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Source: *Journal of Ecology*, Vol. 68, No. 3 (Nov., 1980), pp. 981-998

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2259470>

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EXPERIMENTAL STUDIES ON SLUG–PLANT INTERACTIONS

I. THE ACCEPTABILITY OF THIRTY PLANT SPECIES TO THE SLUG *AGRIOLIMAX CARUANA*E

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SUMMARY

(1) The acceptability of leaves of thirty species from wasteland and grassland to the slug *Agriolimax caruanae* was tested by offering leaf discs. An acceptability index (AI) was calculated as the area eaten from leaf discs of the test species divided by that eaten from leaf discs of lettuce.

(2) Species varied from high acceptability (e.g. *Capsella bursa-pastoris*) to complete rejection (e.g. *Poa annua*).

(3) The AI was generally high for annuals, for species with soft thin leaves and for species not known to contain secondary compounds. Hairiness appeared to have no influence on acceptability.

(4) There are close parallels between the results obtained with *A. caruanae* and those obtained by other workers with different species of slugs and snails but there are some marked differences. It is suggested that it may be possible to distinguish 'general' acceptability (that affecting a range of herbivores) from specific acceptability (in which a host food can be classified as acceptable or not only for a specific herbivore).

(5) Occasional slugs made choices quite different from all the rest. These individuals maintained their deviant behaviour in subsequent tests.

(6) Although slugs are generalized feeders they are 'acceptability-moderated generalists' with a hierarchy of acceptable foods. Their interactions with host plants suggest that coevolutionary specialization may be at an early stage of development.

INTRODUCTION

The distribution and abundance of some plant species appear to be determined at least in part by grazing by herbivores (e.g. Feeny 1970; Janzen 1970; Dollinger *et al.* 1973; Cates 1975; Whelan 1977). Plant species display a variety of physical structures such as hairs, thorns, spines, etc. and may contain chemical compounds such as alkaloids, glucosinolates and tannins which may most easily be explained as defences evolved against herbivores (Brower 1969; Janzen 1969, 1975; Feeny 1970; Gilbert 1971, 1975; Whittaker & Feeny 1971; Levin 1973, 1976).

The reciprocal situation in which the plant defence mechanisms exert selective pressures on herbivores has also been described (e.g. Janzen 1975). The mutual feedback of selective pressures in predator–prey interaction might be expected to produce coevolutionary change, and convincing evidence of such coevolution has been put forward for Lepidoptera

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and their host plants in a seminal paper by Ehrlich & Raven (1965) and for squirrels and pines by Smith (1970). It is difficult to obtain direct evidence of coevolutionary pressures though the presence of 'gene for gene' correspondence in fungal pathogens and their host plants is well known among crops (Flor 1955) and is strong evidence for coevolution, but there seems to be no such evidence from natural communities. Coevolution is usually inferred from retrospective analyses of plant and animal characteristics.

Most animals when faced with a variety of offered foods make choices. The interpretation of such choices may require an analysis of both 'proximal' and 'ultimate' factors (*sensu* Baker 1938). The choices of diet made by a herbivore from a variety of foods offered represent immediate and present behavioural responses. These may or may not have been made before by the individual or by its ancestors. Proximal interpretation of dietary choice is in terms of the present character (taste, appearance, nutritional value) of the food and the present behaviour of the herbivore (learned or inherited). Ultimately however, all biological observations must find their explanation in evolution (Dobzhansky 1973) and the 'ultimate' explanation of a herbivore-plant interaction must lie in the selective forces that acted on ancestors and that leave the present descendants (both plant and animal) behaving as they do. These forces can be revealed only by retrospective argument based on present observation and it is dangerous to assume that any feature, e.g. leaf toughness, which at present appears to hinder a herbivore from feeding on a particular plant, has necessarily been selected by ancestral experience of predation. It may be that selection for toughness was exerted by some quite different herbivore from the one whose proximal behaviour is now observed or that toughness evolved as an aspect of xeromorphy, and now, secondarily, shows itself as conferring resistance to grazing by the herbivore. It is important to bear these caveats in mind in interpreting the experiments described in this paper. No matter how important a plant may have been in the diet of a herbivore or how important herbivores may have been in the predation of plants, these may represent only a fraction of the selective forces leading to present form and behaviour.

The interaction of terrestrial molluscs with their food plants has been poorly documented when compared with that of other terrestrial herbivores (e.g. insects and mammals). Both slugs and snails are reported to eat a wide range of foods (Chatfield 1976), but a closer analysis of published results suggests that particular species of mollusc have quite specific patterns of feeding. The majority are strict herbivores relying either on fresh or senescent material (Runham & Hunter 1970; Chatfield 1976). Faecal analysis has shown that higher plants form the main component of the diet (Grime & Blythe 1969; Pallant 1969; Jennings & Barkham 1975) and although fungi, mosses and liverworts may be present they form a very small part of the diet. Some species of slugs and snails are known to eat lichens (Coker 1967; Peake & James 1967). Some snails are known to be omnivorous (Mason 1970) and Boycott (1934) has shown that the slug *Arion ater* is also omnivorous. I have observed that *A. ater* may be a cannibal under laboratory conditions (also reported by Chatfield 1976) and R. J. Whelan (personal communication) reports similar behaviour in *Arion subfuscus*. True carnivores among the slugs are represented by the three species of *Testacella* (Runham & Hunter 1970, p. 23).

Although analysis of slug faeces has revealed omnivorous feeding behaviour, the strong preference for plant over animal (Pallant 1969, 1972; Mason 1970) and over fungal and fungus-animal food (Jennings & Barkham 1975) seems to be very consistent, although seasonal variation occurs associated with cycles of food availability (Jennings & Barkham 1975). At a finer level there is evidence that both snails (Grime, MacPherson-Stewart & Dearman 1968; Grime, Blyth & Thornton 1970) and slugs (Duval 1971, 1973; Cates &

Orians 1975) choose between species of higher plants or even between morphs of a given plant species (Jones 1962, 1973; Crawford-Sidebotham 1972; Angseesing 1973; Cates 1975).

All this suggests that slugs may be particularly useful for studying plant–animal interaction: the animal is selective in its diet yet not specialized to the extent of complete reliance on a single food plant. This paper describes a series of trials made to determine the acceptability of thirty plant species to the slug *Agriolimax caruanae*. Throughout the discussion the word *acceptability* is used to describe the position of a particular plant or plant part in the hierarchy of choice made by the slug. I avoid the word *palatability* which is commonly used but carries the implication that taste is the determinant of choice.

MATERIALS AND METHODS

The biology of Agriolimax caruanae

Agriolimax caruanae Pollonera (Limacidae) is a species of terrestrial slug whose general biology is poorly documented. The general impression from the sparse literature is that the species is widespread but rarely abundant. The distribution of the species in the British Isles is given by Kerney (1976) and may be changing in response to human activities. It was present in North Wales (at least in the surroundings of Bangor) in considerable numbers in 1977 and 1978 on arable land and in gardens and the density was particularly high in waste places. Search and trapping under ideal conditions of high relative humidity and wet soil showed that the species was absent or in very low density, in areas dominated by grasses, but considerable numbers were found among the ground flora under the shade of trees where grasses were absent or sparse. *Agriolimax caruanae* has an annual life cycle with overlapping generations. Eggs are laid in early summer and mid-autumn and hatch in spring and early summer. Most adults die in the winter or early spring after laying eggs in the autumn. In 1977 the species seemed to be most abundant at the end of the spring but numerous individuals could usually be collected after wet nights at any season of the year.

The collection of slugs for experimental study

All the slugs used in the present experiments were collected in the immediate surroundings of the Pen-y-Ffridd Experimental Station near Bangor (National Grid reference SH 564705). In all experiments mature slugs of comparable size *c.* 3 cm long were used. Animals were collected by laying down wooden flats in an area in which the soil had been dug over with a spade. The collection area was soaked with water frequently so that the bottom of the flats maintained the disturbed surface constantly wet and attracted the animals. Slugs were also collected from under stones in damp areas or after wet periods. The animals were kept in Petri dishes with a moistened filter paper at a constant temperature (15 °C) for a week prior to the experiments, and were fed with a mixture of lettuce and bran cereal.

The collection of plant material

The acceptability of thirty common plant species to *A. caruanae* was investigated in the summers of 1977 and 1978. Most of the plants were collected from waste sites at the Pen-y-Ffridd Experimental Station from which the slugs had also been sampled. Other plant samples were taken from grassy places and other sites from which the slugs were absent or where they were very scarce. Some characteristics of the species investigated and the site of collection are given in the Appendix. Plant acceptability was studied

using mature leaves only. As far as possible the leaves tested came from a single plant. In most cases leaves were used immediately. The rest were kept, moist, in polythene bags stored in a cold room (4 °C) until required.

Acceptability tests

A technique similar to that of Grime, MacPherson-Stewart & Dearman (1968) was used. In order to determine an acceptability index, it was necessary to choose a 'control' plant with which the acceptability of other plant species could be compared. Slugs are pests of many vegetables including lettuce (*Lactuca sativa**). In a pilot experiment to assess the possibility of using lettuce as a control plant, five leaf discs of fresh lettuce, each of area 1.3 cm², were placed in a Petri dish (8.5-cm diameter) containing Whatman No. 1 filter paper moistened with 5 ml of distilled water. One slug was put in the dish and allowed to feed for 12 h during the night at 15 °C. There were five replicate dishes. On average three out of five discs were almost completely consumed in this time (mean area eaten = 3.8 cm²). As soon as the slugs were offered lettuce they ate it avidly. In the rest of the experiments the following procedure was followed.

- (i) Leaf discs of lettuce were used as control in every acceptability trial.
- (ii) In an attempt to reduce variability, slugs were fed with a total of only two-thirds (2.6 cm²) of the average leaf area eaten in 12 h in the pilot experiment.
- (iii) The slugs were starved for 24 h before each trial.
- (iv) The acceptability index (AI) is the quotient of leaf area of test material consumed/leaf area of lettuce consumed (in 12 h).
- (v) On a few occasions a slug totally rejected the test disc and ate less than half of the offered lettuce. Such trials were rejected because, although giving a qualitative measure of acceptability, they were not reliable quantitative measures.

The technique was the same as that in the pilot experiment, except that in each dish one slug was presented with two leaf discs (test plant and control).

Five and ten replicates were used in the 1977 and 1978 acceptability trials respectively.

RESULTS

Acceptability indices

The results of the acceptability trials for each year, and the mean for the two years are shown in Table 1. In 1978 two species (*Anagallis tenella* and *Chenopodium album*) could not be obtained from habitats similar to those sampled in 1977 and hence were not tested. The standard error of replicate trials in 1977 was particularly high in the case of five offered plant species (*Brassica oleracea* (cultivated), *B. nigra*, *Papaver dubium*, *Polygonum aviculare* and *Trifolium pratense*) and in 1978 variation was high in tests involving *Papaver dubium*. The high variation in these tests was caused in every case by a single egregious slug which made choices quite different from the other slugs. Omission of these results from trials on cultivated *Brassica oleracea*, *B. nigra* and *Papaver dubium* in both years resulted in an increase in AI, but omitting such results from trials on *Polygonum aviculare* and *Trifolium repens* caused a decrease in AI.

The modified calculations are shown in parentheses in Table 1. When the egregious slugs were isolated and acceptability tests repeated, the individuals reliably repeated their earlier behaviour. These observations are suggestive of very interesting individual-to-individual variation in feeding choice. The plant species were ranked by their acceptability indices after removal of these anomalies. The results obtained in both years were very

*Nomenclature follows Clapham, Tutin & Warburg (1962).

TABLE 1. Acceptability indices (and ranking) of thirty plant species offered as leaf discs to *Agriolimax caruanae*

Species tested	Species code	Acceptability index \pm S.E.		Mean of 2 yr	Species rank ^a
		1977	1978		
<i>Anagallis tenella</i>	At	0.57 \pm 0.10	–	–	–
^a <i>Bellis perennis</i>	Bp	0	0	0	= 17
<i>Brassica napus</i>	Bn	0.66 \pm 0.23	0.26 \pm 0.07	0.46	6
<i>Brassica nigra</i>	Bni	0.65(0.81) ^b \pm 0.26(0.16)	0.27 \pm 0.07	0.54*	5
<i>Brassica oleracea</i>	Bo	0.14 \pm 0.08	0	0.07	= 11
<i>Brassica oleracea</i> (cultivated)	B(c)	0.26(0.33) \pm 0.13(0.07)	0.36 \pm 0.05	0.35	7
<i>Brassica rapa</i>	Br	0.03 \pm 0.02	0	0.02	= 15
<i>Capsella bursa-pastoris</i>	Cbp	1.05 \pm 0.01	1.0 \pm 0.003	1.03	1
<i>Chenopodium album</i>	Cha	0.20 \pm 0.05	–	–	–
<i>Epilobium hirsutum</i>	Eh	0	0	0	= 17
<i>Epilobium parviflorum</i>	Ep	0	0	0	= 17
<i>Lamium purpureum</i>	Lp	0.07 \pm 0.05	0	0.04	= 13
¹ <i>Lotus corniculatus</i>	Lc	0	0	0	= 17
<i>Papaver dubium</i>	Pd	0.53(0.89) \pm 0.30(0.10)	0.75(0.83 \pm 0.09(0.07)	0.86	3
<i>Plantago lanceolata</i>	Pl	0	0	0	= 17
<i>Plantago major</i>	Pm	0	0	0	= 17
<i>Plantago media</i>	Pmd	0	0	0	= 17
² <i>Poa annua</i>	Pan	0	0	0	= 17
^a <i>Polygonum aviculare</i>	Pa	0.28(0.11) \pm 0.10(0.02)	0.33 \pm 0.11	0.22	8
^a <i>Ranunculus acris</i>	Ra	0.01 \pm 0.002	0.34 \pm 0.7	0.17**	9
^a <i>Ranunculus bulbosus</i>	Rb	0.04 \pm 0.03	0	0.02	= 15
^a <i>Ranunculus repens</i>	Rr	0.10 \pm 0.04	0.03 \pm 0.01	0.07	= 11
^a <i>Senecio jacobaea</i>	Sj	0	0.01 \pm 0.01	0.01	16
^a <i>Senecio squalidus</i>	Ss	0	0	0	= 17
^a <i>Senecio vulgaris</i>	Sv	0.18 \pm 0.04	0.07 \pm 0.03	0.13	10
<i>Stellaria media</i>	Sm	0.91 \pm 0.07	0.42 \pm 0.09	0.67***	4
<i>Taraxacum officinale</i>	T	0.98 \pm 0.11	0.83 \pm 0.14	0.91	2
<i>Trifolium pratense</i>	Tp	0.14(0.08) \pm 0.08(0.02)	0.04 \pm 0.03	0.06	12
<i>Trifolium repens</i>	Tr	0	0.08 \pm 0.03	0.04	= 13
<i>Veronica persica</i>	Vp	0	0.05 \pm 0.03	0.03	14

^a Ranks given to the species are for mean of 2 yr and exclude values from 'anomalous' slugs (see text).

^b Numbers in parentheses show the values obtained when results from 'anomalous' slugs are omitted (see text).

¹ Complete leaflets were used instead of discs.

² Leaf rectangles were used instead of discs.

^a Small leaf discs (0.57 cm²) were used because of the small size of the leaves.

*, 0.05 \geq P > 0.01; **, 0.01 \geq P 0.001; ***, P < 0.001 for the comparison of AI between the two years; values with no asterisk are not significantly different between years.

similar. Although some species changed their actual rank, the order of the species changed little: the difference in rank resulted mainly from a few species whose rank changed considerably. For example, *Ranunculus acris* changed its rank from 18th in 1977 to 5th in 1978 (AI from 0 in 1977 to 0.34 in 1978). The acceptability indices themselves also remained very similar and only three species differed significantly between the two years (*Brassica nigra* and *Stellaria media* appeared to be less acceptable in 1978 than they were in 1977 and *Ranunculus acris* was more acceptable in 1978). It might be relevant that the plants of *Brassica nigra* had been collected from different localities in the two years.

In both years, 12 and 13 (i.e. 42 and 43% respectively) of the 29 dicotyledon species and the grass *Poa annua* were rejected completely by the slugs (AI = 0). The range of AI values suggests an 'all or nothing' feeding response but this was more closely examined by constructing a frequency histogram of acceptability indices (Fig. 1).

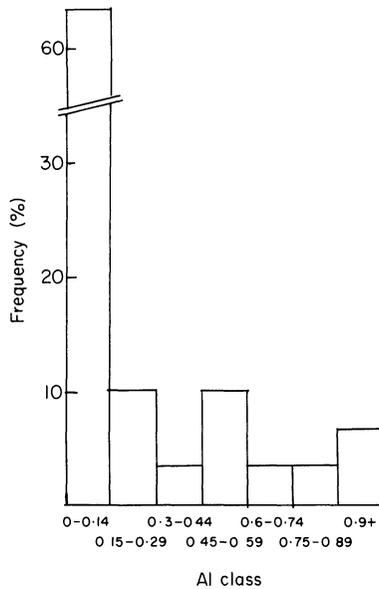


FIG. 1. Distribution of acceptability indices (AI).

Although the sample size does not permit a clear segregation of AI into modal groups, three broad categories are apparent: rejected or rarely chosen, moderately acceptable and very acceptable.

The relationship between plant attributes and acceptability to Agriolimnax caruanae

No very obvious relationships can be detected by comparison of characteristics of the plant species (Appendix) and their acceptability indices (Table 1). To simplify this comparison, species with properties that might be expected to contribute to plant acceptability were grouped and their AI compared. The great proportion of species with AI = 0 makes the distributions strongly skewed and therefore Fisher's Exact Test was used to compare the number of species (with a given property) that fell below or above the median; tests were made both including and omitting the zero values. The properties tested were: (i) texture (soft *v.* tough), (ii) hairs (presence *v.* absence), (iii) growth habit (erect *v.* ground level), (iv) life-history (annuals *v.* biennials and perennials) and (v) habitat (waste sites *v.* grassy sites). When zeros are included, the only comparison that approaches statistical significance is annuals against biennials and perennials (annuals being more acceptable). When the zeros are excluded, this comparison remains nearly significant but species also differ significantly with respect to leaf texture (soft-leaved species being more acceptable). Plants from waste sites were generally more acceptable than those from grassy places, but the difference is not statistically significant ($P = 0.11$). This comparison is further complicated because (i) *Brassica oleracea* and cultivated cabbage cannot be assigned to either habitat category and (ii) seven of the taxa studied were common to both grassy and waste sites. A next step in this analysis would be to combine the different attributes and compare the acceptability indices associated with the combinations. A combinatory system taking into consideration these attributes was applied by means of the technique of Group Average Clustering. This technique

defines clusters based on the Jaccard Similarity Coefficient (JSC) (Jaccard 1912), in which:

$$JSC = AB/(AB + Ab + aB)$$

where AB = number of attributes present in both samples A and B; Ab = number of attributes present in sample A but absent from B; aB = number of attributes present in sample B but absent from A.

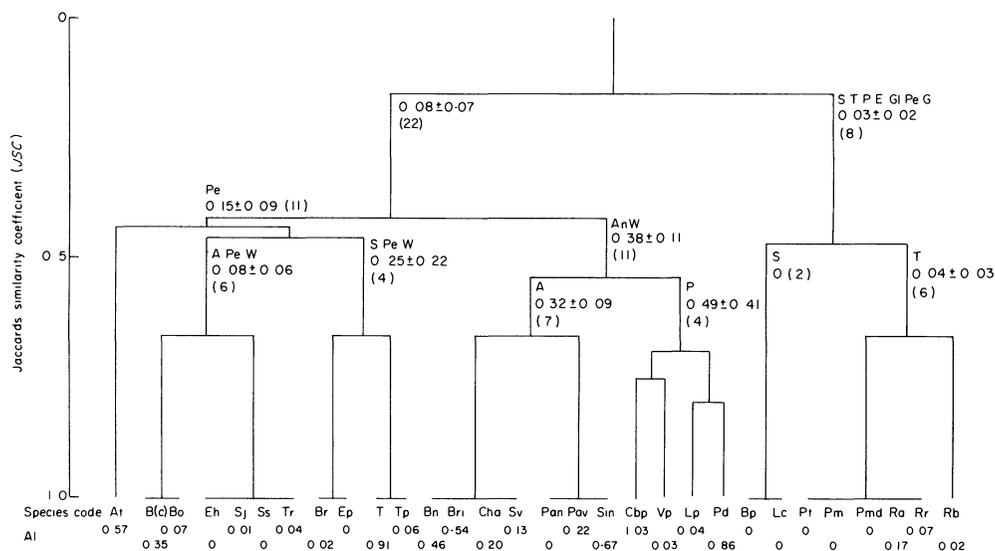


FIG. 2. Grouping of the species studied into clusters of similar attributes (see text) and the mean AI \pm S.E. (n) associated with them; for species code see Table 1. Attributes code: S, soft; T, tough; P, hairs present; A, hairs absent; E, erect; Gl, ground level; An, annuals; Pe, perennials; W, waste sites; G, grassy sites.

The results are shown in Fig. 2. The most noticeable feature of this diagram is the large variation associated with any given cluster. The first division (at $JSC = 0.15$) produces two main clusters, one of low AI in which all but two species possess attributes that might be expected to confer unacceptability. The other group contains species with several combinations of attributes, and this can be split up again into two groups of contrasting AI based solely on plant life-history characteristics, the group of annuals having an average AI 2.5-times that of the group of perennials. *Anagallis tenella* stands conspicuously apart from the remaining species with a JSC of only 0.42. Further divisions occur, in some cases unrelated to the attributes considered. This is not surprising because many qualities that might be important in affecting acceptability were not considered in this analysis, particularly the chemistry of the species investigated. Two simple cases illustrate this point: *Brassica oleracea* and cultivated cabbage have exactly the same attributes ($JSC = 1.0$), but their AI is quite different (see Table 1). This suggests that there may be deterrent chemicals in the wild species which are absent or in lower concentration in the cultivated form. Similar comments might apply to the species-pair *Taraxacum officinale*/*Trifolium pratense* where there may be important chemical differences that account for the differences in acceptability of these two species which otherwise have many features in common. Cyanogenic glucosides could not be detected in the sampled clover plants.

DISCUSSION

A number of constraints have been built into the design of the experiments described in this paper:—

(i) A narrow range of size of slugs was chosen (juveniles and adults almost certainly have some differences in feeding habits and newly hatched juveniles often concentrate on feeding below ground).

(ii) Only leaves were offered as food. Slugs will certainly eat other plant parts, including roots and the perianth of some flowers (e.g. *Taraxacum officinale*, *Galanthus nivalis*). They will also eat hypocotyls and 'fell' young seedlings: their role in determining the nature of vegetation may be exerted most critically at the seedling stage.

(iii) Leaves were removed from the plants before being offered to the slugs. In nature the leaves of shrubs, trees and tall herbs may gain protection because of the distance of travel relative to the reward gained by the mollusc. Moreover the pathway up a stem or trunk may inhibit slug movement either because it is exposed and too dry or because hairs or prickles hinder the movement of slugs. Slugs will sometimes climb trees and a 2-m-high specimen of *Magnolia wilsoni* has been seen almost wholly defoliated by slugs.

(iv) Leaves were offered as cut discs (or leaf segments in *Poa annua*). The presence of cut margins may have removed one major hindrance to mollusc grazing. It is perhaps significant that when (after initial delay) the slugs ate *Poa annua*, they invariably chewed from the cut ends—perhaps the silica deposits in leaf margins prevent normal access to the tissue (Dirzo 1977). Merz (1959) has shown that if the spiny leaf margin of holly (*Ilex aquifolium*) is removed the leaf becomes wholly acceptable to the larvae of *Lasiocampa quercus*.

(v) Young and senescent leaves were not used. It seems obvious that young leaves have greater potential value than do old ones to a plant's continued assimilatory activity—old leaves will often be more accessible to the slug because, in erect plants, they are usually closer to the ground and in more shaded and humid environments than younger leaves.

(vi) All feeding trials were made in Petri dishes and this special environment might alter the food choices made by the slugs, particularly if volatile attractants or deterrents accumulated within the dish.

These constraints must be borne in mind when the results are extrapolated to field situations. Nevertheless, a number of interesting conclusions emerge from the study and these can be compared with the findings of other workers who have used essentially similar test conditions.

The pattern of acceptability shown by *Agriolimax caruanae* in the present studies is closely similar to that obtained by Grime, MacPherson-Stewart & Dearman (1968), and by Grime, Blythe & Thornton (1970) using the snail *Cepaea nemoralis*. They found that 62% of the species tested were rejected ($AI \leq 0.17$), 23% were less acceptable than the control (*Hieracium pilosella*) ($AI < 0.72$) and 15% were highly acceptable ($AI \geq 0.72$). There is some information about acceptability to other species of slug. Gets (1959) examined the food choice made by three species of slug (*Arion circumscriptus*, *Deroceras (Agriolimax) reticulatus* and *D. (A.) laeve*). The species of plants chosen for study were forty-five common plants from abandoned fields in Michigan, U.S.A. About 47% of these were rejected, c. 25% were relatively acceptable and c. 28% were highly acceptable. Duval compared the acceptability of twenty-six common weeds to *Agriolimax reticulatus* (Duval 1971) and to *Arion hortensis* (Duval 1973), but his methods were different from those of Grime, MacPherson-Stewart & Dearman (1968) and from those used in this study. He grouped the plants into four categories: 27% of the plants were 'virtually

rejected' by *Agriolimax reticulatus*, 15% were 'eaten occasionally', 19% were 'eaten less readily' and 39% were 'eaten readily'. This distribution of acceptability is very different from that found by Grime, MacPherson-Stewart & Dearman (1968) for *Cepaea nemoralis* and those reported in the present paper for *Agriolimax caruanae*. However, Duval's results for *Arion hortensis* were 37, 19, 29 and 15%, much closer to those reported in this paper.

Of the thirty-six possible comparisons of the acceptability assessments described in this paper with those of other authors, twenty-four (67%) agree. The remaining twelve (33%) do not agree. Six of these are with the results of Cates & Orians (1975) in which one of the two species of slug used was native to North America and the other (*Arion ater*) had been introduced from Europe.

It is unfortunate that results from the various studies are not given in a form suitable for a detailed comparative analysis. However, the various molluscs that have been studied have in common a general reluctance to eat many plants which are common and a clear acceptability ranking among the plant species that are eaten. Table 2 lists assessments of acceptability to molluscs for different plant species that have been tested by two or more authors. Several interesting features can be seen.

(i) Some plant species (notably *Capsella bursa-pastoris*) appear to be highly acceptable to all the molluscs studied.

(ii) Some appeared to be unacceptable to all the molluscs (e.g. *Epilobium hirsutum*).

(iii) For some plant species AI differed widely between species of mollusc (e.g. *Stellaria media*).

(iv) For any one species of slug different plant species represent quite wide extremes of acceptability.

These different situations pose some interesting questions in both the proximal and ultimate interpretation of the biology of herbivores and their food plants.

(i) What makes some species of plant highly acceptable (e.g. *Capsella bursa-pastoris*) and others highly unacceptable (e.g. *Epilobium hirsutum*) to a range of relatively similar herbivores?

(ii) What characteristics of a plant species make it not equally acceptable to several apparently similar herbivores?

Answers to these questions probably require the introduction of concepts of 'general' acceptability and 'specific' acceptability. A species that has general unacceptability will be one possessing deterrent qualities that are revealed no matter what mollusc is used in the test. Species that possess qualities of specific unacceptability have a specialized relationship with a specific predator. There are interesting parallels that can be drawn between these concepts and those of vertical and horizontal resistance that have been used by plant pathologists to describe the relationships between plants and their pathogens (van der Plank 1963).

In the dietary choices made by *Agriolimax caruanae*, leaf texture appeared to be of great importance in determining acceptability. In general, soft-leaved plants were much more acceptable. This feature again parallels the findings of Grime, MacPherson-Stewart & Dearman (1968) with *Cepaea nemoralis* and Jennings & Barkham (1975) with several species of slug.

Rather surprisingly, leaf hairiness did not appear to have any effect on acceptability. *Capsella bursa-pastoris* has a complicated vesture of hairs on both leaf surfaces (Appendix) and yet was the most acceptable species studied. Several species are both hairy and acceptable. Grime, MacPherson-Stewart & Dearman (1968) have shown that leaf hairs appear to be irrelevant to the acceptability of plants to the snail *Cepaea nemoralis*. This

TABLE 2. Acceptability* to different molluscs of a variety of plant species

Plant species	<i>Agrilolimax caruanae</i> This study	<i>Agrilolimax reticulatus</i> Duval (1971)	<i>Agrilolimax columbianus</i> Cates & Orians (1975)	<i>Arion ater</i> Duval (1973)	<i>Arion hortensis</i> Duval (1973)	<i>Cepaea nemoralis</i> Grime, MacPherson-Stewart & Dearman (1968)
<i>Bellis perennis</i>	AI = 0	0.14-0.29			0.14-0.29	
<i>Capsella bursa-pastoris</i>	AI = 1.03	0.29-0.43	log PI = 1.03	log PI = 1.0	0.29-0.43	
<i>Chenopodium album</i>	AI = 0.20	0.43-0.49	log PI = 1.0	log PI = 1.07	0.43-0.93	
<i>Epilobium hirsutum</i>	AI = 0	0-0.14			0-0.14	
<i>Lamium purpureum</i>	AI = 0.04	0.29-0.43			0.43-0.93	
<i>Lotus corniculatus</i>	AI = 0					PI = 0.04
<i>Plantago lanceolata</i>	AI = 0	0-0.14				PI = 0.07
<i>Plantago major</i>	AI = 0					PI = 0.17
<i>Plantago media</i>	AI = 0					PI = 0.38
<i>Polygonum aviculare</i>	AI = 0.22	0.29-0.43				PI = 0.01
<i>Ranunculus repens</i>	AI = 0.07	0.14-0.29	log PI = 0.59	log PI = 0.61	0.43-0.93	
<i>Senecio jacobaea</i>	AI = 0.01					
<i>Senecio vulgaris</i>	AI = 0.13	0.29-0.43	log PI = 0.76	log PI = 0.81	0.29-0.43	
<i>Stellaria media</i>	AI = 0.67	0.14-0.29			0.29-0.43	
<i>Taraxacum officinale</i>	AI = 0.91	0.43-0.93			0.43-0.93	
<i>Veronica persica</i>	AI = 0	0-0.14			0.29-0.43	

* Assessments of acceptability: AI, PI = area of test material consumed/area of control material consumed; log PI = log area of test material consumed/log area of control material consumed; 0.43-0.93 = accepted in 30/70 to 65/70 instances; 0.29-0.43 = accepted in 20/70 to 30/70 instances; 0.14-0.29 = accepted in 10/70 to 20/70 instances; 0-0.14 = accepted in 0/70 to 10/70 instances.

does not however deny the claimed importance of trichomes for other herbivores (Gilbert 1971; Levin 1973) and hairs may have a role in the acceptability of whole leaves that is removed by using leaf discs.

Poa annua, the only grass included in the present study, was not included among the test plants of other authors. Grass leaves seem to be generally unacceptable to both slugs and snails, possibly due to the presence of silica bodies (phytoliths) in the leaves. *Holcus lanatus* is a notable exception; it occurred as a major component in the diet of the slug *Agriolimax reticulatus* (Pallant 1972) and was also relatively acceptable to the snails *Cepaea nemoralis* (Grime, MacPherson-Stewart & Dearman 1968) and *Arianta arbustorum* (Grime & Blythe 1969).

In these experiments slugs generally refused to eat leaves of those plant species known to contain important secondary compounds (glucosides, alkaloids etc.) (e.g. *Senecio* spp., *Ranunculus* spp., *Trifolium repens* and *Lotus corniculatus*). However, the presence of latex in leaves was no deterrent and both *Taraxacum officinale* and *Lactuca sativa* (the control plant) were highly acceptable. It is interesting that all three species of *Plantago* were quite unacceptable to slugs—though members of this genus have not been reported to contain any secondary chemicals that might act as a defence.

Comparison between plants of different habitats (waste land and grassland) showed that in general the waste-land species were more acceptable to *Agriolimax caruanae* than were the grassland species. *Agriolimax caruanae* appears to be restricted to those habitats in which its preferred food plants are abundant.

Comparisons of the acceptability of species of different life cycles show high acceptability of the annuals. This may be because annual species generally lack chemical defences (Cates & Orians 1975) and are most abundant in the waste areas favoured by *A. caruanae*; similarly, annuals often have growth forms that place the leaves close to ground level and easily accessible to slugs. If the feeding relationships of slugs and their food plants had resulted from coevolution—each exerting powerful selective forces on the evolution of the other—one might expect that predators newly introduced to an area should differ in dietary choices from those that could have coevolved with their local food plants. Cates & Orians (1975) tested this hypothesis with plants that were both native and introduced to the U.S.A. and with two species of slug (one native and one introduced). They found that native plants were sometimes preferred by the native slug and sometimes by the introduced one but that the proportions did not differ from random expectation.

It might be expected that those plants (*r*-species) that occupy early successional stages, e.g. waste ground, might expend less of their limited resources on defence compounds than would *K*-species of stable habitats where continued dispersal and escape from competitors and predators are less important in the life cycle. Several authors have considered this question and found conflicting results. Cates & Orians (1975) tested the hypothesis by direct measurement of the acceptability to two species of slug of early successional annuals and biennials, early successional perennials, and late successional and climax plants; the results neatly fitted the hypothesis outlined above. On the other hand, Otte (1975) studying the acceptability of plants to grasshoppers and Futuyama (1976) analysing the diet of caterpillars, found evidence against the hypothesis. The studies of Otte (1975) and of Futuyama (1976), as well as those of Cates & Orians (1975), have all been criticized on the grounds of inadequate experimental methods (Maiorana 1978). Maiorana suggests that 'successional status and life history form may not be important factors influencing the preferences of these herbivores but factors correlated perhaps with

more basic ones', amongst which she proposed, for example, growth form and relative abundance of the plants, and animal-conditioning to frequently encountered diets. The work reported here avoids most of Maiorana's criticism but does not provide an unequivocal answer to the evolutionary question. On the one hand, 'basic' attributes, particularly toughness, appeared to be of prime relevance in determining herbivore preference. Similarly, evidence of short-term (proximal) conditioning or long-term (ultimate) selection of, and specialization on, frequently available plants was suggested by the tendency of slugs (in 1977 at least) to prefer waste-site plants over species from grassland.

Among highly specialized phytophagous insects it is almost impossible to define with precision the characteristics that make a plant acceptable or not (Ehrlich & Raven 1965). In the study of slugs one is dealing with an acceptability-moderated generalist, that is, a species capable of taking a wide variety of food but showing a distinct order of preference. In these circumstances it may be quite unrealistic to expect that one or even a small group of plant characteristics could be isolated as responsible for the position of a plant in the acceptability hierarchy. The situation is not unlike that of the behaviour of an unspecialized plant pathogen, such as *Pythium* or *Rhizoctonia*. A very great range of host plants is attacked and some species suffer much more than others. Resistance seems most often to be generalized rather than specific and the degree of co-evolved relationship of host and parasite seems slight. In such cases specialized races are rare and the fundamental niche of the pathogen is wide. In the case of non-specialized pathogens it is common to find that lethal damage to the host is most common at the seedling stage. The same is almost certainly true of slug damage. It rarely appears to be lethal to established plants. Much of the information about dietary choices made by *Agriolimax caruanae* suggests that it has not formed closely coevolved relationships with its food plants, yet the range of plants that are acceptable is strictly limited and the slug is not by any means a generalist herbivore. In a few cases it is possible to recognize quite subtle intra-specific variation in plant acceptability; for example, morphs of *Trifolium repens* containing cyanogenic glucosides are not accepted by *Agriolimax caruanae* though acyanogenic forms are eaten readily (R. Dirzo, unpublished).

One remarkable feature emerging from the present study is the existence of the occasional egregious slug amongst a group of replicates. In some comparisons the anomalous slug displayed a particular ability to feed on leaves that were unacceptable to the rest. In other cases occasional slugs refused a food plant that the rest took readily. A similar phenomenon has been described by Bernays *et al.* (1976) who found exceptional insects within populations of *Locusta migratoria* which accepted plant species that most members of the population rejected. If this variation in acceptability is heritable, such polymorphism in feeding behaviour, coupled with the few known examples of polymorphism in acceptability amongst host plants, may suggest that the slugs, although still generalists, are beginning to be caught up in the 'ever-deepening rut' of specialization and that we may be witnessing in slug-plant interactions the early stages of a coevolutionary process. Between-species variation in food choice by slugs may be a significant area for further study, coupled with analysis of the influence on choice-making of dietary conditioning during the life of individuals.

ACKNOWLEDGMENTS

I thank Professor J. L. Harper for his continuous help and guidance. I am grateful to the staff of the Pen-y-Ffridd Experimental Station of the School of Plant Biology for much

help with the experimental work; to A. Vardy for statistical advice and to Dr R. W. Runham for the identification of some slugs. This research was supported by the British Council and the University of Mexico.

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(Received 31 October 1979)

APPENDIX

The plants investigated and characteristics of leaves likely to be important in determining their acceptability to molluscs

Species	Collection site (National Grid reference)	Growth habit	Texture	Leaf characteristics*			Evidence of chemical deterrents
				Upper surface	Lower surface	Veins	
<i>Anagallis tenella</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Prostrate perennial	Fleshy and succulent	Glabrous with sparse, isolated hairs along furrow of main nerve	Glabrous	Central incon- spicuous vein	
<i>Bellis perennis</i>	Grassy places at Cors Goch, Anglesey (SH 501815) in 1977; at Treborth, Bangor (SH 553712) in 1978	Perennial rosette	Soft	Strigose vesture of long, spaced hairs; presence of crystals in both surfaces suggests that hairs may be glandular	As upper but hairs slightly more dense, especially along the main nerve	Central well- developed vein	
<i>Brassica napus</i>	Waste places by roads around Llandudno (SH 775815)	Erect annual or biennial	Relatively soft	Glabrous	Almost glabrous; some hairs present along furrows of the lamina	Reticulate	Gluco-sinolates; 'poisonous substances to higher animals' (Forsyth 1954) Gluco-sinolates
<i>Brassica nigra</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705) in 1977 at Moelfre, Anglesey (SH 514865) in 1978	Erect annual	Soft	Glabrous	Glabrous	Central prominent vein, plus a less conspicuous reticulum	
<i>Brassica oleracea</i>	Sea-cliffs at Llandudno (SH 781835)	Erect biennial or perennial	Fleshy, tough	Glabrous	Glabrous	As <i>B. nigra</i> but veins more fibrous and developed	Gluco-sinolates; 'poisonous substances to higher animals' (Forsyth 1954) Mustard oil, gluco-sinolates
<i>Brassica oleracea</i> (cultivated)	Crop fields at Pen- y-Ffridd, Bangor (SH 564705)	Erect biennial	Fleshy, very furrowed	Glabrous	Glabrous	A reticulum of veins, some very prominent	
<i>Brassica rapa</i>	Waste sites, Pen- y-Ffridd, Bangor (SH 564705)	Erect annual or biennial	Soft	Very sparse vesture of small hairs (pilose- like)	As on upper, but hairs denser along furrows of the nerves	Reticulate	Gluco-sinolates

Species	Collection site (National Grid reference)	Growth habit	Texture	Upper surface	Leaf characteristics*	Evidence of chemical deterrents
<i>Capsella bursapastoris</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Annual rosette	Soft to tough	Densely tomentulose plus a vesture of sparse, longitudinal and stellate hairs	Lower surface As upper surface	Prominent central vein
<i>Chenopodium album</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Erect annual	Soft	Glabrous	Glabrous	Prominent central vein with a few lateral veins
<i>Epilobium hirsutum</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Dense erect shoots, perennial	Soft	Glabrous	Glabrous	A longitudinal vein and some less prominent lateral veins
<i>Epilobium parviflorum</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Erect perennial	Soft	Sparse, small and thin hairs mostly associated with nerves	As upper, but hairs denser along the main nerve	Central vein with a simple system of lateral veins
<i>Lamium purpureum</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Erect shoots, annual	Tough and very rugose	Hirsute vesture of long and dense hairs	As upper surface	Only a conspicuous central vein
<i>Lotus corniculatus</i>	Grassy places at Cors Goch, Anglesey (SH 501815)	Prostrate perennial	Fairly soft	Glabrous	Strigose-like hairs, abundant on the edges of the leaflets	Central veins on the lower surface only
<i>Papaver dubium</i>	Waste sites at Pen- y-Ffridd, Bangor (SH 564705)	Erect annual	Soft and tender	Strigose vesture with long sparse hairs	As upper, but hairs mainly on the veins	Central vein, and a linear reticulum
<i>Plantago lanceolata</i>	Grassy places, Pen- y-Ffridd, Bangor (SH 564705)	Perennial rosette	Tough	Very long hairs emerging from a conspicuous (gland-like) body	As upper, but hairs denser along the veins	Longitudinal very prominent veins
<i>Plantago major</i>	Grassy places, Pen- y-Ffridd, Bangor (SH 564705)	Perennial rosette	Tough	Scabrous vesture of sparse hairs all over the surface	As upper surface	As <i>P. lanceolata</i> ; some more prominent veins

<i>Plantago media</i>	Grassy sites, Menai Strails, Bangor (SH 563715)	Perennial rosette	Tough	Scabrous vesture of sparse hairs all over the surface	As upper surface	As <i>P. lanceolata</i> ; some more prominent veins	Silica in the leaves (Parry & Smithson 1964)
<i>Poa annua</i>	Waste sites, Pen-y-Ffridd, Bangor (SH 564705)	Dense tussocks, annual	Soft	Almost glabrous	Almost glabrous	Parallel veins, the central one most prominent	
<i>Polygonum aviculare</i>	Waste sites, Pen-y-Ffridd, Bangor (SH 564705)	Prostrate annual	Soft to tough	Glabrous	Glabrous	Linear system; central prominent vein	
<i>Ranunculus acris</i>	Grassy places, Treborth, Bangor (SH 553712)	Perennial rosette	Slightly tough	Vellutinous vesture but hairs more concentrated towards the base and tip	As upper, plus gland-like spots from which smaller hairs emerge	Reticulate system with two degrees of vein prominence	Glucosinolates (ranunculin; Harper 1957)
<i>Ranunculus bulbosus</i>	Grassy places, Treborth, Bangor (SH 553712)	Perennial rosette	Slightly tough	Vellutinous vesture but hairs more concentrated towards base and tip	As upper, plus gland-like spots from which hairs emerge	Reticulate system with two degrees of vein prominence	Glucosinolates (ranunculin; Harper 1957)
<i>Ranunculus repens</i>	Grassy places, Treborth, Bangor (SH 553712)	Rosettes with stolons, perennial	Slightly tough	Dense vellutinous vesture	As upper, plus gland-like spots from which smaller hairs emerge	Reticulate system with two degrees of vein prominence	Glucosinolates (ranunculin; Harper 1957)
<i>Senecio jacobaea</i>	Waste sites near Llandudno (SH 775815)	Erect perennial	Soft, but fleshy	Vesture of small hairs plus longer hairs along the veins	As upper surface	Central vein prominent, lateral ones less conspicuous	Alkaloids (Harper & Wood 1957)
<i>Senecio squallidus</i>	Waste sites near Llandudno (SH 775815)	Erect perennial	Soft, but fleshy	Almost glabrous	As upper but some hairs along veins	Central vein prominent, lateral ones less conspicuous	Alkaloids
<i>Senecio vulgaris</i>	Waste sites near Llandudno (SH 775815)	Erect perennial	Soft, but fleshy	Almost glabrous, some hairs along the veins	As upper surface but hairs even less dense	Prominent central vein	Alkaloids
<i>Stellaria media</i>	Waste sites, Pen-y-Ffridd, Bangor (SH 564705)	Semi-creeping shoots, annual	Soft	Smooth, glabrous, some sparse hairs along the nerves	As upper surface, more hairs toward the base of the leaf	Prominent central vein	
<i>Taraxacum officinale</i>	Waste sites, Pen-y-Ffridd, Bangor (SH 564705)	Very dense perennial rosette	Very soft	Tomentulose with sparse longitudinal hairs	As upper surface	Prominent central vein	Latex

Species	Collection site (National Grid reference)	Growth habit	Texture	Upper surface	Lower surface	Veins	Evidence of chemical deterrents
<i>Trifolium pratense</i>	Waste sites, Pen- y-Ffridd, Bangor (SH 564705)	Dense prostrate clones, perennial	Very soft	A vesture of small, thin and isolated hairs	A sericeous vesture of very dense hairs	Central vein with parallel very fibrous secondary veins	
<i>Trifolium repens</i>	Waste sites, Pen- y-Ffridd, Bangor (SH 564705)	Dense prostrate clones, perennial	Very soft	Glabrous	Glabrous	As <i>T. pratense</i> but the secondary veins are more fibrous	Polymorphic for cyanogenic glucosides (Jones 1973)
<i>Veronica persica</i>	Waste sites, Pen- y-Ffridd, Bangor (SH 564705)	Erect shoots, annual	Tough and rugose with dense papillae	Pubescent hairs; scabrous but very sparse	As upper surface but hairs denser on the nerves	Very prominent nerves.	

* Nomenclature for kinds of pubescence follows that of Lawrence (1951; descriptions and diagrams on pp. 746–47). Descriptions of leaf surfaces correspond to observations under dissecting microscope (magnification 12–60×).