings the snails to their food sources. If the snails feed opportunistically, we would expect the day/night dynamics to produce a feeding pattern reflecting the general availability of food plants in the habitat, which is what we found for all sites in July and for the *Petasites*-dominated sites in May (Tables 3, 4). However, it is hard to see how the same predation dynamics could account for the pattern of seasonal or general avoidance as seen for the *Adenostyles* species.

We therefore favour as the most likely explanation for the failure to meet the prediction of maximising food intake with highest plant quality that deterrents and toxins preclude the snails from taking full advantage of the quality of available food sources (Freeland and Janzen 1974). Alternatively, compensatory feeding, e.g. between protein- and carbohydrate-containing diets, could produce a pattern without a simple correlation between high contents of both nutrients and feeding preference (Simpson and Simpson 1990; Simpson et al. 1995). The observation that most snails had at least two different food items in their guts, and had thus switched their diets during the last 24–48 h, however, supports the hypotheses of compensatory feeding behaviour as well as toxin dilution (Speiser and Rowell-Rahier 1993; Hägele and Rowell-Rahier 1999a). Although compensatory feeding might be one of the reasons why the simple measure of plant quality was almost never important in explaining the snails' food choice, it is difficult to imagine how it could have caused the pattern seen in the *Adenostyles* and *Senecio* species. They were either completely (*A. alpina*) or seasonally (*A. alliariae*, *Senecio* sp.) avoided, a pattern that we would expect to be caused by deterrent or toxic plant compounds given that many plant secondary compounds are known to decrease in concentration as the growing season progresses (Gershenson and Croteau 1991).

Nevertheless, however suggestive an observed correlation might be, it cannot prove a causal relationship between the observed patterns. For example, the case made for PAs and their possible influence on snail feeding (Speiser and Rowell-Rahier 1991) had to be rejected when snails were later found to show little response to the isolated compounds (Speiser et al. 1992). STs, however, tested as single compounds by Speiser et al. (1992) and Hägele et al. (1996, 1998) had a significant effect on snail feeding, but in the field, STs of *A. alliariae* and *A. alpina* might only be effective in subterranean plant parts, since the compounds were either not found in the leaves (*A. alliariae*) or in concentrations which were not

deterrent in single-compound tests (*A. alpina*). During a subsequent fractionation of *A. alpina*, however, we discovered at least four leaf-derived and nine rhizome-derived fractions containing unknown compounds with snail-feeding-deterrent activity (B.F. Hägele and J. Harmatha, unpublished results). This finding underlines the need to look at all potential compounds rather than the most obvious ones when looking for functional explanations for specific feeding patterns.

Our results support the hypothesis that apparent and predictable high-quality ephemeral tissue should be specially protected against generalist herbivores (Feeny 1976; Rhoades and Cates 1976; McKey 1979). This is also a prerequisite of van der Meijden's (1996) model, which explains the distribution of secondary compounds in plants within a population. Most of our predictions about seasonal avoidance of plants, based on our knowledge of their secondary compound content, were confirmed. *A. alliariae* and *Senecio* species, which have a seasonally declining concentration of PAs were seasonally avoided, *A. alpina* with both PAs and STs with unknown seasonal dynamics was always avoided, and *P. albus*, with no PAs and a non-deterrent ST, was palatable over the whole season. However, on closer examination, we still lack the ultimate explanation for the observed pattern. Seneciphylline, the main alkaloid in *A. alliariae* and *A. alpina* is not snail deterrent (Donati 1992; Speiser et al. 1992), and adenostylone, cacalol and cacalol-trimer, the only STs present in the leaves of *A. alpina*, but not in *A. alliariae*, are not snail deterrent in the quantities observed (Hägele et al. 1996, 1998; Hägele and Rowell-Rahier 1999b). Therefore, the observed consistency with our original predictions is most likely not a direct consequence of the avoidance of known compounds, but rather a by-product of the avoidance of other snail-deterrent substances, some of which we have begun to identify in the case of *A. alpina* (B.F. Hägele and J. Harmatha, unpublished results).

In summary, although plant availability was the strongest predictor of snail food choice, which would argue for indiscriminate feeding, influenced only by the available biomass, there is circumstantial evidence to suggest that, in addition to plant nutritional quality, plant secondary compounds influence snail food choice: (1) fresh plant consumption increases over the season, as the concentration of many secondary compounds decreases (Gershenson and Croteau 1991; Speiser and Rowell-Rahier 1991); (2) that both plant availability and quality could only explain around half of the observed variation in snail feeding argues for other hidden factors influencing snail feeding; (3) the dynamics of feeding of the various senecionean plants, such that *A. alliariae* and *Senecio* sp. had a seasonal acceptance whereas *P. albus* was always and *A. alpina* never accepted; (4) the detection of a number of snail-deterrent fractions in the leaves of *A. alpina*, a plant which was never found to be consumed in this study.

Our findings argue strongly for the identification and verification of the effects of each compound on each of

the important herbivores, because what might be effective against one (Hägele and Rowell-Rahier 2000) might be ineffective against another (Speiser et al. 1992). This is admittedly a big task, but it might be rewarded with surprising and new insights into the effects of plant compounds and may lead to new hypotheses about their mode of action and ultimately their significance for plant defence.

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