FIELD OBSERVATIONS ON FEEDING OF THE LAND SNAIL
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(Received 16 March 1998; accepted 30 November 1998)

ABSTRACT

Feeding of the land snail Helix aspersa (Müller) was observed at monthly intervals. Three natural populations in Galicia (NW-Spain) were studied. At two sites only a few plants constituted the bulk of the diet and in spring the snails’ diet had the highest diversity (H’). In the third population feeding and distribution of Helix aspersa (Müller) were observed in a small plot with permanent patches of Urtica dioica. Nearly one half of feeding snails fed upon Urtica dioica. Most of the other observations were on Menyanthes trifoliata, Rumex repens and Graminoids. The diversity of the snails’ diet showed seasonal variation with the maximum in the autumn months. Comparison between the availability of the different plant species and their contribution to the snails’ diet showed that the snails did not eat at random; Urtica dioica was eaten much more than expected from its occurrence and grasses were strongly under-represented in the snails’ diet. Temporal changes of availability were significantly correlated with the amounts eaten in the case of Urtica, but not for the other food plants. The distribution of the snails in the plot was significantly correlated with that of Urtica. Chemical analyses of the food plants revealed Urtica as the species with the higher protein, ash and calcium contents. The strong preference of Helix aspersa for Urtica dioica could be explained by the value of Urtica as food or by its suitability as habitat for the snails. The largest proportions of green material in the snails’ diet occurred in the spring and juveniles ate more green material than adults in the three populations.

INTRODUCTION

Land gastropods have traditionally been regarded as generalist herbivores taking a wide variety of plants from the environment (Boycott, 1934; Grime & Blythe, 1969; Mason, 1970; Wolda, 1970; Zweep & Schuijtema, 1971; Richardson, 1975; Jennings & Barkham, 1975; Williamson & Cameron, 1976; Chatfield, 1976; Chang, 1991; Speiser & Rowell-Rahier, 1991; Hatziioannou, Eleutheriadis & Lazaridou-Dimitriadou, 1994). The fact that many land gastropods are capable of eating a wide variety of living and dead plants and of adjusting their diet to the availability of the food items might determine the wide distribution of many species (Pallant, 1972).

Nevertheless, land gastropods show different levels of preference for the different components of their diet, as demonstrated in a number of field (Grime & Blythe, 1969; Pallant, 1969, 1972; Wolda et al., 1971; Williamson & Cameron, 1976; Dan, 1978; Richter, 1979; Speiser & Rowell-Rahier, 1991; Hatziioannou et al., 1994) and laboratory studies (Grime, MacPherson-Stewart & Dearman, 1968; Grime, Blythe & Thornton, 1970; Cates & Orians, 1975; Dirzo, 1980; Richardson & Whittaker, 1982; Rathcke, 1985; Molgaard, 1986; Gallois & Daguzan, 1989; Baur, Bauer & Fröberg, 1994).

Food preferences determine the food ingested by an animal and hence affect its physiological condition and fitness (Carefoot, 1967; Vadas, 1977; Batzli & Lesieutre, 1991). The concept of ‘food preference’ usually comprises two features of the food: attractiveness and palatability. Attractiveness is experimentally measured with choice tests (Dan, 1978; Nicotria, 1980; Rathcke, 1985; Szlavecz, 1986; Gallois & Daguzan, 1989). Palatability is often measured by comparing the quantity of one food item ingested by the consumer in relation to another food (Grime et al., 1968; Cates & Orians, 1975; Molgaard, 1986; Richardson & Whittaker, 1982; Chang, 1991; Egonmwan, 1991) or by means of assimilation rates (Mason, 1970; Jennings & Barkham, 1976; Williamson & Cameron, 1976; Dan, 1978; Staikou & Lazaridou-Dimitriadou, 1989). Vadas (1977) investigated several features related to food preference in sea urchins like chemoreception, feeding rates, assimilation efficiency, caloric value of the foods growth and reproductive capacities of the consumers on different foods, and availability of prey.
items. He concludes that feeding in nature is a compromise between preferences of the consumer and availability of prey items.

The habitat or microhabitat conditions which food plants provide to the consumer may influence its feeding habits (Nicotri 1980), a feature which has not received much attention in gastropods. If any plant species offers the grazer protection from predators, good resting plates, egg-laying sites, overwintering sites, a particular microclimate or any other favourable condition for its life cycle, this might influence the food preference of the consumer. This is specially true in small animals like land gastropods with low mobility and little capacity to defend themselves against predators.

This paper describes the feeding of the land snail *Helix aspersa* in natural populations on the basis of field observations. The importance of direct visual observations in the field for understanding feeding habits in natural conditions has been emphasized (Richardson, 1975; Vadas, 1977; Chang, 1991), but most previous studies on snails’ diet have been based on laboratory feeding experiments or analysis of faeces or crop contents. Since the stinging nettle *Urtica dioica* is often reported as a preferred food plant of land gastropods (Grimé et al., 1968; Grime & Blythe, 1969; Pallant, 1969; Mason, 1970; Grime et al., 1970; Wolda et al., 1971; Cates & Onions, 1975; Jennings & Barkham, 1975, 1976; Chatfield, 1976; Day, 1975; Carter, Jeffery & Williamson, 1979; Staikou & Lazaridou-Dimitriadou, 1989; Lazaridou-Dimitriadou & Kattoulas, 1991; Hatziioannou et al., 1994), we also decided to study in situ whether *Helix aspersa* really prefers *Urtica* over other plant species of the environment and, if so, to search for the causes of that preference.

**MATERIALS AND METHODS**

**Study area**

The study was carried out in two localities in Galicia (NW-Spain), named Cobas and Lapido. The study areas, the climate and the annual activity cycles of *Helix aspersa* at these localities were described in detail by Iglesias, Santos & Castillejo (1996). The three populations will be referred as Cobas, Lapido-I and Lapido-II. The main observation site in Cobas, a plot of 400 m², was abandoned land, the vegetation of which consisted of woody species about 2 m tall, including *Crataegus monogyna*, *Prunus spinosa* and *Rosa* spp., herbs which included mainly *Sanguisorba minor*, *Potentilla splendens*, *Geum sylvaticum*, *Erigeron canadensis*, *Peganum harmala*, *Origanum vulgare* and grasses including *Brachytrichis sp.*, *Poa sp.* and *Lolium sp.* The main observation site for population Lapido-I was an unsurfaced road 90 m long and 4 m wide, the vegetation of which consisted mainly of perennial herbs including *Ranunculus repens*, *Juniperus effusa*, *Menyanthes trifoliata*, *Plantago lanceolata* and *Sonchus asper*, and grasses including *Holcus* sp., *Artemisia vulgaris* sp., *Anchusa officinalis* sp., *Avena sp.*, *Agrostis sp.*, *Bisca sp.* and *Dactylis sp.*

For population Lapido-II the main observation site was a triangular plot of 91 m² delimited by the wall of a house, by a road three meters wide and by an unsurfaced road two meters wide: it was about 400 metres away from the site of population Lapido-I. The vegetation of this plot was very dense but with low diversity, since it consisted almost exclusively of *Menyanthes trifoliata*, *Ranunculus repens*, *Urtica dioica* and grasses including *Dactylis* sp., *Artemisia vulgaris* sp., *Holcus* sp. and *Anchusa officinalis* sp. Some specimens of *Cyperus lutescens*, *Lotus corniculatus*, *Juniperus effusa* and *Plantago lanceolata* were also present, but in very low abundance. The plot was frequently visited before the start of sampling in July 1991, and the existence of a well established population of *Helix aspersa* and of permanent patches of *Urtica dioica* were confirmed. In June 1991, five zones named A, B, C, D (18 m² each) and zone E (19 m²) were delimited with red cords tied to wooden stakes. There were no barriers to prevent snails moving inside the plot or to leave it.

**Sampling**

Cobas and Lapido-I populations were visited monthly from September 1990 to September 1992 (except for May 1991, when only the site of Cobas was visited) on three consecutive nights. Lapido-II population was visited monthly on two consecutive nights from July 1991 to September 1992. Each observation site was carefully explored for 3 hours at least, searching for snails by torchlight. When a snail was seen, we recorded the plant species and whether the snail ate a green or a senescent plant. In Lapido-II we recorded also the position (zone) of the snail. Only observations made on snails feeding upon living or senescent plants were noted. Snails eating dead plant material on the ground, mosses, lichens, fungi, faeces of vertebrates and dead arthropods were also seen, but they were not recorded quantitatively. Observations were noted only when the animals were not disturbed by the observer and when consumption of food was certain from the feeding movements of the animal and/or the feeding marks on the plant. Plant nomenclature was based on Tutin, Heywood, Burges, Moore, Valentine, Walters & Webb (1964), and grass species were pooled. The presence of a solid reflected lip on the peristome of the shell was taken to denote adulthood of snails.

On the day previous to the first night of sampling in Lapido-II, the relative abundance (percentage cover) of the plant species was measured by means of a stratified sampling on 45 points of the plot (9 points/zone). Samples of leaves of the most abundant plant species in this plot (*Menyanthes, Ranunculus, Urtica* and...
Gramineae were collected on four occasions and analyzed for crude protein (Kjeldahl method), raw fibre (Wendel method), soluble sugars (colometry), ash (550°C for 4 hours) and calcium (atomic absorption).

Data analysis

Diversity of the snails' diet and of the vegetation was determined for each sampling by means of the Shannon-Wiener index, \( H' = -\sum (p_i) \log (p_i) \) (Krebs, 1986) where \( p_i \) was the frequency of each plant species in the snails' diet or in the plot. To compare the diversity of adult and juvenile snails' diet, the Mann-Whitney test was performed. A chi-square test with contingency tables was executed to investigate differences between adults and juveniles in relation to green or senescent material. ANOVA and Pricer LSD tests, with arcsine transformation of the data (Sokal & Rohlf, 1981) were performed to compare protein, fibre, soluble sugars, ashes and calcium contents of the different plant species.

With the data of the snails' diet composition and the data of relative abundance of the plants (% cover) in the plot Lapido-II, an electricity index C, according to Peix (1982), was calculated for adults and juveniles in each sampling. The index C is based on 24 and provides a simple way to test the significance of any degree of selection at any sample size. The value of C ranges between -1 and +1, positive values indicating preference, negative values indicating avoidance and C = 0 for random feeding.

In order to examine any relationship between the distribution of the snails and that of the plant species, the percentage distribution of adult and juvenile snails and the percentage distribution of each plant species over the five zones were compared by means of scatter diagrams. The existence of association between the two variables was tested with Kendall's rank correlation coefficient, \( \tau \). The same coefficient was used to investigate any relationship between abundance of each plant species and the amount eaten by the snails.

RESULTS

Snails' diet in the field

In Cobas, a total of 833 observations of snails feeding upon 25 plant species was made (Table 1). The most frequent foods in the diet of Helix aspersa in this site were Fragaria vesca (17.28% of the observations), Gramineae (15.96%), Trifolium angustifolium (12.24%), Hieracium pilosella (10.2%), Eryngium campestre (7.32%)

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<td>Green</td>
<td>Senescent</td>
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<td></td>
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<td>%</td>
<td>13.32</td>
<td>32.17</td>
<td>31.33</td>
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and *Carlina corymbosa* (7.2%); these six plant species represented more than 70% of the feeding observations made in Cobas over the study period. Senescent grasses were the most abundant material in the diet of the snails at Cobas during the autumn, accounting for more than 30% of the observations in September 1990 and November 1991, but in spring, hardly any senescent grasses were eaten. During the spring periods the maximum proportion of one plant species in the diet of the snails was *Fragaria vesca*, with percentages around 20%.

In Lapido-I, a total of 708 observations of snails feeding upon 24 plant species was made (Table 2). *Mentha suaveolens* (20.48%), *Ranunculus repens* (15.39%), Gramineae (15.39%), *Heracleum sphondylium* (8.05%), *Plantago lanceolata* (7.76%) and *Apium nodiflorum* (7.48%) were the most abundant foods, representing more than 70% of the feeding observations made in this plot over the study period. There was not a clear seasonal variation in the contribution of any plant species to the diet of the snails in Lapido-I, the highest contribution of a single plant to the diet was that of *Mentha suaveolens* in November 1991, but the contribution of the most frequent plant in each sampling was in general about 20%.

In Lapido-II, a total of 958 observations of snails feeding were noted during the study period. 95.6% of the observations were made upon the four major foods. Gramineae, *Mentha suaveolens*, *Ranunculus repens* and *Urtica dioica*, and only 4.4% were made upon very scarce plant species in the plot like *Cyperus longus*, *Lotus corniculatus*, *Juncus effusus* and *Plantago lanceolata* (Table 3). The most frequent food in the diet of *Helix aspersa* in this site was *Urtica dioica* with 47.9% of the observations; its contribution to the snails’ diet ranged from 61.9% in August 1991 to 29.8% in November 1991.

For the whole study period, 44.65% of the feeding observations in Cobas were made on green material and 55.35% on senescent plants; in Lapido-I 67.5% of the observations were on green material and 32.5% on senescent plants; in Lapido-II 71.5% of the observations were on green plants and 28.5% on senescent plants. The proportions of adults and juveniles feeding upon green and senescent material during each sampling are shown in Fig. 1. There was a clear

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<th>Juveniles</th>
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Table 3. Field observations on feeding of Helix aspersa in Lapido-II. Others includes Juncus effusus, Cyperus longus, Lotus corniculatus and Plantago lanceolata.

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<th>Juveniles</th>
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<td>18.58</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. Percentages of field observations of adult (left bars) and juvenile (right bars) snails feeding upon green and senescent material during each sampling in the sites Cobas, Lapido-I and Lapido-II.
seasonal variation in the diet with respect to green or senescent material; snails ate mainly green plants during spring, and senescent material during the autumn. Juveniles ate more green material than adults in spring (Cobas $\chi^2 = 35.08$, $P < 0.001$; Lapido-I $\chi^2 = 25.95$, $P < 0.001$), in summer (Lapido-I $\chi^2 = 20.03$, $P < 0.001$) and in autumn (Cobas $\chi^2 = 14.29$, $P < 0.001$; Lapido-I $\chi^2 = 24.73$, $P < 0.001$). In Lapido-II juveniles ate more green material than adults over the whole study period ($\chi^2 = 14.99$, $P < 0.001$), but for the different seasons differences were only significant in summer ($\chi^2 = 10.89$, $P < 0.001$).

Diversity of vegetation and of the snails' diet

The diversity of the snails' diet for the whole study period was $H' = 3.7$ in Cobas and $H' = 3.65$ in Lapido-I, but there was a seasonal variation (Fig. 2) with the maximum diversity in spring and the minimum in autumn.

The diversity of the diet in Lapido-II was $H' = 1.95$; there was also a seasonal variation with the maximum diversity in the autumnal months. The changes in the diversity of the snails' diet, in the diversity of the vegetation and in the abundance (% cover) of Urtica dioica along the study period are shown in Fig. 3, from which it seems that the snails' diet diversity follows an opposite trend to that of the vegetation. Also, the diversity of the snails' diet increased when the abundance of Urtica decreased and vice versa. Kendall's rank correlation test showed that there was no significant association between any of these variables.

Mann-Whitney test showed no statistical difference between adults and juveniles in relation to diet diversity in each site.

Snails' diet in relation to the relative abundance of the plants in Lapido-II

Urtica dioica was preferred by Helix aspersa over the other plant species in the plot (Fig. 4). Rumex crispus and Mentha suaveolens were in a similar rank of abundance as Urtica, but their contribution to the snails' diet was smaller. Gramineae were the most available plant species in the plot, but they were also eaten in a smaller proportion than Urtica.

For the whole population a significant positive association existed between the abundance

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**Figure 2.** Changes in the diversity of the snails' diet in the sites of Cobas and Lapido-I during the study period.

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**Figure 3.** Changes in the diversity of the snails' diet, in the diversity of the vegetation, and in the abundance (% cover) of Urtica dioica along the study period in Lapido-II.
of *Urtica* and the amount eaten by the snails
($\tau = 0.636, P < 0.01, n = 11$), but for the rest of the plant species there was no significant relationship between abundance and the amounts eaten. The association between abundance of plant species and amount eaten was significant only in the case of juveniles and *Urtica* ($\tau = 0.527, P < 0.05, n = 11$).

The monthly values of the electrivity index $C$ for adult and juvenile snails are shown in Table 4. The values of the index $C$, indicate that both adult and juvenile *H. aspera* show a strong preference for *U. dioica* and a strong avoidance for Gramineae. For *Rumex repens*, the values of the electrivity index were always around zero, indicating that this plant species

\[\text{Table 4. Monthly values of the electrivity index } C \text{ for adult and juvenile snails and for the commonest plant species of the site Lapido-II. } \ast = P < 0.05, \ast \ast = P < 0.01. \text{ N.S. = not significant.}\]

<table>
<thead>
<tr>
<th></th>
<th><em>U. dioica</em></th>
<th>Gramineae</th>
<th><em>M. sueveolens</em></th>
<th><em>R. repens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Jul-91</td>
<td>Adults</td>
<td>0.15 **</td>
<td>−0.10 *</td>
<td>−0.01 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.45 **</td>
<td>−0.21 **</td>
<td>−0.08 N.S.</td>
</tr>
<tr>
<td>Aug-91</td>
<td>Adults</td>
<td>0.34 **</td>
<td>−0.23 **</td>
<td>0.00 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.36 **</td>
<td>−0.26 **</td>
<td>0.02 N.S.</td>
</tr>
<tr>
<td>Sep-91</td>
<td>Adults</td>
<td>0.33 **</td>
<td>−0.19 **</td>
<td>0.01 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.50 **</td>
<td>−0.29 **</td>
<td>0.01 N.S.</td>
</tr>
<tr>
<td>Oct-91</td>
<td>Adults</td>
<td>0.23 **</td>
<td>−0.14 **</td>
<td>0.01 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.28 **</td>
<td>−0.31 **</td>
<td>0.18 **</td>
</tr>
<tr>
<td>Nov-91</td>
<td>Adults</td>
<td>0.11 *</td>
<td>−0.13 *</td>
<td>0.10 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.30 **</td>
<td>−0.21 **</td>
<td>0.12 *</td>
</tr>
<tr>
<td>Apr-92</td>
<td>Adults</td>
<td>0.24 **</td>
<td>−0.19 **</td>
<td>0.01 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.35 **</td>
<td>−0.32 **</td>
<td>0.12 *</td>
</tr>
<tr>
<td>May-92</td>
<td>Adults</td>
<td>0.25 **</td>
<td>−0.13 **</td>
<td>−0.04 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.37 **</td>
<td>−0.29 **</td>
<td>0.03 N.S.</td>
</tr>
<tr>
<td>Jun-92</td>
<td>Adults</td>
<td>0.25 **</td>
<td>−0.13 **</td>
<td>−0.03 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.34 **</td>
<td>−0.17 **</td>
<td>0.00 N.S.</td>
</tr>
<tr>
<td>Jul-92</td>
<td>Adults</td>
<td>0.24 **</td>
<td>−0.15 **</td>
<td>0.01 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.36 **</td>
<td>−0.16 **</td>
<td>−0.09 N.S.</td>
</tr>
<tr>
<td>Aug-92</td>
<td>Adults</td>
<td>0.10 *</td>
<td>−0.13 **</td>
<td>0.06 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.43 **</td>
<td>−0.29 **</td>
<td>−0.01 N.S.</td>
</tr>
<tr>
<td>Sep-92</td>
<td>Adults</td>
<td>0.10 *</td>
<td>−0.10 *</td>
<td>0.04 N.S.</td>
</tr>
<tr>
<td></td>
<td>Juveniles</td>
<td>0.39 **</td>
<td>−0.30 **</td>
<td>−0.01 N.S.</td>
</tr>
</tbody>
</table>
was eaten proportionally to its abundance. *Mentha suaveolens* was neither preferred nor avoided by adult snails, but juveniles showed preference for this plant species in October and November 1991 and also in April 1992, coinciding with low abundance of *Urtica*.

*Spatial distribution of the snails in relation to the relative abundance of the plants in Lapido-II*

The scatter diagrams for the percentage distribution of *Urtica dioica* and the percentage distribution of snails among the five zones of the plot on each sampling occasion are shown in Fig. 5. There was a significant positive association between the percentage distribution of snails among the five zones of the plot and that of *Urtica dioica*, both for adult (**τ** = 0.742, **P** < 0.001, **n** = 55) and juvenile snails (**τ** = 0.734, **P** < 0.001, **n** = 55).

The distribution of snails over time and that of *Urtica* were strongly related; the abundance of snails in zones A and B, where *Urtica* was relatively abundant over the study period, was not related to the temporal changes in the abundance of nettles; in zones C and E, where *Urtica* was absent (zone C) or scarce (zone E) before the winter, the increase in the abundance of nettles after the winter was accompanied by an increase in the abundance of snails (adults and juveniles in zone C, only juveniles in zone E).

There existed a significant negative relation among the distribution of *Urtica* and that of Gramineae in the plot (**τ** = −0.670, **P** < 0.001, **n** = 55), and therefore the percentage distribution of snails also showed a significant negative association with the percentage distribution of Gramineae among the five zones of the plot (for adults, **τ** = −0.613, **P** < 0.001; for juveniles, **τ** = −0.651, **P** < 0.001; **n** = 55 in both cases). Furthermore, the distribution of the snails was never significantly related to the distribution of *Mentha suaveolens* and *Ranunculus repens*.

*Composition of the plant species*

Table 5 shows the contents of protein, fibre, soluble sugars, ashes and calcium for the four commonest plant species of the plot Lapido-II. Fisher LSD tests showed that *Urtica dioica* differed statistically (**P** < 0.05) from the other plant species because of its high protein, ashes and calcium contents: Gramineae were differentiated because of their high fibre and low calcium contents, and *Ranunculus repens* was differentiated because of its high soluble sugars content. No other statistical differences were found.

![Figure 5](image)

**Figure 5.** Scatter diagrams for the percentage distribution of *Urtica dioica* and the percentage distribution of adult and juvenile snails among the five zones of the plot Lapido-II. Each point represents one sampling occasion, in the abscissa the percentage of *Urtica* in one zone with respect to the cover of *Urtica* in the whole plot, and in the ordinate the percentage of snails in the same zone and the same sampling with respect to the total number of snails in the whole plot.
Table 5. Protein, fibre, soluble sugars, ashes and calcium contents of the four commonest plant species of the site Lapido-II. Values are % dry weight (mean ± S.D.), sample size = 4 in all cases except soluble sugars in M. suaveolens and R. repens, where n = 3. Figures within the same column followed by the same letter are not significantly different (P < 0.05) by Fisher LSD test.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Calcium</th>
<th>Ash</th>
<th>Crude protein</th>
<th>Raw fibre</th>
<th>Soluble sugars</th>
</tr>
</thead>
<tbody>
<tr>
<td>U. dioica</td>
<td>3.83 ± 0.84 a</td>
<td>20.09 ± 4.16a</td>
<td>30.50 ± 1.77a</td>
<td>12.30 ± 0.97a</td>
<td>5.11 ± 2.79a</td>
</tr>
<tr>
<td>M. suaveolens</td>
<td>1.62 ± 0.56b</td>
<td>13.05 ± 2.14b</td>
<td>22.01 ± 4.63b</td>
<td>10.89 ± 3.77a</td>
<td>2.57 ± 0.75a</td>
</tr>
<tr>
<td>R. repens</td>
<td>1.21 ± 0.13b</td>
<td>11.65 ± 1.47bc</td>
<td>22.12 ± 4.18b</td>
<td>12.76 ± 1.40a</td>
<td>11.44 ± 2.30b</td>
</tr>
<tr>
<td>Gramineae</td>
<td>0.51 ± 0.13c</td>
<td>9.23 ± 2.04c</td>
<td>20.49 ± 4.44b</td>
<td>26.96 ± 2.68b</td>
<td>3.49 ± 0.87a</td>
</tr>
</tbody>
</table>

**DISCUSSION**

The results of this work agree well with previous studies on food and feeding of land gastropods. For a given species of land gastropod, the range of foods eaten under natural conditions may vary widely depending on the food available (South, 1992). For example, the slug *Deroceras reticulatum* feeds mainly on *Rumianthus repens* and *Urtica dioica* in a oak grove (Pallant, 1969), and on grasses in rough grassland (Pallant, 1972). Grime & Blythe (1969) found that senescent grasses form the bulk of the diet of *Cepaea nemoralis* in grassland, but animals living in a nettle (*Urtica dioica*) patch eat large proportions of green *Urtica*. The same was found for *Monacha cantiana* by Chatfield (1976).

The fact that plants which are frequent in the field are also eaten frequently and the occurrence of seasonal changes in the diet related to availability have been reported for other species of slugs and snails (Chatfield, 1976; Williamson & Cameron, 1976; Richter, 1979; Slavicek, 1986; Speiser & Rowell-Rahier, 1991; Hatziioannou et al., 1994). The seasonal changes in the percentages of green material in the diet reported here probably reflect also seasonal changes of the plant community and in the abundance of different food items: during spring, when a variety of green plants were present, the snails' diet showed the highest percentage of green material. The same applies for diet diversity in the sites Cobas and Lapido-I where maximum diet diversity occurred in spring. On the contrary, diet diversity in Lapido-II followed an opposite trend to that of diversity of vegetation, and it seems that diet diversity in this plot was related to the abundance of the highly preferred food *Urtica dioica*: low abundance of *Urtica* coincided with high diet diversity and vice versa, although there was no significant relationship between these variables.

The avoidance of grasses by slugs and snails has frequently been shown (Grime et al., 1970; Wolda et al., 1971; Williamson & Cameron, 1976; Carter, Jeffery & Williamson, 1979; Cottam, 1985; Slavicek, 1986; Chang, 1991; Speiser & Rowell-Rahier, 1991), although a number of studies pointed out the grasses as the main diet components of some species like *Cepaea nemoralis* (Grime & Blythe, 1969), *Deroceras reticulatum* (Pallant, 1972) and *Helix aspersa* (Dan, 1978). In these three studies, the Gramineae were the most abundant plants in the habitat and their predominance in the diet probably arises from high availability. Also, the three studies were based on the frequency of presence of each food item in faeces or stomach contents, and grasses are the most readily identifiable and detectable plants in the analyses due to the shape and arrangement of the stomata and due to low degradation in the digestive process (Grime & Blythe, 1969; Chatfield, 1976; Jennings & Barkham, 1976). The fact that grasses comprised the bulk of the diet does not mean that they were preferred food. In the present study grasses were also abundant in the three sites and they always occupied the second place in the rank of feeding observations, although the values of the electivity index C clearly show a strong avoidance for Gramineae in site Lapido-II. The rejection of grasses by slugs and snails is usually attributed to the high silica content of the leaves (Wadham & Wynn Parry, 1981) or to their toughness (Grime et al., 1968; Dirzo, 1980; Reingold & Gelperin, 1980; Speiser & Rowell-Rahier, 1991).

On the other hand a number of studies have shown that *Urtica dioica* is one of the most preferred food plant for slugs and snails. Stinging nettles are highly acceptable for *Cepaea nemoralis* (Grime et al., 1968, 1970; Carter et al., 1979). *Cepaea hortensis* (Carter et al., 1979), *Deroceras reticulatum* (Pallant, 1969), *Arion ater* (Cates & Orans, 1975; Jennings & Barkham, 1975), *Ariolimax colombianus* (Cates

Also, the association between the distribution of nettles and that of snails has been found in several studies: Grime & Blythe (1969) make reference to high densities of *Arianta arbustorum* in patches of *Urtica dioica*, and the same was seen by Mason (1970) with *Trichia striolata* and *Chatfield* (1976) with *Monacha cantiana*. Baur (1986) found densities of 11.3–17.3 snails/m² in patches of *Urtica dioica* for a population of *Arianta arbustorum*. Cam, Cook & Currey (1990) with *Cepaea nemoralis* found higher densities of snails in nettle patches than in the surrounding grassland and they report that changes in the cover of *Urtica* were accompanied by changes in the snails’ density. Oliveira Silva (1992) found 4–5 adult *Helix aspersa* on each plant of *Urtica*.

The question that arises from this study is whether *Helix aspersa* is associated with *Urtica dioica* for the food value of the plant or whether this association is caused by other reasons like habitat suitability. The high ingestion and assimilation rates and the high acceptability of *Urtica dioica* for land gastropods, seem to indicate that the food value of the plant may be the reason for the preference of these animals for the nettles. Thus, the association between the distribution of nettles and *Helix aspersa* in the present case may be caused by *Urtica dioica* being the best available food plant for the snails.

The value of *Urtica* as food for land snails is supported by reasons related to both attractiveness and nutritional properties. In relation to attractiveness, the ability of land snails for olfactory orientation towards foods has been demonstrated (Farkas & Shorey, 1976; Gallois & Daguizan, 1989), and Grime et al. (1970) found, in laboratory experiments with *Cepaea nemoralis*, the existence of a strong attraction towards the odour of *Urtica*. In the field, when people cut the weeds of road margins, we observed how land snails come in hordes to the remains of *Urtica*, which give off a strong odour. In the herbivorons prosobranch *Littorina littorea*, the olfactory and/or gustatory cues which determine attractiveness of food items are the primary determinant of food preference (Imrie, Hawkins & McGrohan, 1983).

*Urtica dioica* is a nitrophilous plant (Olsen, 1927) which possesses high nutrient quality; it is well known for its high content of proteins (Pollard & Briggs, 1984), minerals (Vulink & Drost, 1991), calcium (Pramila, Kumar & Raghuvanshi, 1991) and vitamins A and C (Pollard & Briggs, 1984). The analyses of the different plant species of the plot showed that *Urtica* differed statistically from the other species because of its high protein, ash and calcium contents. The optimum protein content of the diet of *Helix aspersa* ranges between 15.5% (Bonnet, Aigner & Vrillon, 1990) and 17.5% (Sanz Sampelospy, Fonolla & Gil Extremeira, 1991) and none of the four commonest plant species of the plot reach these levels on a fresh-weight basis. But *Urtica* was the plant with the highest protein content. Also the higher ash and calcium contents of *Urtica* in comparison with the other plant species of the plot could be of prime importance in determining the preference of the snails, since Williamson & Cameron (1976) consider that the need for minerals can explain the food preference of *Cepaea nemoralis* in the field in better than other factors like the energetic value of the food. Calcium has been traditionally considered the most important element for land snails, and the availability of calcium is directly related to the vitality, growth, reproduction and survival of land snails (Govan, 1983). Snails usually eat soil and are able to extract calcium from acid or neutral soils (Crowell, 1973), but distribution and abundance of land snails may be limited by calcium (Wareborn, 1970; Mason, 1974). Mason (1974) pointed out that land snails often appear associated with calcium sources in non-calcareous areas. In Ceylon, where the soils are very acid, *Achatina* shows a great preference for the tea plants, which have a high content of calcium (Mead, 1961). The soil of the plot studied here is also acid (pH = 5.9) and *Urtica* was the plant species with the highest calcium content, so this could be a primary determinant in the snails’ preference for *Urtica dioica*.

Another aspect not studied here is the presence of secondary compounds in the
plants, which are important factors determining food preference in Arianta arbustorum (Speiser & Rowell-Rahier, 1991). This could also be related to the preference of Helix aspersa for nettles, since there is no evidence that Urtica dioica contains any internal defensive compounds (Pullin & Gilbert, 1989).

However, it is also possible that snails select the nettle patches for reasons not related to the food value of the plant, and then eat Urtica for its closeness and availability. Bailey (1989) found that terrestrial gastropods often remain in the same food patch and eat the first food item encountered; Paine & Vadas (1969) and Arrontes (1990) consider that food preference in marine herbivores is a response to availability more than a response to the nutritive value of the food.

Animals with high mobility can select an area to live for its physical characteristics and then move to preferred feeding areas, but in less mobile animals, habitat selection may be a compromise between the physical characteristics of the area and the value of the existing food.

Nettle patches may be a suitable habitat for land snails because Urtica dioica is a perennial plant which survives well under heavy grazing pressure (Pullin & Gilbert, 1989) and which can provide to the snails protection from predators (Cain & Currey, 1967) and from eventual human harvest. The stinging trichomes of Urtica are an effective deterrent for most vertebrate herbivores (Pollard & Briggs, 1984; Pullin & Gilbert, 1989) but not for slugs and snails (Grime et al., 1968; Mølgaard, 1986; Pullin & Gilbert, 1989) and thus the potential competition for food with other herbivores must be reduced. The other plant species in the plot, Gramineae, Mentha suaveolens and Rumex crispus repens can not offer the same advantages to the snails, although they are also perennial and predictable plants.

In this study, all the evidence suggests that Urtica dioica is the most suitable plant species in the plot for Helix aspersa, both as food because of its higher protein ash and calcium contents, and also as habitat because it is the only plant which can offer to the snails protection from predators and a reduction of the potential competition for food with other herbivores, besides good resting places. Whether snails give more value to the nutritive value of Urtica or to the habitat suitability of the nettle patches, cannot be determined from the present results.

A number of previous studies (Grime & Blythe, 1969; Mason, 1970; Grime et al., 1970; Wolda et al., 1971; Richardson, 1975; Williamson & Cameron, 1976; Chaffield, 1976; Richter, 1979; Carter et al., 1979; Szlavecz, 1986; Speiser & Rowell-Rahier, 1991; Hatzioannou et al., 1994) have reported a predominance of senescent material in the natural diet of land gastropods, but references in the literature about different diets among adults and juveniles are scarce and ambiguous. Wolda et al. (1971) found that some plant species are eaten by juvenile Cepaea nemoralis rather than by adults and vice versa, and Williamson & Cameron (1976) found that juveniles of the same species show significantly less food selection than adults. Hatzioannou et al. (1994), in a study of the diet and food preferences of five coexisting species of land snails, found that adult Brachypodium pinnatum eat more senescent material than juveniles in autumn, but with respect to the other species and the rest of the year, they found no differences between adults and juveniles. To our knowledge this is the first time that a consistent difference between adult and juvenile diets have been pinpointed. It seems obvious that the soft and tender green vegetables may be easier to eat for the young snails, and green plants often contain more nitrogen, but more research is needed to confirm this result and to look into the possible causes.

ACKNOWLEDGEMENTS

I am grateful to Dr. Bernd Speiser for his comments on a draft of the manuscript, and to the anonymous referees who made useful suggestions. Also thanks are due to the Agricultural and Phytopathological Laboratory of Galicia for the analyses of plants.

REFERENCES


FEEDING OF *HELIX ASPERNA* IN THE FIELD


