

Food, Feeding Rates and Assimilation in the Land Snail *Cepaea nemoralis* L.

A. M. M. Richardson

Department of Biological Sciences, University of Exeter,
Hatherly Laboratories, Exeter, Devon

Received January 6, 1975

Summary. The natural diet of a population of *Cepaea nemoralis* living in a sand dune system in southwest England was investigated by field observations and examination of crop and faeces contents. The food consisted of dead material from the commoner plants on the site. Very little green matter was eaten and there was little evidence for seasonal variation in the diet.

Consumption and egestion rates were measured gravimetrically on natural foods (dead leaves of *Taraxacum officinale* and *Ononis repens*) and artificial foods. Consumption rates were temperature dependent over the measured range of 5–20° C and also varied with the food substrate, an artificial food (rat food pellets) being consumed at the highest rate. High variability in the results can probably be linked to the live weight and activity cycles of the snails.

Assimilation was estimated as the difference between consumption and egestion, since a trial of the ash-ratio method proved unsuitable with this animal. Assimilation efficiency did not vary with temperature over the range studied, but was dependent on food substrate, the two artificial foods (rat food pellets and lettuce leaves) being assimilated more efficiently (71–73%) than natural foods (30–44%).

Faeces produced from the digestive gland could be distinguished and were measured separately. The amount produced was very small compared to the gut faeces, but increased significantly when a relatively indigestible food was used.

Introduction

To make realistic estimates of the feeding rates of animals the natural food sources must be known. The diet of *Cepaea nemoralis* L. has been studied previously by Grime and his associates (Grime *et al.*, 1968, 1970; Grime and Blythe, 1969) and Wolda *et al.* (1971) using animals from limestone grassland in Derbyshire and an artificial population in the Netherlands respectively. Both recorded the diet of the animals in these habitats, but did not measure the rate of feeding or assimilation. Using the IBP symbols as defined by Petruszewicz and Macfadyen (1970), population assimilation can be calculated either as:

$$A = C - FU$$

or:

$$A = P + R.$$

The apparent simplicity of measuring population assimilation (energy flux) in terms of consumption minus rejecta is deceptive, and in most ecological studies, it is calculated as the sum of production and respiration. Usually, field measure-

ments of production are more accurate than information from laboratory feeding studies (Petrušewicz and Macfadyen, 1970), and Phillipson (1967) discusses the likely errors in laboratory feeding studies. However, in support of field studies, Crossley (1966) found good agreement between laboratory studies and field radioisotope experiments in herbivorous insects. As in respiration measurements, it is critical that experimental conditions should reproduce those in the field as closely as possible (Macfadyen, 1967).

The following study is part of an overall investigation of energy flux in a *Cepaea* population.

Methods

Study Area. Field studies were carried out in the Braunton Burrows sand dune system, North Devon (Nat. Grid. Ref.: SS458356), close to the National Nature Reserve. The structure of the dune has been described by Kidson and Carr (1960), the vegetation by Willis *et al.* (1959a, b), and the mineral status of the soils by Willis (1963, 1965) and Willis and Yemm (1961).

The site was situated landward to the main dune ridge, in an undulating slack and dune-pasture complex, dominated in the drier areas by the grasses *Ammophila arenaria* Link. and *Festuca rubra* L. Over 60 other angiosperm species were identified on the site. The absence of short turf with much *Thymus drucei* indicates that heavy grazing by rabbits does not occur (Willis *et al.*, 1959a, b) and although the land is common, no stock were grazed on the site.

Besides *Cepaea nemoralis*, 12 other molluscs were collected during the study. Of these, only the population of *Helix aspersa* Muller approached the biomass of *C. nemoralis*. *C. hortensis* was not present.

Diet. Although nocturnal, *C. nemoralis* is relatively easy to observe and direct observations of feeding were made on three occasions in 1971 (June 10–11, July 23–24, August 4–5). Animals were observed in nine 1 m² quadrats once every hour for the nightly activity period.

Samples of the animals crop contents and faeces were also taken on a regular basis. They were mounted in glycerine jelly and compared under the microscope with scrapings from the epidermis and stems of the commoner plants on the site (over 20 sp.).

Feeding Rate. Assimilation was estimated as the difference between consumption and rejecta, measured gravimetrically. Before the experiment snails were fed filter paper which resulted in white marker faeces. The animals were then exposed to the experimental food for 24 hrs. The food was either dried and weighed beforehand (MRC2 diet pellets) or a similar aliquot was kept away from the animals over the 24 hrs and then weighed afterwards to estimate the water loss from the food. After the experiment, the animals were again given filter paper and the faeces were collected for weighing until the white marker faeces appeared. Food and faeces were dried in a vacuum oven at 40° C before weighing. Calorific contents of food and faeces were determined in a Gallenkamp ballistic bomb calorimeter.

Two natural and two artificial foods were used: dead leaves and stems of *Ononis repens* L., dead leaves of *Taraxacum officinale* (L.) Link., discs cut from fresh leaves of Lettuce (*Lactuca sativa* L.) and pellets of Charles Rivers MRC2 rat diet.

The experiments were carried out on individual animals in 300 cm³ dishes. Humidity and water were supplied by a layer of water soaked cotton wool covered with nylon mesh. A variety of temperatures were used with natural light regimes.

Assimilation Efficiency. Mason (1970) used the ash ratio method of Conover (1966) to measure the assimilation efficiency of snails. Since it required no quantitative collection of food and faeces, a trial experiment of this method was carried out. 10 adult animals were used and their assimilation efficiency was estimated using the gravimetric method described above. Samples of the food (lettuce discs) were dried to constant weight at 40° C in a vacuum oven and then ashed in a muffle furnace at 500° C for 48 hrs. The experiment was repeated twice. The assimilation consumption ratio (*U*) was calculated by the gravimetric method (*e.g.* Phillipson, 1960) and the ash ratio method using the following formulae:

Table 1. Major components of the diet of *Cepaea nemoralis* in sand dunes. Material from crop and faeces combined compared with field observations of feeding

Plant species	% Occurrence in crop contents and faeces	% Occurrence in field observations
<i>Festuca rubra</i>	1	26
<i>Ammophila arenaria</i>	13	21
<i>Ononis repens</i>	9	10
<i>Hieracium pilosella</i>	9	5
<i>Leontodon taraxacoides</i>	12	2
<i>Hypochoeris glabrata</i>	8	2
<i>Senecio jacobaea</i>	3	5
<i>Carlina vulgaris</i>	3	0
<i>Plantago lanceolata</i>	1	0
<i>Lotus corniculatus</i>	5	8
<i>Agrostis stolonifera</i>	4	2
<i>Medicago lupulina</i>	3	0
<i>Ranunculus bulbosus</i>	3	0
<i>Vicia</i> sp.	2	2
<i>Veronica</i> sp.	4	0
<i>Taraxacum officinale</i>	2	2
<i>Potentilla anserina</i>	3	2
<i>Ajuga reptans</i>	2	0
<i>Crepis taraxacifolia</i>	1	2
<i>Sonchus asper</i>	2	0
Rabbit faeces	0	3
Moss	10	7
Arthropod remains	6	0
Fungal hyphae	8	0

$$U = \frac{F - E}{F} \times 100 \quad (\text{Gravimetric method})$$

$$U = \frac{f - e}{(1 - e)f} \times 100 \quad (\text{Ash ratio method})$$

Where F is the estimated dry weight of food eaten, E is the dry weight of faeces produced, f is the ash free dry weight: dry weight ratio for food and e is the same for faeces.

Results

Diet

No major food components were found which were present in the crop samples but not in the faeces and consequently the results from these two sources were lumped together for comparison with the direct observations. These results are shown in Table 1. A clear difference between the two sets of results is the near absence of *Festuca rubra* in the crop/faeces data compared with its major occurrence in the direct observations. This could either represent a high digestibility of the grass or a failure to detect it. Its apparent absence in the crop material and its lack of prominent epidermal features would indicate the latter possibility.

The following foods occurred over 5% of observations in either of the two methods:

Festuca rubra
Ammophila arenaria
Ononis repens
Leontodon taraxacoides
Hypochoeris glabrata
Lotus corniculatus
 Moss
 Fungal hyphae

All these observations refer to dead material and little green material was observed in the faeces. Moss leaves were by far the commonest green material eaten, the only other plant eaten green with any consistency being *Lotus corniculatus*.

The results were examined for any seasonal variation in the diet. Of the eight items listed above, *Festuca rubra* was only detected in the three sets of direct observations. *Ammophila*, *Leontodon* and *Hypochoeris* show no distinct seasonal changes. *Ononis* only occurs in the diet from June to September which corresponds with the appearance and disappearance of the foliage on the site. In August it is the dominant plant over large areas but its remains are almost completely eaten by decomposers before the spring of the next season. *Lotus* shows a slight tendency to be eaten early in the year and in the case of moss this is quite marked.

Animal material was found only rarely in the shape of unidentified arthropod remains and occasionally small intact mites (Acarina). The very small amounts would indicate that these are only taken by chance.

In conclusion, the diet of *C. nemoralis* at Braunton consists of the dead parts of the commoner plants. There is no evidence to suggest that the snails avoid any particular plants and the commoner plants were eaten most frequently.

Feeding Rate

The summarised results of individual feeding experiments (nearly 150) are shown in Table 2. Sufficient results are available with lettuce as the food to investigate the relationship between feeding rate and temperature. An analysis of variance with regression (Sokal and Rohlf, 1969) was carried out:

Source of variation	d.f.	SS	MS	F	Sig.
Among temps.	5	0.0494	0.0099	7.13	$P < 0.001$
Linear regression	1	0.0434	0.0434	28.93	$0.01 < P > 0.001$
Deviations from regression	4	0.0060	0.0015	1.07	n.s.
Within temps.	36	0.0499	0.0014		
Total	41	0.1487			

The calculated regression line and equation are shown in Fig. 1.

Table 2. Summarised results (\pm SE) of individual feeding experiments

Substrate	Temp. (° C)	Consumption rate g g DW ⁻¹ Day ⁻¹	Egestion rate		Assimi- lation efficiency
			Gut	g g DW ⁻¹ Day ⁻¹ Digestive gland	
Lettuce	23.5	0.1286 \pm 0.0233		0.0334 \pm 0.0049	70.9 \pm 3.09
	23.0	0.0820 \pm 0.0137		0.0195 \pm 0.0036	76.5 \pm 1.67
	12.6	0.0493 \pm 0.0094		0.0104 \pm 0.0017	77.2 \pm 2.58
	12.0	0.0395 \pm 0.0107		0.0081 \pm 0.0023	79.5 \pm 7.17
	9.8	0.0393 \pm 0.0098		0.0191 \pm 0.0024	44.2 \pm 12.03
	5.0	0.0271 \pm 0.0061		0.0049 \pm 0.0003	81.9 \pm 8.05
<i>Ononis</i>	10.0	0.0306 \pm 0.0119	0.0122 \pm 0.0060	0.0022 \pm 0.0005	54.3 \pm 6.51
	9.8	0.0653 \pm 0.0075	0.0389 \pm 0.0054	0.0055 \pm 0.0013	31.8 \pm 6.19
	9.5	0.0895 \pm 0.0291		0.0511 \pm 0.0105	39.5 \pm 5.71
	8.2	0.0749 \pm 0.0066		0.0521 \pm 0.0052	46.0 \pm 6.15
	8.1	0.0602 \pm 0.0067	0.0313 \pm 0.0059	0.0020 \pm 0.0005	
<i>Taraxacum</i>	8.1	0.1050 \pm 0.0067	0.0593 \pm 0.0046	0.0094 \pm 0.0014	33.0 \pm 4.88
	10.0	0.1137 \pm 0.0159	0.0642 \pm 0.0159	0.0049 \pm 0.0024	21.9 \pm 5.39
Rat food	8.3	0.2230 \pm 0.0192	0.0720 \pm 0.0077	0.0018 \pm 0.0004	65.5 \pm 3.50
	8.3	0.2101 \pm 0.0446	0.0414 \pm 0.0081	0.0014 \pm 0.0002	80.3 \pm 3.08

The food substrate has a marked effect on consumption rate and assimilation efficiency. The overall mean consumption rates (g g⁻¹ DW day⁻¹), excluding data above 20° C, and the significance of the difference between the means are shown below:

Food	Rat food >	<i>Taraxacum</i> >	<i>Ononis</i> =	Lettuce
Mean consumption rate	0.217	0.108	0.056	0.040
F value and significance		14.9***	16.09**	2.62n.s.

*** $P < 0.001$; ** $P = 0.01 - 0.001$; n.s. = not significant.

The assimilation efficiencies (%) can be examined similarly:

Food	Rat food =	Lettuce >	<i>Ononis</i> >	<i>Taraxacum</i>
Mean assimilation %	73.0	70.7	43.8	29.6
F value and significance		0.26n.s.	51.02***	7.38***

There was no relationship between assimilation efficiency and temperature. The low assimilation efficiency on *Taraxacum* is of interest since the animals used for that trial had all been collected from a large isolated *Taraxacum* plant in the field. The assimilation efficiency of the same group on *Ononis* was significantly higher ($F = 5.59$, d.f. 1/21, $P < 0.5$). This may indicate either high resistance to digestion in *Taraxacum* or that there is little food specialisation in *Cepaea*.

The improved assimilation efficiency on "artificial" substrates probably reflects the selection which has gone on to improve their digestibility. The dif-

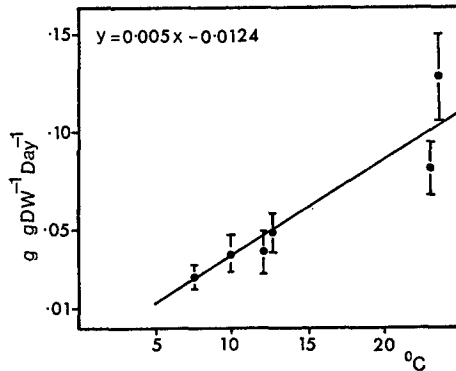


Fig. 1. Relationship between consumption rate of lettuce (*Lactuca sativa*) and temperature for adult *Cepaea nemoralis*. The vertical bars represent 1 Standard Error above and below the mean

ferences in consumption rate may be related to the texture and geometry of the food source. In the field, snails have been observed to feed on a single pellet of rabbit dung for a whole night and a pellet of rat food probably presents the same easily-radulated surface and unlimited supply. The thin stems of *Ononis*, on the other hand, have a rather limited surface area, whereas the lamina of a *Taraxacum* leaf is easily attacked. Lettuce is a special case since green material is rarely eaten in the field.

Two types of faeces were produced by the snails: the main bulk of "gut" faeces and at intervals a fine, brown, granular material which is the residue of intra-cellular digestion in the digestive gland. Intra-cellular digestion is a slower process than extra-cellular and faeces from this source were often produced many days after a meal. Production of digestive gland faeces was measured in some instances and the rates are shown in Table 2. The amount produced is very small compared to the bulk gut faeces but it is significantly higher when *Taraxacum* is the food source ($F = 38.31$, d.f. 1/44, $P < 0.001$). This may be related to the low digestibility of *Taraxacum* already mentioned. The appearance of digestive gland faeces long after a meal (hence not collected as faeces from that meal) means that estimates of assimilation efficiency may be inflated.

Food consumption rates, egestion rates, and assimilation efficiencies are presented in energy terms in Table 3. Since the energy content of faeces is consistently higher than that of food, these assimilation efficiencies are lower than those estimated gravimetrically. Mean values for *Taraxacum* were 29.7% and for *Ononis* 33.6%.

Assimilation Efficiency

The results from the trial of the ash-ratio method are shown in Table 4. The frequent failure to obtain any results from the ash-ratio method was due to the appearance of values of e greater than f . This implies that the ash content of the faeces was lower than that of the food and consequently a negative assimilation.

Table 3. Summarised results (\pm SE) of individual feeding experiments in energy terms

Substrate	Temp. (° C)	Consumption rate kJ g DW ⁻¹ Day ⁻¹	Egestion rate		Assimi- lation efficiency
			Gut	kJ g DW ⁻¹ Day ⁻¹ Digestive gland	
Lettuce	23.5	2.0873 \pm 0.3782		0.6698 \pm 0.0983	67.91
	23.0	1.4263 \pm 0.2383		0.4038 \pm 0.0746	71.69
	12.6	0.8098 \pm 0.1544		0.2427 \pm 0.0397	70.03
	12.0	0.6507 \pm 0.1763		0.1613 \pm 0.0458	75.21
	9.8	0.6635 \pm 0.1655		0.3832 \pm 0.0482	42.25
	5.0	0.4276 \pm 0.0963		0.1066 \pm 0.0065	75.07
<i>Ononis</i>	10.0	0.5526 \pm 0.2149	0.2597 \pm 0.1277	0.0554 \pm 0.0126	42.98
	9.8	1.2377 \pm 0.1422	0.7757 \pm 0.1077	0.1148 \pm 0.0271	28.05
	9.5	1.5300 \pm 0.4975		1.0164 \pm 0.2088	33.57
	8.2	1.3575 \pm 0.1196		1.0151 \pm 0.1013	25.22
	8.1	1.1664 \pm 0.1298	0.6862 \pm 0.1293	0.0394 \pm 0.0099	37.79
<i>Taraxacum</i>	10.0	1.7437 \pm 0.2438	1.0839 \pm 0.2533	0.0815 \pm 0.0399	33.17
	8.1	1.7196 \pm 0.1097	1.0981 \pm 0.0852	0.1700 \pm 0.0253	26.26
Rat food	8.3	3.9783 \pm 0.3425		1.4293 \pm 0.1491	64.07
	8.3	3.8758 \pm 0.8227		0.8421 \pm 0.1594	78.27

Table 4. Results of comparison between gravimetric and ash-ratio methods for determining assimilation efficiency

Snail num- ber	Snail live weight (g)	Dry weight food eaten (mg)	Ash content food (%)	Dry weight faeces produced (mg)	Ash content faeces (%)	% Assimi- lation Gravi- metric	% Assimi- lation Ash-ratio
1	4.4	14.02	21.06	5.02	18.7	64.19	
2	2.8	21.79	13.24	4.36	20.9	79.99	42.14
3	2.8	28.67	21.41	6.42	14.2	77.61	
4	3.3	24.51	23.12	4.11	18.0	83.23	
5	2.4	14.21	19.97	3.35	25.1	76.43	25.42
6	2.5	5.78	21.82	1.65	35.8	71.45	49.86
7	3.4	19.71	19.82	2.99	23.4	84.83	19.13
8	2.0	20.01	20.03	3.52	23.9	82.41	20.07
9	3.1	21.48	11.89	7.55	13.8	64.85	15.50
10	3.4	21.73	21.41	6.62	21.8	69.54	2.00
2	2.7	22.23	17.36	4.51	22.62	79.71	28.14
3	2.6	20.98	17.36	5.59	16.99	73.36	
4	3.4	27.43	17.36	8.75	49.14	68.05	78.27
5	2.1	16.52	17.36	5.00	6.60	69.75	
6	2.7	23.36	17.36	6.51	43.32	72.13	72.51
7	3.5	21.32	17.36	6.99	9.30	67.21	
8	1.9	22.51	17.36	6.75	11.11	70.01	
9	3.2	12.44	17.36	5.69	40.77	54.26	69.48
10	3.3	23.70	17.36	5.39	22.82	77.26	28.95
Mean	2.92	20.13		5.30		72.96	37.62

Comparison of individual assimilation efficiencies by the two methods show wide differences and the mean values also differ significantly ($t = 5.82$, d.f. 29, $P < 0.001$).

Discussion

Boycott (1934) describes the feeding habits of terrestrial molluscs as follows: "The normal food consists of the decayed remains of the higher plants, fungi, lichens and algae ... The partly digested vegetables of rabbit and sheep dung are much appreciated. Well grown wild green plants are very seldom eaten ... they are usually protected by hairs, oxalate crystals and the like, or by juices which are offensive to snails ... Cultivated plants ... are not protected in the same way ... the slugs which are adapted to garden life eat them freely." This summarises the findings of this study and also those of Grime *et al.* (1968, 1969, 1970) and Wolda *et al.* (1971).

Grime *et al.* (1968, 1969, 1970) studied the palatability of fresh plant material to *C. nemoralis* by comparing the amounts of a large variety of green plants consumed with the amount of a reference material (leaf discs of *Hieracium pilosella*) consumed and calculating a palatability index for each plant taking *H. pilosella* as unity. *Lotus corniculatus*, one of the few plants eaten green by the Braunton snails, gave a palatability index of 0.04 in Grime's experiments, whereas *Cirsium arvense*, *Hypochoeris radicata* and *Leontodon hispidus*, amongst others, gave high palatability indices (all 1.0) but were never seen to be eaten green in this study. This confirms the suggestion that green material is rarely eaten in the wild. Wolda *et al.* (1971) also found little green material eaten by their artificial *Cepaea* population, but did find that a *Lotus* sp (*Lotus uliginosus*) and moss comprised an important part of the green food. Both these studies (Grime *et al.*, 1968, 1969, 1970; Wolda *et al.*, 1971) found that the nettle *Urtica dioica* was often eaten green but this species was rare on the Braunton site.

Wolda *et al.* (1971) detected seasonal changes in the snails diet and their results show that mosses form a greater percentage of the diet in April than in their other samples (July, August and September). This may suggest a shortage of the preferred dead food at the end of the winter or perhaps that the moss is merely more accessible to the snails before the other plants have grown.

A subjective assessment of the amount of food available at Braunton seems to indicate that there is always more than snails could consume and Boycott (1934) states that "food has no influence either by its quality or quantity on the recurrence of our land molluscs". There is a little evidence that *Cepaea* turns to moss as a food early in the year, perhaps because of a shortage in some component in the seemingly excess food available. Wolda *et al.* (1971) point out that more than an energy source is required and it may be that trace elements or other compounds are limiting. Grime *et al.* (1970) concluded that a shortage of phosphorus was limiting the numbers of *C. nemoralis* on the south face of the Winnats Pass in Derbyshire and Willis (1963) found that the vegetation at Braunton was limited by two nutrients: nitrogen and phosphorus. Nothing is known of the nutritional requirements of *Cepaea*, but studies by Howes and Whellock (1937) on the growth of *Helix pomatia* showed that they needed vitamins A and B and also some sterols.

Wagge (1952) found that adult *Helix* require sitosterol. It seems possible that the *Cepaea* population may be limited by the quality of its energy source.

Few quantitative feeding studies on terrestrial molluscs have been made and the only published results for *Cepaea* are those of Lindquist (1941), which were only a small part of a wider study. He found that a large *C. nemoralis* ate about 125 mg of food per week. If the dry weight of a large snail is taken as 0.3 g, this represents a daily consumption rate of 59.5 mg/g DW, which compares with a figure of 55.6 mg/g DW for snails in the present study feeding on *Ononis* at 20° C. Reichle (1968) expressed consumption rate as a percentage of dry weight for 11 litter-dwelling invertebrates and found that the values all fell close to a mean of 2.5%. Mason (1970) expressed the consumption of his litter snails similarly and found a mean of 2.83% (range 5.19–0.58).

When the mean consumption rates in this study were expressed similarly the percentages were rather higher:

Food	Consumption as % of dry tissue weight
Rat food	21.66
<i>Taraxacum</i>	10.77
<i>Ononis</i>	5.56
Lettuce	3.96

Mason (1970) found that consumption rate was positively related to temperature, most strongly between 5 and 10° C but also between 10 and 15° C. Hunter (1968) also found that feeding activity of slugs was directly related to temperature, but that it declined above 25° C.

The high variability of the results presented here is probably related to the cyclical changes in live weight linked to changes in metabolic activity that were described in helicid molluscs by Howes and Wells (1934). These weight cycles and their effect on the metabolism of *C. nemoralis* are discussed elsewhere (Richardson, 1972). In his study of three slug species, Hunter (1968) noted that only 50–60% of the population were feeding on any given night. This compares with about 80% of feeders in this study, probably as a result of better water conditions in the laboratory.

The contribution of the digestive gland to the nutrition of *C. nemoralis* is difficult to assess. The cells of the "gland" certainly absorb both protein and lipid particles (Sumner, 1965a, b) and the production of the brownish-yellow lipofuchsin granules has been observed by the same author. Sumner (pers. comm.) states that the digestive gland material is produced continuously even when the animal is not feeding, and that material may remain in the gland cells for up to 14 days. The fact that production of digestive gland faeces increases after a meal of relatively low digestibility may indicate that when feeding on foods which are poorly digested extra-cellularly, the animal is able to increase the proportion of assimilation carried out in the digestive gland cells.

These and the present results indicate the necessity for long-term feeding experiments to assess the importance of this assimilation site. Calow (1970) has demonstrated the importance of the digestive gland as an assimilation site in *Lymnaea pereger* but this animal is a microphagous feeder with a gut adapted to comminute food, whereas *Cepaea* has a radula only capable of ingesting relatively

Table 5. Assimilation efficiencies from various feeding studies on non-carnivorous molluscs

Mollusc species	Food substrate	Assimilation efficiency (%)	Range	Source
<i>Cepaea nemoralis</i>	Lettuce	70.74	95.9—14.2	Present study
„	Rat food	72.95	96.7—50.2	„
„	<i>Ononis repens</i>	43.54	77.2—10.5	„
„	<i>Taraxacum officinale</i>	29.58	50.6— 7.43	„
<i>Discus rotundatus</i>	Leaf litter	49.12	58.0—43.07	Mason (1970)
<i>Hygromia striolata</i>	„	38.23	± 4.71 (SE)	„
„	Fresh <i>Urtica</i>	52.40	± 8.78 (SE)	„
<i>Oxychilus cellarius</i>	Lettuce	70.20	± 4.40 (SE)	„
<i>Helix aspersa</i>	„	53.50	± 6.04 (SE)	„
<i>Agriolimax reticulatus</i>	Fresh <i>Ranunculus repens</i>	78.4	93.2—45.6	Pallant (1970)
<i>Aplysia punctata</i>	Marine algae	62.7	45.0—75.0	Carefoot (1967)
<i>Littorina littorea</i>	Marine algae	57.0	41.0—69.0	Grahame (1973)
<i>Tegula funebris</i>	Marine algae	70.8	69.6—70.3	Paine (1971)

large lumps of food and is probably relying on the battery of hydrolytic enzymes in its gut secretion (Myers and Northcote, 1958) for its nutrition.

Although Mason (1970) was able to use the ash-ratio method to determine the assimilation efficiency of his snails, he also found the $e > f$ anomaly in some experiments. The anomaly implies that the ash content of the faeces was lower than that of the food, indicating the uptake of ash material in the gut. It is known that *C. nemoralis* is capable of considerable shell repair (Wagge and Mittler, 1953) and that *Helix aspersa* undergoes shell thickening after increase in shell size has ceased (Wagge, 1952). If calcium is being absorbed from the food, the anomaly can be explained. Champion (1961) has described glands from the foot and mantle of *H. aspersa* which secrete calcium granules into the mucus, and although calcium carbonate absorption through the foot has been reported in aquatic molluscs (Rao and Goldberg, 1954; Kapur and Gibson, 1968), it is unlikely that a terrestrial mollusc would obtain calcium in this way. Cowell (1928) reported a calcium content of 10 mg per gram in cabbage leaves and if lettuce contains similar quantities complete absorption would be sufficient to explain the ash content differences. Grahame (1973) reported the presence of calcium spherules in the faeces of *Littorina littorea* and discusses the effect on assimilation estimates. It would appear that the ash-ratio method is unreliable in shelled molluscs where active movement of calcium is taking place.

The assimilation efficiencies calculated here compare favourably with the range of values found by Mason (1970) in several terrestrial snails. Wolda *et al.* (1971) express surprise at the high assimilation efficiencies recorded by Mason on the

grounds that there was no apparent difference between the state of the food found in the crop and the faeces of specimens of *C. nemoralis* examined by them. The gravimetric assimilation efficiencies found here are compared with those of other herbivorous molluscs in Table 5. The values for snails feeding on dead plant material are lower than those feeding on green plant matter, but they are higher than the assimilation efficiencies of other leaf litter organisms, such as millipedes: 6–15% (van der Drift, 1961; Bocoock, 1963) or oniscid isopods: 15–33% (White, 1968). This may reflect the presence of powerful hydrolytic enzymes in the molluscan gut.

Acknowledgments. I should like to thank Professor David Nichols for the facilities provided in his department, Mr. G. G. Vickers for his encouragement, advice and criticism and Dr. J. H. Lawton who read and criticised the work in thesis form.

The work was completed under the tenure of an N.E.R.C. post graduate research award.

References

- Baker, R. A.: The ecology of the Wrinkled Snail, *Helicella caperata* Mont., on the Braunton Burrows sand dune system. *Proc. malac. Soc. Lond.* **38**, 41–54 (1968)
- Bocoock, K. L.: The digestion and assimilation of food by *Glomeris*. In: J. Doeksen, J. van der Drift, eds., *Soil organisms*, p. 85–91. Amsterdam: North Holland 1963
- Boycott, A. E.: Habitats of land molluscs in Great Britain. *J. Ecol.* **22**, 1–38 (1934)
- Calow, P.: Studies on the natural diet of *Lymnea pereger obtusa* (Kobelt) and its possible ecological implications. *Proc. malac. Soc. Lond.* **39**, 203–215 (1970)
- Campion, M.: The structure and function of the cutaneous glands in *Helix aspersa*. *Quart. J. micr. Sci.* **102**, 195–216 (1961)
- Conover, R. J.: Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.* **11**, 338–345 (1966)
- Cowell, E.: A note on the calcium content of cabbage. *Biochem. J.* **26**, 1422 (1928)
- Crossley, D. A.: Radioisotope measurement of food consumption by a leaf beetle species *Chrysomela knabi* Brown. *Ecology* **47**, 1–8 (1966)
- van der Drift, J.: Analysis of the animal community in a beech forest floor. *T. Ent.* **94**, 1–168 (1951)
- Grahame, J.: Assimilation efficiency of *Littorina littorea* (L.) (Gastropoda: Prosobranchiata). *J. Anim. Ecol.* **42**, 383–390 (1973)
- Grime, J. P., Blythe, G. M.: An investigation of the relationship between snails and vegetation at the Winnats Pass. *J. Ecol.* **57**, 45–66 (1969)
- Grime, J. P., Blythe, G. M., Thornton, J. D.: Food selection by the snail *Cepaea nemoralis* L. In: A. Watson, *Animal populations in relation to their food resources*, p. 73–99. *Brit. Ecol. Soc. Symp. No. 10*. London-Edinburgh: Blackwell 1970
- Grime, J. P., MacPherson-Stewart, S. F., Dearman, R. S.: An investigation of leaf palatability using *Cepaea nemoralis*. *J. Ecol.* **56**, 405–420 (1968)
- Howes, N. H., Wells, G. P.: The water relations of snails and slugs. I. Weight rhythms in *Helix pomatia* L. *J. exp. Biol.* **11**, 327–343 (1934)
- Howes, N. H., Whellock, R. B.: A semi-synthetic diet for *Helix pomatia*. *Biochem. J.* **31**, 1489 (1937)
- Hunter, P. J.: Studies on slugs of arable ground. III. Feeding habits. *Malacologia* **6**, 391–399 (1968)
- Kapur, S. P., Gibson, M. A.: A histochemical study of calcium storage in the foot of the freshwater gastropod, *Helisoma duryi eudiscus* (Pilsbry). *Canad. J. Zool.* **46**, 987–990 (1968)
- Kidson, C., Carr, A. P.: Dune reclamation at Braunton Burrows. *Chart. Surv.* **93**, 298–303 (1960)
- Lindquist, B.: Experimentelle Untersuchungen über die Bedeutung einiger Landmollusken für die Zersetzung der Waldstreu. *K. Fysiogr. Sällsk. Lund. Forh.* **11**, 144–156 (1941)

- Macfadyen, A.: Methods of investigation of productivity of invertebrates in terrestrial ecosystems. In: K. Petruszewicz, ed., Secondary productivity of terrestrial ecosystems. Principles and methods, p. 383-412. Warszawa-Krakow: Institute of Ecology, Polish Academy of Sciences 1967
- Mason, C. F.: Food, feeding rates and assimilation in woodland snails. *Oecologia (Berl.)* **5**, 215-239 (1970)
- Myers, F. L., Northcote, D. H.: A survey of the enzymes from the gastrointestinal tract of *Helix pomatia*. *J. exp. Biol.* **35**, 639-648 (1958)
- Paine, R. T.: Energy flow in a natural population of the herbivorous gastropod *Tegula funebris*. *Limnol. Oceanogr.* **16**, 86-98 (1971)
- Petrusewicz, K., Macfadyen, A.: Productivity of terrestrial animals: principles and methods. IBP Handbook No. 13. Oxford-Edinburgh: Blackwell 1970
- Phillipson, J.: A contribution to the feeding biology of *Mitopus morio* (F). *Phalangiida. J. Anim. Ecol.* **29**, 35-43 (1960)
- Phillipson, J.: Secondary productivity in invertebrates reproducing more than once in a lifetime. In: K. Petruszewicz, ed., Secondary productivity in terrestrial ecosystems: principles and methods, p. 459-475. Warszawa-Krakow: Institute of Ecology, Polish Academy of Sciences 1967
- Rao, K. P., Goldberg, E. D.: Utilization of dissolved calcium by a pelecypod. *J. cell. comp. Physiol.* **43**, 283-292 (1954)
- Reichle, D. E.: Relation of body size to food intake, oxygen consumption and trace element metabolism in forest floor arthropods. *Ecology* **49**, 538-542 (1968)
- Richardson, A. M. M.: A study of the energy flux through a natural population of the polymorphic land snail *Cepaea nemoralis* L. Unpublished Ph. D. thesis, University of Exeter (1972)
- Sokal, R. R., Rohlf, F. J.: Biometry. San Francisco: Freeman 1969
- Sumner, A. T.: Experiments on phagocytosis and lipid absorption in the alimentary system of *Helix*. *J. roy. micr. Soc.* **84**, 415-421 (1965a)
- Sumner, A. T.: The cytology and histochemistry of the digestive gland cells of *Helix*. *Quart. J. micr. Soc.* **106**, 173-192 (1965b)
- Wagge, L. E.: Quantitative studies of calcium metabolism of *Helix aspersa*. *J. exp. Zool.* **120**, 311-342 (1952)
- Wagge, L. E., Mittler, T.: Shell regeneration in some British molluscs. *Nature (Lond.)* **171**, 528 (1953)
- White, J. J.: Bio-energetics of the woodlouse *Tracheoniscus rathkei* Brandt in relation to litter decomposition in a deciduous forest. *Ecology* **49**, 694-704 (1968)
- Willis, A. J.: Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* **51**, 353-374 (1963)
- Willis, A. J.: The influence of mineral nutrients on the growth of *Ammophila arenaria*. *J. Ecol.* **53**, 735-745 (1965)
- Willis, A. J., Folkes, B. F., Hope-Simpson, J. F., Yemm, E. W.: Braunton Burrows: the dune system and its vegetation. I. *J. Ecol.* **47**, 1-24 (1959a)
- Willis, A. J., Folkes, B. F., Hope-Simpson, J. F., Yemm, E. W.: Braunton Burrows: the dune system and its vegetation. II. *J. Ecol.* **47**, 249-288 (1959b)
- Willis, A. J., Yemm, E. W.: Braunton Burrows: mineral nutrients status of the dune soils. *J. Ecol.* **49**, 377-390 (1961)
- Wolda, H., Zweep, A., Schuitema, K. A.: The role of food in the dynamics of populations of the land snail *Cepaea nemoralis*. *Oecologia (Berl.)* **7**, 361-381 (1971)

Dr. A. M. M. Richardson
Department of Zoology
University of Tasmania
P.O. Box 252 C
Hobart 7001, Tasmania, Australia