The study of the food preferences of snails on a magnesian limestone habitat

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by

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I. Introduction

I.1. General consideration

It is true that the distribution and abundance of some plant species are determined to certain extent by the grazing of herbivores (Feeny 1970; Cates 1975; Strong et al. 1984). Many studies of the plant-animal interactions have suggested that plant species display a variety of defensive mechanisms and modifications effective in reducing loss of photosynthetic tissue to their grazers. Among these triats are the physical barriers such as hairs, thorns, spines, etc. and the production of a wide range of secondary plant substances which provide various degrees of protection against the herbivores (Brower 1969; Levin 1973). Much research has been devoted to the study of the feeding ecology of insects and mammals such as the work done on bettle (Bentley and Whittaker 1979), damselfly (Lawton 1970), sheep (Milton 1933), rabbit (Gilham 1955) and cow (Long 1924). In comparison, relatively less work has been done to investigate the feeding habits of terrestrial molluscs. Though recently more studies have been carried out on the food preferences of snails (Grime et al. 1968) and slugs (Dirzo 1980), still little attention has been paid to account for the various degrees of palatabilities among the plant species to the animals.

The aims of the present study were twofolds. Firstly, the food preferences of the snails on a magnesian limestone habit were examined. Secondly, it was intended to investigate the barriers erected by the plants against the snails feeding on them. Achieving the first aim required the palatability test of the plant species. In order to be more realistic as in the natural habitat, the palatability of the plant species was compared with one another instead of comparing with a reference material. The tests were carried out in such a way that the hierarchical food preferences of the snails were also examined. The second part of the study concentrated on the investigation of the defensive mechanisms of the plants. It involved the study of the chemical nature and the physical features of the plants which could probably provide protection against the consumption by the animals. Obviously the conditions of the experiments performed in the laboratory could never imitate exactly the same as those in the natural habitat, field observations of the feeding habits of the snails were also made in the hope that a more complete picture of the interaction between the plants and the animals could be revealed.

I.2. Study area

The present project was carried out in the area of the Bishop Middleham Reserve which is a disused magnesian limestone quarry to the north of Bishop Middleham village (Fig.1) (Grid reference NZ332327). It was first designated by the Nature Conservancy Council as a Site of Special Scientific Interest (S.S.S.I.) in 1968 (D.C.C. 1979). The importance of the magnesian limestone grassland is due to the presence of the unique plant communities made up of Arctic/Alpine species which are at the southernmost limit and the southern lowland plants at their northern limits. Bishop Middleham has been described as one of the most botanically important disused limestone quarries in Britain as it contains a wide range of

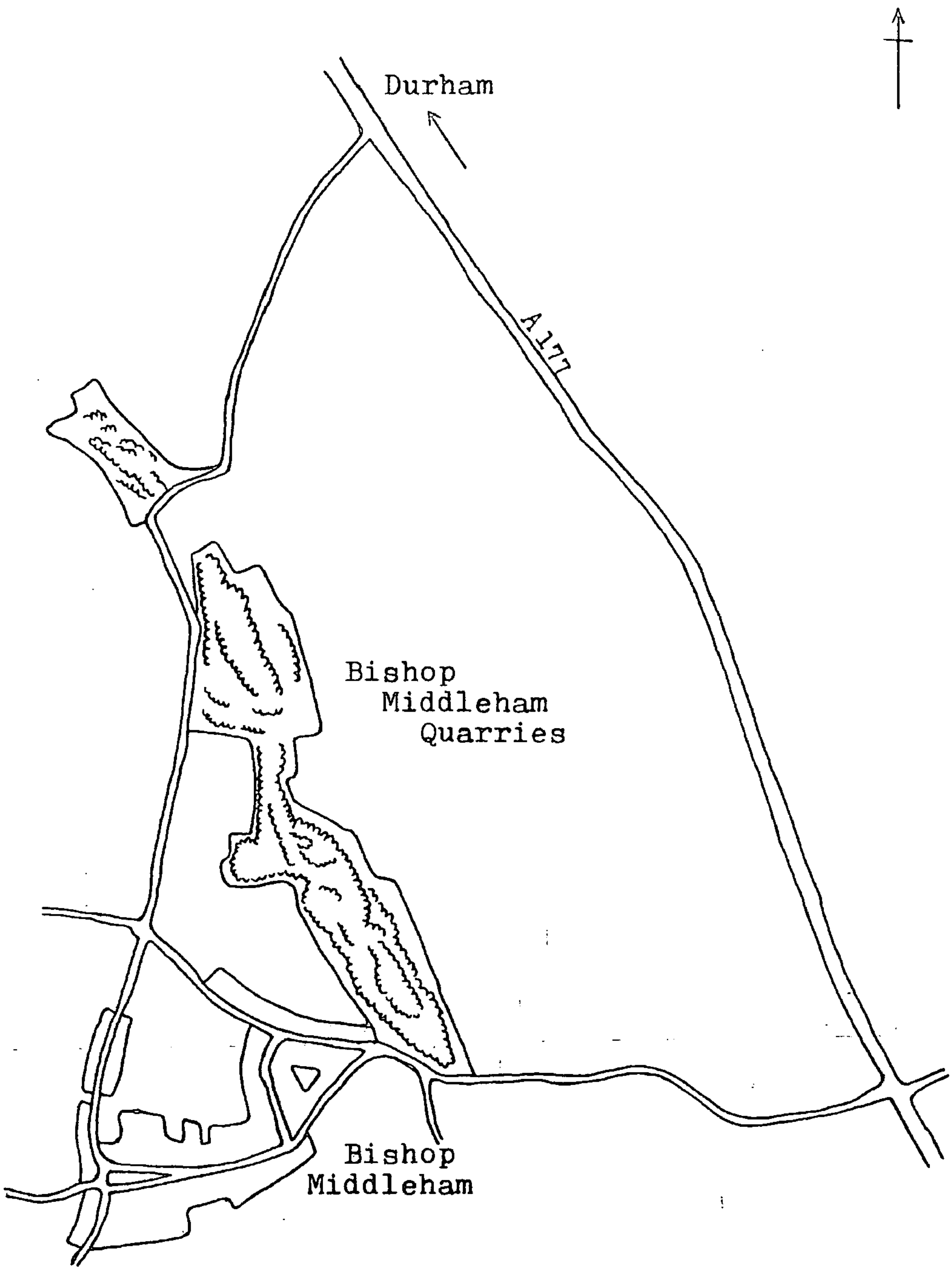

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Fig. 1. Map of the locality of the study site

plant and animal species characteristic of limestone soils. (D.C.C.T. 1984).

The quarry is bordered to the west, north and east by agricultural land and to south by an active limestone quarry. All the work was confined to the northern part of the quarry because of easy accessibility and large snail populations.

I.3. Species studied

Four snail species were found in the quarry. They were Helix aspersa Müller, Cepaea nemoralis (L.), Helicella itala (L.) and Hygromia striolata (Pfeiffer). The first two species were more abundant and larger whilst the other two were rather small and inconspicuous. Attempt was made to collect the smaller snails by thorough searching and all the work was carried out on these four species found in the site.

Helix aspersa (Plate 1) is the second largest snail found in Britain. The height and width can be very variable but usually both are about 30-35 mm. Pairing takes place from April throughout the summer. They spend over half the year in hibernation with their apertures of the shells closed by membranous epiphragms. Normally they are biennial but have been known to attain ten years in captivity (Taylor 1913). They are found in many habitats, from dunes to woodland, and particularly abundant in gardens, stony places and calcareous soils.

Cepaea nemoralis (Plate 2) is the most variable British snail, and is especially inconsistent in the number, pigmentation and arrangement of the bands. The height of the shell can attain 17 mm. and breadth 22 mm. The snails breed in spring and summer. Like Helix aspersa, its life span is usually two years. It is also widespread, living among grasses, herbage, shrubs, hedges, quarries, gardens and waste places. Though it is not an obligate calicole, it prefers limestone habitat. Much work has been done on its polymorphism but not until recently more studies have been carried out on its other aspects of ecology.

Helicella itala (Plate 3) is a smaller snail attaining the size of height 5-12 mm. and breadth 9-25 mm. These snails breed in late summer and autumn, and usually live for about one year. It appears to be an obligatory calicole as described by Boycott (1934). It is also a xerophile species, found on dunes and calcareous grassland. It spends its time in dry weather attached to the stalks of grasses, thistles, knapweed and other plants. It feeds when the herbage is damp. Relatively little work has been done on this species.

Hygromia striolata (Plate 4) is the smallest of the four snail species found in the study area. The height of the shell is 7-10 mm. and the breadth 11-14 mm. Hygromia striolata breeds from spring to autumn. The shell has a colour polymorphism but brown shells are the most common. They are mostly abundant in moist places such as in the hedges, gardens and woods. Boycott (1934) has suggested that this species prefers a calcareous habitat, but is also sometimes found in non-calcareous places.

Plate 1. Photograph of adult <u>Helix aspersa</u> (scale in mm.)

Plate 2. Photograph of adult <u>Cepaea nemoralis</u> (scale in mm.)

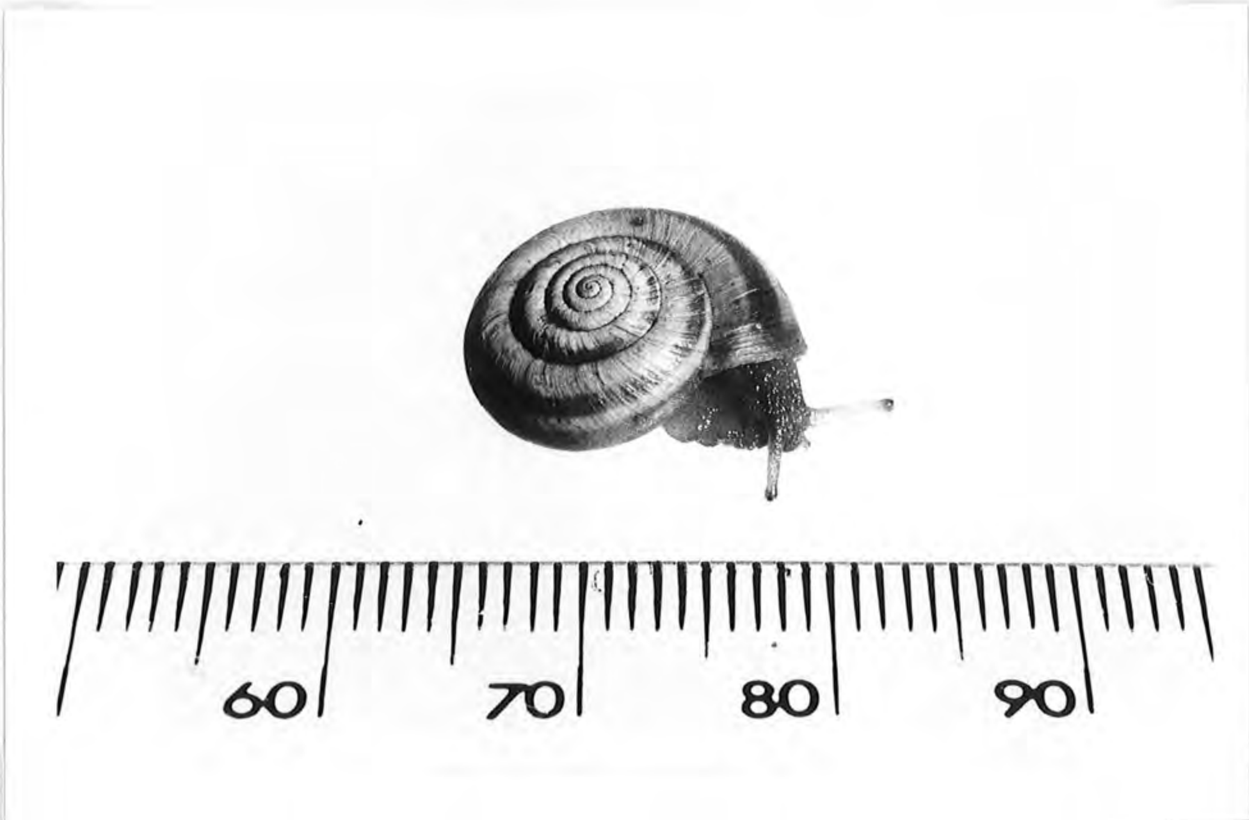

Plate 3. Photograph of adult Helicella itala (scale in mm.)

Plate 4. Photograph of adult Hygromia striolata (scale in mm.)

II. Methods

II.1. Collection of snails and foliage

Snails were collected in the beginning of May. They were found among the vegetation, stones and crevices in the rock. After sampling they were identified in the laboratory and different species were kept in separate containers. The large species, Helix aspersa and Cepaea nemoralis, were placed in large tanks whereas the smaller snails, Helicella itala and Hygromia striolata, were kept in plastic jars with air holes on the lids. The containers were put near the window to have normal diffused light. It was thought that these conditions were more similar to the natural habitat than conditions of constant temperature and illumination by fluorescent tubes. No snails died throughout the whole experimental period. Between experimental tests the snails were fed with the same variety of lettuce. (Lactuca sativa)

Most of the plants were collected from the same area from where the snails were sampled. Plants frequent in the habitat and those of known palatability to snails or other herbivores were chosen for the palatability experiments. Six plant species were studies in detail with respect to their palatabilities and barriers to the snails. The leaves were stored in polythene bags at 5°C and fresh materials were collected in the field when necessary.

II.2. Palatability tests with fresh materials

The palatabilities of the plant species were tested with four different snail species. Each plant species was compared with every other test plants in a pairwise pattern. Difficulties were encountered in persuading all of the snails to eat and reducing the variations of the snails during the palatability tests. Sometimes, the formation of an epiphragm suggested that the snail did not feed on the test plants was not due to the low palatability of the plants but rather because of the dry condition. The situation was improved by keeping the containers moist enough for the activities of the snails and activating them on wet surfaces before the experiments. The variations in the later experiments were minimized by feeding each snail approxomately the same quantity of food every day. In order to ensure that the snails have enough food to choose between the two plants, the results where over two thirds of either plants was consumed were discarded. Fortunately, after appropriate adjustment had been made, only a few tests needed to be repeated.

Due to the fact that the smaller snail species, Helicella itala and Hygromia striolata, consumed so little that it was difficult to measure quantitatively in terms of the weight or area of the plant eaten, different techniques were employed for the palatability tests between the large species and the smaller snail species.

(a) Experiments with large snail species

For the large snail species, Helix aspersa and Cepaea nemoralis, the method of palatability test was adopted from Grime et al. (1968). Individual snails were placed on the bottom of plastic containers with equal amount of two different plant materials on the opposite sides. The plant materials used for Helix aspersa was 700 mg. and Cepaea nemoralis 500 mg.

The inside of the container was wetted with distilled water to maintain a high humidity for the continuous snail activity during the experiment. The feeding period lasted for 16 hours and the remains of the two plant materials were dried separately at 105°C and then weighed. Control plant samples were similarly dried and weighed in order to obtain the dry weight to fresh weight ratio for the calculation of the quantities consumed by the snails. Five replicates were used for each comparison between the plant species and the palatability ratio was calcultaed in the following units:

$$\text{Palatability Ratio} = \frac{\text{Weight of species A consumed, mg.}}{\text{Weight of species B consumed, mg.}}$$

(b) Experiments with small snail species

Prior to the experiment, the snails were activated in a dark chamber. Two different plant species were tested with five snails placed onto the middle of a Petri dish which was divided into four quadrants with the same plant materials in the opposite quadrants. The plant materials used were 20 mm. x 20 mm. squares. The experiment was prolonged for 3 hours and the numbers of snails feeding on the two plant species were recorded. Six replicates totalling of 30 snails were used for each test. The preference ratio between two plant species was expressed as follow:

$$\text{Preference Ratio} = \frac{\text{No. of snails feeding on species A}}{\text{No. of snails feeding on species B}}$$

II.3. Palatability tests with leaf extracts

Leaf extract was prepared by grinding 1 g. of fresh material in 10 ml. of distilled water and filtering through a Whatman No.1 filter paper. In the case of working with large snail species, 0.08 ml. of filtered extract was added to 625 mm^2. squared filter paper whereas 0.05 ml. of filtered extract and 400 mm^2. squared filter paper were used for smaller snail species. The filter paper was then dried at 40°C and two more additions of the extract were made. The test procedures were basically the same as those for testing fresh materials. The filter paper consumed by the snails was measured using graph paper and the palatability ratio was expressed in terms of area eaten, but the same units of calculation were used for the small snail species.

II.4. Removal of leaf epidermal hairs

Attempt was made to investigate the protective effect of epidermal hairs against the grazing by the snails. The techniques used here followed the work of Neama (1982). The leaf was washed with distilled water, dried with tissue paper and fixed on a flat glass plate by clips. An ordinary razor blade was used to shave the hairs from the surface of the leaf avoiding damage to the epidermal tissues. The palatability of the shaved leaves was then compared with the hairy leaves of the same species. The same procedures were carried out as in the palatability test.

II.5. Feeding observations in the field

Surveys of snails feeding in the site were carried out in August at which time the smaller snails reached maturity. Since the snails were active only at night or after rain, observations were made in the wet days. Records were only made on the active snails actually feeding on the plants, and in which cases, lifting up the snails revealed the sign of damage caused by the animals.

III. Results

III.1. Palatability of fresh materials

In the palatability tests of fresh materials, plants were consumed preferentially by the snails. The palatabilities of the plant species with respect to the four snail species were ranked according to the total numbers of preferences made by the snails (Tables 1-4).

The palatability ratios of all the paired comparisons between the plants tested with *Helix aspersa* are shown in Table 5. This snail preferred *Hieracium vulgatum* most and *Urtica dioica* least. There were no significant differences in the preferences between *Hieracium vulgatum*, *Sonchus asper* and *Taraxacum officinale*; *Sonchus asper*, *Taraxacum officinale* and *Leontodon hispidus*; and *Leontodon hispidus* and *Tussilago farfara*. The rest of other comparisons showed highly significant differences.

Although there were some differences in the ranking, *Cepaea nemoralis* showed similar preferences as *Helix aspersa* with *Taraxacum officinale*, *Hieracium vulgatum* and *Sonchus asper* were the top three and *Leontodon hispidus*, *Urtica dioica* and *Tussilago farfara* the lower three in the preference order. Their palatability ratios are presented in Table 6. There were no significant differences among the top three plants, nor with the comparisons between *Hieracium vulgatum* and *Leontodon hispidus*, *Sonchus asper* and *Leontodon hispidus*, and *Urtica dioica* and *Tussilago farfara*.

The preference ratios of the plants with respect to Helicella itala are shown in Table 7. Like Helix aspersa, Helicella itata also preferred Hieracium vulgatum most and Urtica dioica least. However, it has to be pointed out that this snail showed exceptionally high preference for Leontodon hispidus as comparing with the other three snail species. Five comparisons showed no significant differences and most of which were the pairs of plants adjacent in the ranking.

Hygromia striolata responsed differently. It preferred Urtica dioica, the least preferable plant to the other three snail species. The preference ratios of the plants are shown in Table 8. Out of fifteen comparisons, only three were not significantly different. This may reflect that this snail is rather specific in feeding among the tested plants.

Table 1. The number of the preferences made by Helix aspersa in the palatability tests of fresh materials

Plants	Total no. of preferences
Hieracium vulgatum	23
Sonchus asper	19
Taraxacum officinale	16
Leontodon hispidus	11
Tussilago farfara	6
Urtica dioica	0

Table 2. The number of the preferences made by *Cepaea nemoralis* in the palatability tests of fresh materials

Plants	Total no. of preferences
Taraxacum officinale	23
Hieracium vulgatum	20
Sonchus asper	16
Leontodon hispidus	11
Urtica dioica	4
Tussilago farfara	1

Table 3. The number of the preferences made by *Helicella itala* in the palatability tests of fresh materials

Plants	Total no. of preferences
Hieracium vulgatum	104
Leontodon hispidus	95
Taraxacum officinale	87
Sonchus asper	67
Tussilago farfara	60
Urtica dioica	37

Table 4. The number of the preferences made by *Hygromia striolata* in the palatability tests of fresh materials

Plants	Total no. of preferences
Taraxacum officinale	113
Urtica dioica	95
Hieracium vulgatum	79
Sonchus asper	73
Leontodon hispidus	52
Tussilago farfara	38

Table 5. Palatability ratio of fresh leaves with respect to *Helix aspersa*

	Palatability ratio
Hieracium vulgatum/*Sonchus asper*	1.09 n.s.
H. vulgatum/*Taraxacum officinale*	1.89 n.s.
H. vulgatum/*Leontodon hispidus*	2.78 ++
H. vulgatum/*Tussilago farfara*	5.33 +++
H. vulgatum/*Urtica dioica*	8.20 +++
Sonchus asper/*Taraxacum officinale*	2.10 n.s.
S. asper/*Leontodon hispidus*	1.55 n.s.
S. asper/*Tussilago farfara*	3.99 +++
S. asper/*Urtica dioica*	6.85 +++
Taraxacum officinale/*Leontodon hispidus*	1.07 n.s.
T. officinale/*Tussilago farfara*	2.31 ++
T. officinale/*Urtica dioica*	5.34 +++
Leontodon hispidus/*Tussilago farfara*	1.86 n.s.
L. hispidus/*Urtica dioica*	3.16 +++
Tussilago farfara/*Urtica dioica*	2.89 ++

Significant level assessed by t-test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

Table 6. Palatability ratio of fresh leaves with respect to *Cepaea nemoralis*

	Palatability ratio
Taraxacum officinale/*Hieracium vulgatum*	1.10 n.s.
T. officinale/*Sonchus asper*	1.91 n.s.
T. officinale/*Leontodon hispidus*	2.31 +
T. officinale/*Urtica dioica*	7.06 +++
T. officinale/*Tussilago farfara*	8.17 +++
Hieracium vulgatum/*Sonchus asper*	2.04 n.s.
H. vulgatum/*Leontodon hispidus*	1.72 n.s.
H. vulgatum/*Urtica dioica*	6.12 +++
H. vulgatum/*Tussilago farfara*	6.97 +++
Sonchus asper/*Leontodon hispidus*	1.23 n.s.
S. asper/*Urtica dioica*	4.56 +++
S. asper/*Tussilago farfara*	5.49 ++
Leontodon hispidus/*Urtica dioica*	2.15 ++
L. hispidus/*Tussilago farfara*	2.09 ++
Urtica dioica/*Tussilago farfara*	1.29 n.s.

Significant level assessed by t-test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

Table 7. Preference ratio of fresh leaves with respect to *Helicella itala*

	No. consumed	Preference ratio
Hieracium vulgatum/ *Leontodon hispidus*	17 : 13	1.31 n.s.
Hieracium vulgatum/ *Taraxacum officinale*	19 : 11	1.73 n.s.
Hieracium vulgatum/ *Sonchus asper*	21 : 9	2.33 ++
Hieracium vulgatum/ *Tussilago farfara*	22 : 8	2.75 +++
Hieracium vulgatum/ *Urtica dioica*	25 : 5	5.00 +++
Leontodon hispidus/ *Taraxacum officinale*	16 : 14	1.14 n.s.
Leontodon hispidus/ *Sonchus asper*	21 : 9	2.33 ++
Leontodon hispidus/ *Tussilago farfara*	21 : 9	2.33 ++
Leontodon hispidus/ *Urtica dioica*	24 : 6	4.00 +++
Taraxacum officinale/ *Sonchus asper*	19 : 11	1.73 n.s.
Taraxacum officinale/ *Tussilago farfara*	20 : 10	2.00 +
Taraxacum officinale/ *Urtica dioica*	23 : 7	3.29 +++
Sonchus asper/ *Tussilago farfara*	17 : 13	1.31 n.s.
Sonchus asper/ *Urtica dioica*	21 : 9	2.33 ++
Tussilago farfara/ *Urtica dioica*	20 : 10	2.00 +

Significant level assessed by Chi-squared test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

Table 8. Preference ratio of fresh leaves with respect to *Hygromia striolata*

	No. consumed	Preference ratio
Taraxacum officinale/ *Urtica dioica*	18 : 12	1.50 n.s.
Taraxacum officinale/ *Hieracium vulgatum*	21 : 9	2.33 ++
Taraxacum officinale/ *Sonchus asper*	23 : 7	3.29 +++
Taraxacum officinale/ *Leontodon hispidus*	24 : 6	4.00 +++
Taraxacum officianle/ *Tussilago farfara*	27 : 3	9.00 +++
Urtica dioica/ *Hieracium vulgatum*	17 : 13	1.31 n.s.
Urtica dioica/ *Sonchus asper*	21 : 9	2.33 ++
Urtica dioica/ *Leontodon hispidus*	23 : 7	3.29 +++
Urtica dioica/ *Tussilago farfara*	22 : 8	2.75 +++
Hieracium vulgatum/ *Sonchus asper*	14 : 16	0.88 n.s.
Hieracium vulgatum/ *Leontodon hispidus*	21 : 9	2.33 ++
Hieracium vulgatum/ *Tussilago farfara*	22 : 8	2.75 +++
Sonchus asper/ *Leontodon hispidus*	20 : 10	2.00 +
Sonchus asper/ *Tussilago farfara*	21 : 9	2.33 ++
Leontodon hispidus/ *Tussilago farfara*	20 : 10	2.00 +

Significant level assessed by Chi-squared test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

On one hand there are obvious different preference orders among the four snail species, on the other hand, the results appear to reveal that *Leontodon hispidus*, *Urtica dioica* and *Tussilago farfara* are less preferable to other plants as any two of them are always the least two preferred food to the four snail species as a whole (Table 9).

Table 9. Preference order of the plants among the four snail species

Plant species	Preference order			
	Helix aspersa	*Cepaea nemoralis*	*Helicella itala*	*Hygromia striolata*
Hieracium vulgatum	1	2	1	3
Taraxacum officinale	3	1	3	1
Sonchus asper	2	3	4	4
Leontodon hispidus	4	4	2	5
Urtica dioica	6	5	6	2
Tussilago farfara	5	6	5	6

III.2. Palatability of leaf extracts

It is of interest to study the effects of the chemical nature of the plants on the feeding of snails. Similarly, the preference orders were ranked on the basis of the total numbers of choices made by the snails (Tables 10-13). Subsequently, the rankings of the fresh materials and leaf extracts were compared by Kendall's rank correlation assessment for each snail species (Tables 14-17) (Kendall 1948).

Table 10. The number of the preferences made by *Helix aspersa* in the palatability tests of leaf extracts

Plants	Total no. of preferences
Sonchus asper	23
Hieracium vulgatum	21
Tussilago farfara	15
Taraxacum officinale	10
Leontodon hispidus	5
Urtica dioica	1

Table 11. The number of the preferences made by *Cepaea nemoralis* in the palatability tests of leaf extracts

Plants	Total no. of preferences
Hieracium vulgatum	24
Taraxacum officinale	20
Urtica dioica	16
Sonchus asper	9
Leontodon hispidus	5
Tussilago farfara	1

Table 12. The number of the preferences made by *Helicella itala* in the palatability tests of leaf extracts

Plants	Total no. of preferences
Hieracium vulgatum	103
Taraxacum officinale	97
Leontodon hispidus	86
Sonchus asper	67
Tussilago farfara	62
Urtica dioica	35

Table 13. The number of the preferences made by *Hygromia striolata* in the palatability tests of leaf extracts

Plants	Total no. of preferences
Taraxacum officinale	107
Urtica dioica	91
Leontodon hispidus	83
Hieracium vulgatum	73
Sonchus asper	54
Tussilago farfara	42

Table 14. Rank correlation of preferences between fresh materials and leaf extracts with respect to *Helix aspersa*

Plants	Preference order	
	Fresh materials	Leaf extracts
Hieracium vulgatum	1	2
Sonchus asper	2	1
Taraxacum officinale	3	4
Leontodon hispidus	4	5
Tussilago farfara	5	3
Urtica dioica	6	6

$r = 0.6$

$N = 6$ $P > 0.05$

Table 15. Rank correlation of preferences between fresh materials and leaf extracts with respect to *Cepaea nemoralis*

Plants	Preference order	
	Fresh materials	Leaf extracts
Taraxacum officinale	1	2
Hieracium vulgatum	2	1
Sonchus asper	3	4
Leontodon hispidus	4	5
Urtica dioica	5	3
Tussilago farfara	6	6

$r = 0.60$

$N = 6$ $P > 0.05$

Table 16. Rank correlation of preferences between fresh materials and leaf extracts with respect to *Helicella itala*

Plants	Preference order	
	Fresh materials	Leaf extracts
Hieracium vulgatum	1	1
Leontodon hispidus	2	3
Taraxacum officinale	3	2
Sonchus asper	4	4
Tussilago farfara	5	5
Urtica dioica	6	6

$r = 0.87$

$N = 6$ $P < 0.05$

Table 17. Rank correlation of preferences between fresh materials and leaf extracts with respect to *Hygromia striolata*

Plants	Preference order	
	Fresh materials	Leaf extracts
Taraxacum officinale	1	1
Urtica dioica	2	2
Hieracium vulgatum	3	4
Sonchus asper	4	5
Leontodon hispidus	5	3
Tussilago farfara	6	6

$r = 0.73$

$N = 6$ $P > 0.05$

For the leaf extracts, Helix aspersa showed some degree of variations in preferences from the fresh materials. The palatability ratios of the fifteen comparisons between the tested plants are recorded in Table 18. Most of the comparisons (11 pairs) indicated significant differences in palatability between the paired plants. There was no significant correlation of preferences between the fresh materials and the leaf extracts ($r = 0.60$, $N = 6$, $P > 0.05$). This may suggest that some factors other than the chemical nature of the plants are operating in the determination of the food preferences of the snails.

Not surprisingly, Cepaea nemoralis also changed its preference order between the fresh materials and leaf extracts. The palatability ratios of each plant to every other plant species are presented in Table 19. Apart from four comparisons, the other comparisons of the palatabilities between the tested pairs of plants were highly significantly different. The rank correlation ($r = 0.60$, $N = 6$, $P > 0.05$) suggested that there was no significant correlation between the fresh materials and leaf extracts. Although there was no analysis of each plant species attribute to the ranking differences, the increase in preference of Urtica dioica from the second last to third position could be observed.

On the contrary, Helicella itala responsed similarly as in the fresh materials tests. The preference ratios of the paired comparisons of the plants are shown in Table 20. Six comparisons showed no significant differences in the preferences between the tested pairs of plants. The rank correlation of preferences between the fresh materials and leaf extracts was significant ($r = 0.87$, $N = 6$, $P < 0.05$). Apparently, it seems to suggest that chemical nature of the plant is one of the most important factors affecting the feeding of this snail, but caution is necessary to explain this situation as other determinant factors may also be well correlated with the chemical nature of the plants in determining the food preferences of the snails.

The preference ratios of the plants with respect to Hygromia striolata are presented in Table 21. Four out of fifteen comparisons resulted in no significant differences. The rank correlation of preferences between the fresh materials and leaf extracts was not significant ($r = 0.67$, $N = 6$, $P > 0.05$). However, the preference of the leaf extract of Leontodon hispidus was obviously raised when comparing with the fresh materials tests.

III.3. Removal of leaf epidermal hairs

Despite the chemical effects on feeding, physical barriers have no doubt playing an important part in determining the palatabilities of the plants to some snails. The low palatabilities of the hairy Leontodon hispidus and stinging Urtica dioica leaves seem to suggest that hairness is an effective deterrent to feeding. However, it is worth noticing that the effectiveness of the hairs, if any, could be very different from one snail species to another. Attempt was made to compare the palatabilities of shaved leaves with the normal leaves. Helix aspersa was apparently unaffected by the

Table 18. Palatability ratio of leaf extracts with respect to *Helix aspersa*

	Palatability ratio
Sonchus asper/*Hieracium vulgatum*	1.04 n.s.
S. asper/*Tussilago farfara*	2.86 ++
S. asper/*Taraxacum officinale*	3.01 ++
S. asper/*Leontodon hispidus*	3.94 +++
S. asper/*Urtica dioica*	5.78 +++
Hieracium vulgatum/*Tussilago farfara*	1.76 n.s.
H. vulgatum/*Taraxacum officinale*	3.38 ++
H. vulgatum/*Leontodon hispidus*	3.06 ++
H. vulgatum/*Urtica dioica*	4.11 +++
Tussilago farfara/*Taraxacum officinale*	1.17 n.s.
T. farfara/*Leontodon hsipidus*	2.55 ++
T. farfara/ *Urtica dioica*	3.44 +++
Taraxacum officinale/*Leontodon hispidus*	1.11 n.s.
T. officianle/*Urtica dioica*	2.74 ++
Leontodon hispidus/*Urtica dioica*	2.06 +

Significant level assessed by t-test: n.s., not significant; +, $P<0.05$; ++, $P<0.01$; ++, $P<0.001$

Table 19. Palatability ratio of leaf extracts with respect to *Cepaea nemoralis*

	Palatability ratio
Hieracium vulgatum/*Taraxacum officinale*	1.13 n.s.
H. vulgatum/*Urtica dioica*	2.24 ++
H. vulgatum/*Sonchus asper*	3.17 +++
H. vulgatum/*Leontodon hispidus*	4.86 +++
H. vulgatum/*Tussilago farfara*	5.22 +++
Taraxacum officinale/*Urtica dioica*	1.78 n.s.
T. officinale/*Sonchus asper*	3.12 +++
T. officinale/*Leontodon hispidus*	3.06 +++
T. officinale/*Tussilago farfara*	4.45 +++
Urtica dioica/*Sonchus asper*	2.17 ++
U. dioica/*Leontodon hispidus*	2.85 ++
U. dioica/*Tussilago farfara*	2.92 +++
Sonchus asper/*Leontodon hispidus*	1.07 n.s.
S. asper/*Tussilago farfara*	2.31 ++
Leontodon hispidus/*Tussilago farfara*	1.33 n.s.

Significant level assessed by t-test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

Table 20. Preference ratio of leaf extracts with respect to *Helicella itala*

	No. consumed	Preference ratio
Hieracium vulgatum/ *Taraxacum officinale*	16 : 14	1.14 n.s.
Hieracium vulgatum/ *Leontodon hispidus*	18 : 12	1.50 n.s.
Hieracium vulgatum/ *Sonchus asper*	20 : 10	2.00 +
Hieracium vulgatum/ *Tussilago farfara*	23 : 7	3.29 +++
Hieracium vulgatum/ *Urtica dioica*	26 : 4	6.50 +++
Taraxacum officinale/ *Leontodon hispidus*	17 : 13	1.31 n.s.
Taraxacum officinale/ *Sonchus asper*	19 : 11	1.73 n.s.
Taraxacum officinale/ *Tussilago farfara*	22 : 8	2.75 +++
Taraxacum officinale/ *Urtica dioica*	25 : 5	5.00 +++
Leontodon hispidus/ *Sonchus asper*	18 : 12	1.50 n.s.
Leontodon hsipidus/ *Tussilago farfara*	20 : 10	2.00 +
Leontodon hispidus/ *Urtica dioica*	23 : 7	3.29 +++
Sonchus asper/ *Tussilago farfara*	13 : 17	0.76 n.s.
Sonchus asper/ *Urtica dioica*	21 : 9	2.33 ++
Tussilago farfara/ *Urtica dioica*	20 : 10	2.00 +

Significant level assessed by Chi-squared test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

Table 21. Preference ratio of leaf extracts with respect to *Hygromia striolata*

	No. consumed	Preference ratio
Taraxacum officinale/ *Urtica dioica*	17 : 13	1.31 n.s.
Taraxacum officinale/ *Leontodon hispidus*	20 : 10	2.00 +
Taraxacum officinale/ *Hieracium vulgatum*	21 : 9	2.33 ++
Taraxacum officinale/ *Sonchus asper*	23 : 7	3.29 +++
Taraxacum officinale/ *Tussilago farfara*	26 : 4	6.50 +++
Urtica dioica/ *Leontodon hispidus*	14 : 16	0.88 n.s.
Urtica dioica/ *Hieracium vulgatum*	20 : 10	2.00 +
Urtica dioica/ *Sonchus asper*	21 : 9	2.33 ++
Urtica dioica/ *Tussilago farfara*	23 : 7	3.29 +++
Leontodon hispidus/ *Hieracium vulgatum*	16 : 14	1.14 n.s.
Leontodon hispidus/ *Sonchus asper*	20 : 10	2.00 +
Leontodon hispidus/ *Tussilago farfara*	21 : 9	2.33 ++
Hieracium vulgatum/ *Sonchus asper*	20 : 10	2.00 +
Hieracium vulgatum/ *Tussilago farfara*	20 : 10	2.00 +
Sonchus asper/ *Tussilago farfara*	18 : 12	1.50 n.s.

Significant level assessed by Chi-squared test: n.s., not significant; +, $P < 0.05$; ++, $P < 0.01$; +++, $P < 0.001$

epidermal hairs as there were no significant differences between the shaved and unshaved leaves for both Leontodon hispidus and Urtica dioica (Table 22). In contrast, Cepaea nemoralis showed a significant preference for the shaved leaves to the unshaved ones for both plant species (Table 23). For Helicella itala, the results showed that there were no significant differences between the shaved and unshaved leaves for the two plant species although the shaved leaves were slightly preferable (Tables 24a & b). As far as Hygromia striolata is concerned, the increase in palatability between the fresh leaf and leaf extract of Leontodon hispidus would expect that the epidermal hairs act as a hinderance to feeding. I failed to find any significant difference between the shaved and unshaved leaves of Leontodon hispidus nor the leaves of Urtica dioica (Tables 25a & b). Probably, other mechanisms are involved and further investigations to be sought.

Table 22. Comparison of the palatability between shaved and unshaved leaves of Leontodon hispidus and Urtica dioica with respect to Helix aspersa

Plants	Palatability ratio shaved/unshaved	t-value	d.f.	value of P
Leontodon hispidus	1.05	-1.197	9	$P > 0.05$
Urtica dioica	0.97	0.1291	9	$P > 0.05$

Table 23. Comparison of the palatability between shaved and unshaved leaves of _Leontodon hispidus_ and _Urtica dioica_ with respect to _Cepaea nemoralis_

Plants	Palatability ratio shaved/unshaved	t-value	d.f.	Value of P
Leontodon hispidus	1.21	-6.505	9	$P < 0.001$
Urtica dioica	1.32	-4.468	9	$P < 0.01$

Table 24a. Comparison of the palatability between shaved and unshaved leaves of _Leontodon hispidus_ with respect to _Helicella itala_

	Untouched	Consumed	Total
Shaved _Leontodon hispidus_	11	19	30
Unshaved _Leontodon hispidus_	19	11	30

$\chi^2 = 3.267$

d.f. = 1 $P > 0.05$

Table 24b. Comparison of the palatability between shaved and unshaved leaves of _Urtica dioica_ with respect to _Helicella itala_

	Untouched	Consumed	Total
Shaved _Urtica dioica_	14	16	30
Unshaved _Urtica dioica_	16	14	30

$\chi^2 = 0.067$

d.f. = 1 $P > 0.05$

Table 25a. Comparison of the palatability between shaved and unshaved leaves of *Leontodon hispidus* with respect to *Hygromia striolata*

	Untouched	Consumed	Total
Shaved *Leontodon hispidus*	12	18	30
Unshaved *Leontodon hispidus*	18	12	30

$\chi^2 = 1.667$

d.f. = 1 $P > 0.05$

Table 25b. Comparison of the palatability between shaved and unshaved leaves of *Urtica dioica* with respect to *Hygromia striolata*

	Untouched	Consumed	Total
Shaved *Urtica dioica*	13	17	30
Unshaved *Urtica dioica*	17	13	30

$\chi^2 = 0.600$

d.f. = 1 $P > 0.05$

III.4. Field observations

The feeding habits of the snails in the field depend on the relative abundance and the accessibility of the plant species. Therefore the results of the field observations may not be comparable to the palatability tests in the laboratory, especially only six plant species were tested in this study. Consequently, the data obtained in the field function as complementary information to the laboratory work. It also widens the picture of the food preferences of the snails, showing the whole spectrum of the food consumed by the herbivores. Nevertheless, the overall results were consistent with the experiments in terms of the similar preference order of the six plants tested in the laboratory and observed in the field. Among the four snail species, Helix aspersa was the most general feeder, consuming more than twenty different plant species (Table 26). Cepaea nemoralis and Helicella itala were more specific in feeding than Helix aspersa (Tables 27 & 28). Hygromia striolata seemed to be an oligophagous herbivore feeding on less than ten plant species (Table 29). This snail was more restricted in its distribution and also the least abundant of the four snail species found in the field.

On the whole, the more preferable plants were the members of the Compositae such as the Hieracium spp., Taraxacum spp. and Centaurea spp. (Table 30). Some of the members in the Rosaceae and Papilionaceae were also favoured. In general, the hard, hairy and rough surface leaves were less palatable than the soft-textured and smooth leaves. For the large snail species, they appeared to prefer the rosette leaves such as Taraxacum officinale and Hieracium vulgatum to those which were above ground level, unless they were rigid enough, like Sonchus asper and Cirsium vulgare, to support the snails.

Table 26. The number of observations of the plant species consumed by Helix aspersa in the field

Plant species	No. of observations
Sonchus asper	14
Urtica dioica	8+
Taraxacum officinale	6
Hieracium vulgatum	4
Heracleum sphondylium	4
Lamium album	4
Cirsium vulgare	4
Ononis repens	4
Chrysanthemum leucanthemum	4
Galium aparine	3
Tussilago farfara	2
Leontodon hispidus	2
Epilobium augustifolium	2
Centaurea scabiosa	2
Silene vulgaris	1
Hieracium exotericum	1
Plantago lanceolata	1
Plantago media	1
Trifolium medium	1
Sesleria caerulea	1
Bryophyte sp.	1
	70

+ Juveniles

Table 27. The number of observations of the plant species consumed by *Cepaea nemoralis* in the field

Plant species	No. of observations
Taraxacum officinale	9
Hieracium vulgatum	6
Sonchus asper	6
Epilobium augustifolium	5
Leontodon hispidus	4
Centaurea scabiosa	3
Chrysanthemum leucanthemum	3
Centaurea nigra	2
Galium aparine	2
Silene vulgaris	2
Urtica dioica	2
Heracleum sphondylium	1
Ononis repens	1
Hieracium exotericum	1
Hieracium pilosella	1
Plantago media	1
Bryophyte sp.	1
	50

Table 28. The number of observations of the plant species consumed by *Helicella itala* in the field

Plant species	No. of observations
Hieracium vulgatum	13
Centaurea scabiosa	8
Centaurea nigra	5
Chrysanthemum leucanthemum	5
Taraxacum officinale	4
Hieracium exotericum	4
Hieracium pilosella	3
Sonchus asper	3
Tussilago farfara	3
Leontodon hispidus	2
Plantago lanceolata	2
Ononis repens	2
Fragaria vesca	2
Lotus corniculatus	2
Poterium sanguisorba	1
Bryophyte sp.	1
	60

Table 29. The number of observations of the plant species consumed by *Hygromia striolata* in the field

Plant species	No. of observations
Taraxacum officinale	15
Heracleum sphondylium	13
Urtica dioica	8
Hieracium vulgatum	3
Fragaria vesca	3
Centaurea nigra	3
Epilobium augustifolium	2
Sonchus asper	2
Poterium sanguisorba	1
	50

Table 30. Number of species in different families of the flowering plants consumed by the snails

Families	No. of species
Compositae	11
Papilionaceae	3
Rosaceae	2
Plantaginaceae	2
Umbelliferae	1
Urticaceae	1
Onagraceae	1
Labiatae	1
Rubiaceae	1
Caryophyllaceae	1
Gramineae	1
	25

III.5. Behaviour of the snails

In assessing the consistence and agreement of the food preferences made by the snails, Kendall paired comparisons test was used (Kendall 1984). The agreement of preferences among the snails within the same species are shown in Tables 31 to 34. For Helix aspersa, the coefficients of agreement were 0.68 and 0.71 in the fresh material and leaf extract tests respectively. Cepaea nemoralis also exhibited high degree of agreement. The coefficients of agreement were 0.73 and 0.79 in the two sets of tests. Despite the different and perhaps less sensitive experimental techniques used for the smaller snail species, they also showed positive coefficients of agreement although the values were lower. In the fresh material and leaf extract experiments, the coefficients of agreement were 0.13 and 0.14 for Helicella itala and 0.17 and 0.12 for Hygromia striolata. All these results were significant suggesting that the snails were not allotting their choices randomly but instead displaying a preferential consumption on the tested plants.

Besides the agreement among the snails, the consistency of individual snails is also important when considering the hierachical food preferences of the snails. An incosistent snail may display its preferences for the plants in a non-transitive way. This is reflected in the circular triads of food preferences made by the individual snails. The frequency and distribution of circular triads in the palatability tests of the four snail species are shown in Tables 35 to 38. With six objects for comparison, the maximum number of circular triads is eight. Since the mean of triads made by the individual snails is low (less than 3), except for a few individuals, the snails are capable of discriminating the food plants and making their choices consistently.

Table 31a. Paired comparisons of the preferences of fresh materials with respect to *Helix aspersa*

	H	S	Ta	L	Tu	U	Total
H	-	4	4	5	5	5	23
S	1	-	4	4	5	5	19
Ta	1	1	-	4	5	5	16
L	0	1	1	-	4	5	11
Tu	0	0	0	1	-	5	6
U	0	0	0	0	0	-	0
							75

H = *Hieracium vulgatum*
S = *Sonchus asper*
Ta = *Taraxacum officianle*
L = *Leontodon hispidus*
Tu = *Tussilago farfara*
U = *Urtica dioica*

Coefficient of agreement = 0.68
χ^2 = 101.3
d.f. = 33 $P < 0.001$

Table 31b. Paired comparisons of the preferences of leaf extracts with respect to *Helix aspersa*

	S	H	Tu	Ta	L	U	Total
S	-	3	5	5	5	5	23
H	2	-	4	5	5	5	21
Tu	0	1	-	4	5	5	15
Ta	0	0	1	-	4	5	10
L	0	0	0	1	-	4	5
U	0	0	0	0	1	-	1
							75

S = *Sonchus asper*
H = *Hieracium vulgatum*
Tu = *Tussilago farfara*
Ta = *Taraxacum officinale*
L = *Leontodon hispidus*
U = *Urtica dioica*

Coefficient of agreement = 0.71
χ^2 = 104.0
d.f. = 33 $P < 0.001$

Table 32a. Paired comparisons of the preferences of fresh materials with respect to *Cepaea nemoralis*

	Ta	H	S	L	U	Tu	Total
Ta	-	4	4	5	5	5	23
H	1	-	4	5	5	5	20
S	1	1	-	4	5	5	16
L	0	0	1	-	5	5	11
U	0	0	0	0	-	4	4
Tu	0	0	0	0	1	-	1
							75

Ta = *Taraxacum officinale*
H = *Hieracium vulgatum*
S = *Sonchus asper*
L = *Leontodon hispidus*
U = *Urtica dioica*
Tu = *Tussilago farfara*

Coefficient of agreement = 0.73
χ^2 = 106.7
d.f. = 33 $P < 0.001$

Table 32b. Paired comparisons of the preferences of leaf extracts with respect to *Cepaea nemoralis*

	H	Ta	U	S	L	Tu	Total
H	-	4	5	5	5	5	24
Ta	1	-	4	5	5	5	20
U	0	1	-	5	5	5	16
S	0	0	0	-	4	5	9
L	0	0	0	1	-	4	5
Tu	0	0	0	0	1	-	1
							75

H = *Hieracium vulgatum*
Ta = *Taraxacum officinale*
U = *Urtica dioica*
S = *Sonchus asper*
L = *Leontodon hispidus*
Tu = *Tussilago farfara*

Coefficient of agreement = 0.79
χ^2 = 112
d.f. = 33 $P < 0.001$

Table 33a. Paired comparisons of the preferences of fresh materials with respect to *Helicella itala*

	H	L	Ta	S	Tu	U	Total
H	-	17	19	21	22	25	104
L	13	-	16	21	21	24	95
Ta	11	14	-	19	20	23	87
S	9	9	11	-	17	21	67
Tu	8	9	10	13	-	20	60
U	5	6	7	9	10	-	37
							450

H = *Hieracium vulgatum*
L = *Leontodon hispidus*
Ta = *Taraxacum officinale*
S = *Sonchus asper*
Tu = *Tussilago farfara*
U = *Urtica dioica*

Coefficient of agreement = 0.13
$\chi^2 = 76.15$
d.f. = 17 $P < 0.001$

Table 33b. Paired comparisons of the preferences of leaf extracts with respect to *Helicella itala*

	H	Ta	L	S	Tu	U	Total
H	-	16	18	20	23	26	103
Ta	14	-	17	19	22	25	97
L	12	13	-	18	20	23	86
S	10	11	12	-	13	21	67
Tu	7	8	10	17	-	20	62
U	4	5	7	9	10	-	35
							450

H = *Hieracium vulgatum*
Ta = *Taraxacum officinale*
L = *Leontodon hispidus*
S = *Sonchus asper*
Tu = *Tussilago farfara*
U = *Urtica dioica*

Coefficient of agreement = 0.14
$\chi^2 = 79.43$
d.f. = 17 $P < 0.001$

Table 34a. Paired comparisons of the preferences of fresh materials with respect to *Hygromia striolata*

	Ta	U	H	S	L	Tu	Total
Ta	-	18	21	23	24	27	113
U	12	-	17	21	23	22	95
H	9	13	-	14	21	22	79
S	7	9	16	-	20	21	73
L	6	7	9	10	-	20	52
Tu	3	8	8	9	10	-	38
							450

Ta = *Taraxacum officinale*
U = *Urtica dioica*
H = *Hieracium vulgatum*
S = *Sonchus asper*
L = *Leontodon hispidus*
Tu = *Tussilago farfara*

Coefficient of agreement = 0.17
χ^2 = 94.72
d.f. = 17 $P < 0.001$

Table 34b. Paired comparisons of the preferences of leaf extracts with respect to *Hygromia striolata*

	Ta	U	L	H	S	Tu	Total
Ta	-	17	20	21	23	26	107
U	13	-	14	20	21	23	91
L	10	16	-	16	20	21	83
H	9	10	14	-	20	20	73
S	7	9	10	10	-	18	54
Tu	4	7	9	10	12	-	42
							450

Ta = *Taraxacum officinale*
U = *Urtica dioica*
L = *Leontodon hispidus*
H = *Hieracium vulgatum*
S = *Sonchus asper*
Tu = *Tussilago farfara*

Coefficient of agreement = 0.12
χ^2 = 71.57
d.f. = 17 $P < 0.001$

Table 35a. The distribution of circular triads made by *Helix aspersa* in the palatability tests of fresh materials

No. of triads	Frequency
0	2
1	2
2	1
	5

Total number of triads = 4
mean = 0.8

Table 35b. The distribution of circular triads made by *Helix aspersa* in the palatability tests of leaf extracts

No. of triads	Frequency
0	3
1	1
2	1
	5

Total number of triads = 3
mean = 0.6

Table 36a. The distribution of circular triads made by *Cepaea nemoralis* in the palatability tests of fresh materials

No. of triads	Frequency
0	3
1	1
2	1
	5

Total number of triads = 3
mean = 0.6

Table 36b. The distribution of circular triads made by *Cepaea nemoralis* in the palatability tests of leaf extracts

No. of triads	Frequency
0	3
1	2
	5

Total number of triads = 2
mean = 0.4

Table 37a. The distribution of circular triads made by *Helicella itala* in the palatability tests of fresh materials

No. of triads	Frequency
0	5
1	4
2	10
3	5
4	5
5	1
	30

Total number of triads = 64
mean = 2.13

Table 37b. The distribution of circular triads made by *Helicella itala* in the palatability tests of leaf extracts

No. of triads	Frequency
0	4
1	3
2	10
3	6
4	6
5	1
	30

Total number of triads = 70
mean = 2.33

Table 38a. The distribution of circular triads made by *Hygromia striolata* in the palatability tests of fresh materials

No. of triads	Frequency
0	5
1	5
2	11
3	5
4	3
5	1
	30

Total number of triads = 59
mean = 1.97

Table 38b. The distribution of circular triads made by *Hygromia striolata* in the palatability tests of leaf extracts

No. of triads	Frequency
0	6
1	8
2	6
3	6
4	4
	30

Total number of triads = 54
mean = 1.80

IV. Discussion

IV.1. Method used

I used paried comparison tests of each plant species with every other plant species. This technique has been commonly used in the studies of animal behaviour (Appleby 1980; Bernstein 1969) and in the psychological research work (Thurstone 1927). Basically, this method of paired comparisons serves two purposes. In contrast to using a standard reference material as in many studies of food palatability of herbivores (Grime et al. 1968; Dirzo 1980), paired comparisons allow the animals to express their preferences in a more realistic situation. It is especially important from the ecological point of view that animals do not feed preferentially on food based on a reference material in their natural habitats. Furthermore, paired-comparisons method gives a picture of the interrelationships of the objects under preference. A paired-comparisons scheme is more informative than mere ranking against a standard, for with the latter when A is preferred to B and B preferred to C automatically implies that A is preferred to C; whereas with paired comparisons it might happen that C was preferred to A forming a circular triad. The existence of these departures from the ranking situation may due to various reasons. In fact, preference is a complicated comparison being made with reference to several factors simultaneously, and thus another reason for using paired comparisons is to give such effects a chance to show themselves. However, it should be pointed out that the method of paired comparisons is tedious when the number of objects for comparison is even moderately large. A compensatory design of incomplete block may then be used in such situation (Wilkinson 1957; Dykstra 1960). Though hardly any ecological studies have employed this method of paired comparisons, there is no good reason why it cannot be used in the present investigation of the feeding habits of the snails.

IV.2. Interactions between snails and plants

Of the six plant species which were tested, all were palatable to the snails but to varying degrees. It is clear that a perfect hierachical order of food preferences cannot be obtained unless there are complete consistence and agreement of the snails. However, on the whole, the results show that the snails do consume the plants preferentially. The rankings of plant palatabilities based on the total number of preferences made by the snails are supported by the palatability ratios data which show greater ratios exist between plants further apart as well as no significant differences between those adjacent in the ranking (See section III.1.). From the palatability tests, it is obvious that different snail species exhibit different preferences for the plants. However, some plant species, such as Hieracium vulgatum, Taraxacum officinale and Sonchus asper, are highly palatable to all the snails; whilst some other plants, for example, Leontodon hispidus, Urtica dioica and

Tussilago farfara, are low in palatability. The most interesting phenomena are the exceptionally high palatabilities of Urtica dioica and Leontodon hispidus to the snails Hygromia striolata and Helicella itala respectively. Interpretation of these situations probably requires the introduction of the concepts of 'general' acceptability and 'specific' acceptability (Dirzo 1980). Species of plants that possess qualities of specific acceptability have a specialized relationship with a specific predator. That Urtica dioica is highly preferable to Hygromia striolata is in agreement with the work of Mason (1970a) who has found that this snail has special preference for Urtica dioica when compared with other snail species. The leaf surface of Urtica dioica is protected by stinging hairs but consumption of this plant by the snails is induced by a chemical stimulus which is, at least in part, olfactory (Grime et al. 1970). In addition, Urtica dioica is nutritious as it is associated with habitats that have high levels of phosphorus (Pigott and Taylor 1964). Since it has been shown that the stinging hairs on the leaves of Urtica dioica have no effect on the feeding of Hygromia striolata (See table 25b), it is not surprising that Urtica dioica is preferable to Hygromia striolata. Similar interpretation is applicable to Cepaea nemoralis except that the feeding of this snail is affected by the stinging hairs (See table 23). This parallels with the findings of Grime et al. (1969, 1970) suggesting that the movement of Cepaea nemoralis is hindered on rough surfaces and epidermal hairs deter consumption of the plant. This explains why the fresh leaf of Urtica dioica is low in palatability whilst the leaf extract is highly preferable to Cepaea nemoralis, illustrating mechnical barriers also play an important role in determining food preferences. On the other hand, it is not clear why Helix aspersa and Helicella itala are not attracted to Urtica dioica. The fact that both of these snail species are not affected by the stinging hairs (See tables 22 and 24b) suggests other complicated factors are operating. It may be argued that the age of the leaf is an important factor as most snails prefer senescent leaves (Wolda et al. 1971; Elton 1966). One possible reason may be due to the relative importance of the effects of various factors between a generalist feeder, like Helix aspersa, and specialist feeder such as Hygromia striolata. It has been shown in insect that specialist species prefer high nitritious tissues in spite of other deterrent effects whereas generalist species, in the similar situation, avoid deterrent effects even though the tissues are the most nitritious (Cates and Rhoades 1977). It is of interest that a correlation between polyphagy and nitritive value also apparently existed in snails used in this study and certainly deserves further investigation. Moreover, in the present study only six plant species were compared. Since Urtica dioica is not totally rejected by the snails, it might be very preferable, in a relative term, when comparing with many other apparently repulsive plant species.

The palatability of Leontodon hispidus, like Urtica dioica, differs widely between species of snails. It is clear that

Helicella itala has special preference for Leontodon hispidus is partly due to its capability to overcome the physical barrier (See table 24a). More positively, Williamson et al. (1976) has demonstrated that the growth rate of the snails feeding on Leontodon hispidus is the highest when compared with five other plants. He argued that the mineral need for the snails appeared to be of major importance and energy content was irrelevant. Again, the reason why Helix aspersa and Hygromia striolata, which are not affected by the epidermal hairs of Leontodon hispidus, show low preference for this plant is somewhat obscure. Probably, different snail species require different quantity and quality of nourishment such as minerals and vitamins provided by the plants; just like the growth of Helix pomatia requires vitamins A and B (Howes and Whellock 1937), whereas Helix aspersa needs sitosterol and vitamin D for growth (Wagge 1952).

When comparing the palatabilities between fresh leaves and leaf extracts, there are no significant correlations except in Helicella itala. This illustrates the point that chemical nature of the plants is also an important factor but its relative significance varies with different snail species and also depends on what kind of plants are chosen for the test. Apart from chemical factors, the differences in preferences between fresh materials and leaf extracts are mainly due to mechanical barriers. For example, the epidermal hairs of Urtica dioica and Leontodon hispidus present an obstacle to the feeding of Cepaea nemoralis (See table 23). However, the low palatability of fresh materials and the absence of noxious materials in the leaf extracts does not necessarily mean that the mechanism is entirely physical. Conversely, it is also true that a physical effect may not be detected in a plant in which the cell sap is unpleasant. For instance, the palatabilities of *Tussilago farfara* are low, both in fresh material and leaf extract, to the snails. It is not certain whether the thick and tough leaf surface of this species present any barrier to grazing. Perhaps the slight increase in preference of leaf extract of *Tussilago farfara* with respect to *Helix aspersa* suggests this possibility. Since no attempt has been made to investigate the effect of thickness of leaf on feeding, the actual mechanisms account for the low palatability of *Tussilago farfara* remain to be found.

There is little doubt that the palatabilities of food are largely determined by the characters of the plant, but the validity of the preference order depends on the behaviour of the animal. This is indicated by the degree of agreement among the snails within the same species. The results show that all the snail species exhibit a positive coefficient of agreement although the value is not very high. This suggests that a general food preference order exists among the snails of the same species. However, it is clear that there are also some degrees of variations of individual preferences for the plants and this may relate to the polymorphism in feeding behaviour of the snails (Dirzo 1980). Moreover, the reliability of the preference order may require the examination of the consistency of individual snails.

This indicates the capability of individual snails in making distinctions between the plants. Very little is known about the underlying principles relating to the consistency of the feeding habits of herbivores. Probably, a specialized feeder may be more consistent in feeding but the confirmation of this notion calls for further study.

The materials selected and eaten by the snails in the laboratory may not be similarly consumed in the field because the ecosystem as a whole is more complicated in the natural habitat. Besides physical and chemical factors, the susceptibility of a plant species to herbivore attack also depends on its ecological environment. The significant effects of intra- and inter-specific interactions are not unusual. For examle, the presence of repellent substances released into the air by some species of plants may provide some degree of protection to other plant species in the vicinity. Moreover, herbivores are more likely to find and remain on hosts growing in less diverse habitat because of resource concentration. Area-species relationship may contribute another factor governing the consumption of plants by herbivores (May 1981). Although interspecific competition for food is not an important factor in many circumstances (Richardson 1975; Eisenberg 1970), recent studies have shown that the mucus secreted by the snails reduces the activities of other individuals of the same species or related species (Cameron and Cater 1979). Despite all these discrepancies between the laboratory conditions and natural environment, some remarkable features are revealed from the field observations in the present study. Of the four snail speices, Helix aspersa is the most generalist feeder and Hygromia striolata an oligophagous herbivore. That Hygromia striolata has higher selectivity for species of food plant is consistent with the palatability tests in which the number of comparisons having no significant differences between plants is the least when comparing with other snail species. The ecological advantages of a specialist appear to be the reductions of metabolic costs of the animal as it is closely adapted to the nutritional conditions of the hosts as well as less energy spent to detoxify a narrow range of defensive chemicals present in the plants; whereas polyphagy is costly in these senses and leads to longer development time as consequences. This may relate to the fact that Helix aspersa which is a biennial species requires one year to reach maturity whilst Hygromia striolata takes a few months to grow into full size. Moreover, Mason (1970b) has found that Hygromia striolata is one of the snails having the highest ingestion and assimilation rate among twenty-one species studied.

Another aspect noted in the field is the attachment problem encountered by the snails. All Helix aspersa feeding on the leaves of Urtica dioica in the field were juveniles (See table 26). There are several explanations. It may be due to different tastes between adult and juvenile snails. It has been shown that juvenile snails of Cepaea nemoralis are less selective in feeding (Williamson and Cameron 1976), and adult snails of Helix pomatia are less mobile (Pollard 1975). This may also be applicable to Helix aspersa. Since, however, *Helix aspersa* does consume considerable quantity of *Urtica dioica* in the laboratory, it is not difficult to imagine that probably the leaves of *Urtica dioica* are not rigid enough to support the heavy, adult snails. On the other hand, a herbivore well attached on a plant does not necessarily imply that the animal will feed on that plant readily. It is not uncommon to find many snails resting on the plants which are not food plants. In the present study, no examination has been carried out on the differences of feeding habits between adult and juvenile snails, further experimentation would certainly enlighten this aspect.

Ultimately, all biological observations should find their explantations in evolution. The present phenomena of the herbivore-plant interactions must be the outcomes of the selective forces that acted on the ancestors of both plant and animal. However, these forces are difficult to be demonstrated and they are usually inferred from retrospective analysis of plant and animal characteristics. Harborne (1978) has argued that the enormous diversity of secondary chemical substances produced by the plants is the consequence of the selection pressures exerted by the herbivores. Ehrlich and Raven (1964) visualise a process of coevolution, with both plants and their herbivores continually adapting to changes in each other. Perhaps the evolutionary trend in herbivore-plant interaction has been towards increasing specialization and minimizing interspecific competition. Although these speculations are plausible, it is important to realize that the underlying assumptions have not been proved. Strong *et al*. (1984) argue that the reciprocal and intense interactions for coevolution to be possible are rare. Furthermore, it is dangerous to assume that any feature which at present appears to hinder a herbivore from grazing must be evolved from the pressure of grazing. For example, the selection for epidermal hairs of a particular plant might be originally evolved to the response of xeromorphy, and now, secondarily, serve as a deterrent effect to grazing. No matter how intense an interaction between a plant and a herbivore has been, it may represent only a fraction of the selective forces leading to the present form and behaviour. Similarly, it seems never can we attribute a precise or unique function to a plant product or structure. Finally, I would admit that there remains a vast amount of fascinating investigation which is necessary before the complexities of interaction between plants and snails are thoroughly understood.

V. Summary

Six plant species were tested with four snail species, using paired comparisons method to show the preference orders exhibited by the snails. Palatabilities between fresh leaf and leaf extract of the plants were compared. The effect of hairness of two plant species, *Urtica dioica* and *Leontodon hispidus*, was also examined. The feeding habits of the snails were further inferred from field observations.

The palatabilities of some plants (e.g. *Hieracium vulgatum*) were very high to all the snails; whilst some species (e.g. *Tussilago farfara*) were low to all the snail species; and others (e.g. *Urtica dioica*) were very different with respect to different snail species. Despite only few plant species were tested, it is suggested that it may be possible to distinguish 'general' palatability from 'specific' palatability of the plants.

The palatabilities of the plants were determined by various factors. Chemical and physical factors were obvious, and the nutritive value of the plant was of no less importance. Plants with soft and smooth leaves were generally more palatable than those with hard, thick and hairy leaves. The behaviours of the snails, on the whole, were consistent showing a distinct preference order for the plants.

Apart from chemical and physical barriers, the consumption of plants by the snails in the field was also influenced by the environmental factors, such as the

abundance and accessibility of the plants to the herbivores, the structure of the community and the interactions with other organisms. It was observed that some food plants might not be rigid enough to support the snails and this probably enabled the plants to escape from the consumption by the snails.

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VII. References

Appleby, M.C. (1980). Social rank and food access in red deer stags. Behaviour, 74, 294-309.

Bentley, S. & Whittaker, J.B. (1979). Effect of grazing by a chrysomelid bettle, Gastrophysa viridula, on competition between Rumex obtusifolius and Rumex crispus. Journal of Ecology, 67, 79-90.

Bernstein, I.S. (1969). Stability of the status hierarchy in a pigtail monkey group (Macaca nemestrina). Anim. Behav., 17, 452-458.

Boycott, A.E. (1934). The habitats of land mollusca in Britain. Journal of Ecology, 22, 1-37.

Brower, L.P. (1969). Ecological chemistry. Scientific American, 220, 22-29

Cameron, R.A.D. & Carter, M.A. (1979). Intra- and inter-specific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). Journal of Animal Ecology, 48, 237- 246.

Cates, R.G. (1975). The interface between slugs and wild ginger: some evolutionary aspects. Ecology, 56, 391-400.

Cates, R.G. & Rhoades, D.F. (1977). Prosopis leaves as a resource for insects. In: Mesquite (ed. B.B. Simpson). Dowden, Hutchinson and Ross, Inc., Stroudsberg, Pennsylvania.

Dirzo, R. (1980). Experimental studies on slug-plant interactions. I. The acceptability of thirty plant species to the slug Agriolimax caruanae. Journal of Ecology, 68, 981-998.

Durham County Conservation Trust (1984). Bishop Middleham Nature Reserve: Five Year Management Plan. Durham.

Durham County Council (1979). Magnesian Limestone Escarpment Plan. Report of survey, Durham.

Dykstra, O.Jr. (1960). Rank analysis of incomplete block designs: a method of paired comparisons employing unequal repetitions of pairs. Biometrics, 16, 176-188.

Ehrlich, P.R. & Raven, P.H. (1964). Butterflies and plants: a study in coevolution. Evolution, 18, 588-608.

Eisenberg, R.M. (1970). The role of food in the regulation of the pond snail Lymnaea elodes. Ecology, 51, 680-684.

Elton, Ch.S. (1966). The Pattern of Animal Communities. London: Methuen.

Feeny, P.P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology, 51, 565-581.

Gilham, M.E. (1955). Ecology of the Pembrokeshire Islands. III. The effect of grazing on the vegetation. Journal of Ecology, 43, 172-206.

Grime, G.P. & Blythe, G.M. (1969). An investigation of the relationships between snails and vegetation at the Winnats Pass. Journal of Ecology, 57, 45-66.

Grime, G.P., Blythe, G.M. & Thornton, J.D. (1970). Food selection by the snail Cepaea nemoralis L. in Watson ed. Animal populations in relation to their food resources. Blackwell Scientific Publications, Oxford.

Grime, G.P. MacPherson-Stewart, S.F. & Dearman, R.S. (1968). An investigation of leaf palatability using snail Cepaea nemoralis L. Journal of Ecology, 56. 405-420.

Harborne, J.B. (1978). Biochemical Aspects of Plant and Animal Coevolution. Academic press, London.

Howes, N.H. & Whellock, R.B. (1937). A semi-synthetic diet for Helix pomatia. Biochem. J., 31, 1489.

Kendall, M.G. (1948). Rank Correlation Methods. London: Charles Griffin.

Kendall, M.G. (1984). Statistics: Theory and Practice. London: Charles Griffin.

Lawton, J.H. (1970). Feeding and food energy assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulz.) (Odonata: Zygoptera). Journal of Animal Ecology. 39, 669-689.

Levin, D.A. (1973). The role of trichomes in plant defence. Quaterly Review of Biology, 48, 3-15.

Long, H.C. (1924). Plants Poisonous to Livestock. 2nd edn. Cambridge.

Mason, C.F. (1970a). Food, feeding rates and assimilation in woodland snails. Oecologia, 4, 358-360.

Mason, C.F. (1970b). Snail populations, beech litter production, and the role of snails in litter decomposition. Oecologia, 5, 215-239.

May, R.M. (1981). Theoretical Ecology. Blackwell Scientific Publications, Oxford.

Milton, W.E. (1933). The palatability of self-establishing species in grassland. Emp. J. exp. Agric., 1, 347-360.

Neama, J.D. (1982). Physiological and ecological studies on altitudinal distribution in the genus Salix. Unpublished Ph.D. Thesis, University of College, Cardiff.

Pigott, C.D. & Taylor, K. (1964). The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soils. Journal of Ecology (Supplement), 52, 175-185.

Pollard, E. (1975). Aspects of the ecology of Helix pomatia L. Journal of Animal Ecology, 44, 305-329.

Richardson, A.M.M. (1975). Food, feeding rates and assimilation in the landsnail Cepaea nemoralis L. Oecologia, 19, 59-70.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984). Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific Publications, Oxford.

Taylor, J.W. (1913). Monograph of the Land and Freshwater Mollusca on the British Isles. Leeds.

Thurstone, L.L. (1927). The method of paired comparisons for social values. J. Abnorm. Psychol., 21, 384-400.

Wagge, L.E. (1952). Quantitative studies of calcium metabolism of Helix aspersa. J. exp. Zool., 120, 311-342.

Wilkinson, J.W. (1957). An analysis of paired comparison designs with incomplete repetitions. Biometrika, 44, 97-113.

Williamson, P. & Cameron, R.A.D. (1976). Natural diet of the landsnail Cepaea nemoralis. Oikos, 27, 493-500.

Wolda, H., Zweep, A. & Schuitema, K.A. (1971). The role of food in the dynamics of population of the landsnail Cepaea nemoralis. Oecologia, 7, 361-381.