Published in Functional Ecology 7, issue 4, 403-410, 1993
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# Does the land snail *Arianta arbustorum* prefer sequentially mixed over pure diets?

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## Summary

**1.** Most herbivores have a very restricted host range (the specialists), but some (called generalists) include a large number of different food plants in their diet. Here, we investigate the land snail *Arianta arbustorum* (Helicidae) to discover whether eating several plant species is more advantageous than eating one plant species only.
**2.** In the faeces of field-collected *Arianta arbustorum*, the plant species eaten were identified anatomically. Over 89% of the snails had eaten more than one food item within the period of 1–3 days, for which the faeces are representative.
**3.** In the laboratory, *Arianta arbustorum* was presented with two different food plants in sequence and the amounts eaten were measured (sequentially mixed diet group). The controls were fed only one plant species throughout the experiment (pure diet group). When the snails of the sequentially mixed diet group received the food plants *Circaea lutetiana* (Onagraceae) or *Stachys silvatica* (Lamiaceae) together with *Adenostyles alliariae* (Asteraceae) (irrespective of order of presentation) they ate more than the snails from the pure diet group. However, when the snails of the sequentially mixed diet group received *Senecio fuchsii* (Asteraceae) together with *Adenostyles alliariae* (irrespective of order of presentation) they ate similar amounts as the snails from the pure diet group.
**4.** *Adenostyles alliariae* and *S. fuchsii* belong to the same subtribe Senecioneae and contain very similar secondary compounds, while *C. lutetiana* and *S. silvatica* belong to different plant families from *Adenostyles alliariae* and contain completely different secondary compounds. This suggests that secondary compounds may be important in causing snails to eat sequentially mixed diets. However, nutrient complementation and sampling cannot be ruled out as additional factors responsible for the maintenance of sequentially mixed diets.

*Key-words:* Feeding behaviour, gastropod, generalist herbivore

## Introduction

The great majority of all herbivores have a very restricted host plant range, and less than 10% of them are generalists (Bernays & Graham 1988). Generalists often seem to include the largest possible number of food plants in their diet. Indeed, their diet often contains more different plants than predicted by simple optimal foraging models (e.g. Pulliam 1975; Westoby 1978; Clark 1982). Here, we call diets consisting of one food type 'pure', and diets consisting of more than one food type 'mixed'. Mixed diets are eaten by very different animals (e.g. protozoans: Rapport 1980; molluscs: Kitting 1980; spiders: Greenstone 1979; leaf cutter ants: Rockwood 1976; orthopterans: Pickford 1962, Popov *et al.* 1978, Freeland 1975; reptiles: Stamps, Tanaka & Krishnan 1981, Eason 1990, Bjorndal 1991; birds: Krebs & Avery 1984, Jordano 1988; mammals: Jenkins 1978, Clark 1982, Owen-Smith & Novellie 1982, Kincaid & Cameron 1985, Maizeret 1988; many additional references can be found in Greenstone 1979, Clark 1982 and Waldbauer & Friedman 1991). In most of these studies, the mechanisms causing the animals to eat a mixed diet are unknown.

In this study, we investigate the feeding behaviour of the generalist, herbivorous land snail *Arianta arbustorum* (L.) (Helicidae). Unlike browsing herbivorous mammals, snails can only eat one plant at a time. However, they can maintain a mixed diet by eating different plant species sequentially. Among the

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gastropods, some slugs grow better on a mixed than on a pure diet (Richter 1979). Graber & Suter (1985) suggest that slugs prefer to eat mixed diets, but they do not present data supporting this.

First, we determined whether this snail maintains a sequentially mixed diet in nature over a given time span. For this purpose, snails were collected in the field and the plant species found in their faeces were determined anatomically. Secondly, we investigated whether feeding on a given plant is influenced by the previous food plant. If sequentially mixed diets are advantageous, the snails should eat more of a given plant when they were previously fed another plant than when they were previously fed the same plant. We therefore compared snails which were fed one plant species on 4 consecutive days (the pure diet group) with snails which were fed two different plant species for 2 days each (the sequentially mixed diet group).

If two different food plants are offered to the snails in sequence, the second plant should be eaten in the largest quantity soon after the diets are switched and the gut still contains the first food. We therefore predicted that the intake of sequentially mixed diets would be especially high on the first day on which the second food is given to the snails of the mixed diet group. This latter prediction is a peculiarity of sequentially mixed diets and is not applicable to animals which eat a mixed diet simultaneously (e.g. some browsing mammals).

## Materials and methods

### FAECES EXAMINATION

A total of 203 snails was collected in the field at the site Blauen (Switzerland) and allowed to defecate in the laboratory. Faeces were examined microscopically to determine the plant species (or other food items) eaten by the snails. Here, we analyse the data to determine the number of food items eaten by individual snails [for other results see Speiser & Rowell-Rahier (1991)]. Most of the snails evacuated all their gut contents within 24 h, occasionally 48 h were necessary. In the field, defecation might be slower due to lower temperatures. We therefore assume that the total contents of the snail gut (as analysed here) represent approximately 1–3 days' feeding.

At the field site, 15 plant species were present, 12 of which were identifiable in the snail faeces after test feeding. Of these, 10 were eaten by the wild snails. The snail's diet is a mixture of fresh and decaying plant material, leaf litter, soil, limestone and insects. Brown plant material might contain lower levels of secondary compounds than green material because of bacterial/chemical decomposition. Because of this, and for comparability with the feeding experiments (in which only green leaves were used), only green plant material was counted when the plant species composition in the faeces was analysed.

### COLLECTION AND MAINTENANCE OF SNAILS

One hundred and ten juvenile and adult individuals of *Arianta arbustorum* (Helicidae) were collected in June and July 1991 at the site Zastler (Feldberg, Germany), described in Speiser, Harmatha & Rowell-Rahier (1992). These ranged from 10 to 23 mm in shell diameter. They were kept individually in a climate chamber at 18 °C and 16 h light / 8 h darkness.

### EXPERIMENTAL DESIGN

Six comparisons of sequentially mixed and pure diets were made (Table 1). Sample sizes ranged from 22 to 30 snails per treatment. The symmetric use of each plant both as test plant and as plant for mixing allowed us to distinguish between effects due to the advantages of mixed diets and effects due to different hunger levels building up on days 1 and 2 (see Discussion). Pairs of reciprocal experiments were always done simultaneously. In the field, the frequency of change of food plants is about one change/day (if only green plant material is considered; see Results) and thus comparable to the frequency used in our experiments.

On every experimental day, each snail was given one leaf disc (diameter = 2·5 cm) and was then allowed to feed for 24 h. After this, the area of the uneaten remains was measured with a video camera connected to an image analysis system. For details see Speiser *et al.* (1992).

Plants which are known to be major constituents of the diet of *Arianta* at one study site (see Speiser & Rowell-Rahier 1991) were selected for these experiments. These were: *Adenostyles alliariae* ((Gouan) Kerner) (Asteraceae: Senecioneae), *Circaea lutetiana* (L.) (Onagraceae), *Stachys silvatica* (L.) (Lamiaceae) and *Senecio fuchsii* (Gmelin) (Asteraceae: Senecioneae). *Adenostyles* and *Senecio* belong to the same subtribe of the Asteraceae and have a similar

**Table 1.** Design of the feeding experiments. The food given on days 1 and 2 is separated by a dash from the food given on days 3 and 4. Experiment 1 is reciprocal to experiment 4, no. 2 to no. 5 and no. 3 to no. 6. Plant species are abbreviated as follows: A = *Adenostyles*, C = *Circaea*, St = *Stachys* and Se = *Senecio*

| Experiment no. | Pure diet | Mixed diet |
|---|---|---|
| 1 | A–A | C–A |
| 2 | A–A | St–A |
| 3 | A–A | Se–A |
| 4 | C–C | A–C |
| 5 | St–St | A–St |
| 6 | Se–Se | A–Se |

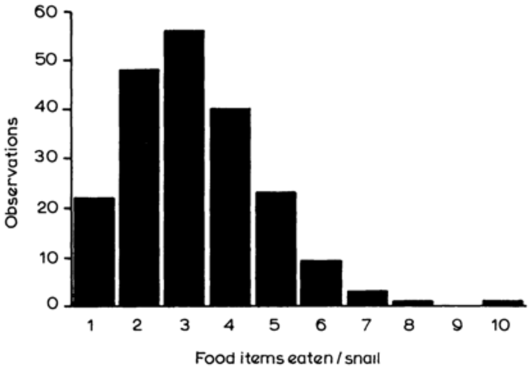

**Fig. 1.** Numbers of different food items consumed per snail during the estimated period of 1–3 days, determined with microscopic examination of faeces. Non-plant and brown plant material are included in this figure but excluded from the analysis given in Table 2.

secondary chemistry (pyrrolizidine alkaloids and sesquiterpenes). The other two plants tested belong to separate families and are chemically distinct. *Circaea* is characterized by polyphenols, flavonoids and calcium oxalate (Hegnauer 1969, 1990), while *Stachys* contains iridoids, rosmarinic acid, diterpenes, flavonoids, protoalkaloids and heterosides (Hegnauer 1966, 1989). The relative nitrogen content is: *Adenostyles* = 1; *Circaea* = 1·17; *Stachys* = 1·20; *Senecio* = 1·33 (data from Speiser & Rowell-Rahier 1991). Thus, *Adenostyles* and *Senecio* are the most similar plants with respect to secondary compounds and the most dissimilar with respect to nitrogen content. With one exception, all experiments were performed with freshly picked plants from the site Blauen described in Speiser & Rowell-Rahier (1991). For the *Stachys* experiment, *Adenostyles* leaves were collected at the Zastler site every second day, because the *Stachys* experiment was performed late in the season, when the *Adenostyles* leaves from Blauen were already senescing, while those from Zastler were still in good condition. *Adenostyles* leaves from the two sites had a similar fresh weight per unit area and the amounts consumed in a pure diet were also similar (see Results). We therefore will not differentiate them in the text.

The same snails were used for all experiments, but they were assigned to different treatments in different experiments. To prevent carryover effects from one experiment to the next, each experiment was preceded by the following pretreatment. Two days before the experiment, each snail was given a large disc of lettuce. One day before the experiment, any remaining lettuce was removed and the snails deprived of food for 1 day (before the *Senecio* experiment, the period of food deprivation lasted for 3 days). Analysis shows that the treatment on days 3 and 4 of the previous experiment never had a significant effect on consumption on day 1 of the next experiment. If a snail did not eat any lettuce in the pretreatment, it was considered unhealthy and its consumption data were removed from the data set of the previous experiment.

### DATA HANDLING

The leaf area eaten was calculated by subtracting the area of the uneaten remains from the total area of the discs. This was then converted to mg fresh weight eaten by multiplying by a factor determined by weighing all the leaf discs used in an experiment. Leaf area of 1 $cm^2$ corresponded to 20·1 mg *Adenostyles*, 11·5 mg *Circaea*, 12·4 mg *Stachys* and 22·9 mg *Senecio*.

Because larger snails eat more than smaller ones, the consumption data were standardized. For this, the fresh weight consumed was divided by each snail's shell diameter and multiplied by 16 mm, the size of a 'standard snail' (i.e. the average size of the snails used in the experiments). Shell diameter of *Arianta* is highly correlated with other parameters which are probably good indicators of metabolism, e.g. shell volume, soft body dry weight or total egg dry weight (Baur & Raboud 1988). On each experimental day a considerable proportion of the snails ate nothing, so non-parametric statistical tests were used to analyse the feeding experiments, and the medians rather than the means are plotted in the figures.

## Results

### DIET OF FIELD-COLLECTED SNAILS

Figure 1 gives the number of different food items found in the faeces. Of all snails, 89% had eaten more than one food item. These may include green and brown plant material, soil, arthropods, etc. (Speiser & Rowell-Rahier 1991). About one-half of the faeces is made up of plant material, which in turn consists of brown or green plant material. Based on green plant material only, the numbers of snails which had eaten different combinations of plant species are given in Table 2. Among the snails which had or had not eaten *Adenostyles* or *Stachys*, we distinguished between those that had eaten either one or more than one plant species (i.e. a pure or a mixed diet). *Adenostyles* was eaten more frequently than expected by those snails that had eaten at least two plants, but this trend is not significant. *Stachys* was eaten significantly more than expected by those snails that had eaten at least two plants. For *Circaea* and *Senecio*, this analysis could not be made because of small sample sizes.

### LABORATORY FEEDING TESTS

The size-corrected consumption data of juvenile and adult snails were similar and will not be differentiated hereafter.

**Table 2.** Counts of snails which had eaten pure or mixed diets (i.e. either one or more than one green plant species) in the presence or absence of *Adenostyles* or *Stachys*. Among the snails which had eaten *Adenostyles* more snails had eaten a mixed diet than among the other snails, but the tendency is not quite significant ($\chi^2 = 3{\cdot}09$, $P = 0{\cdot}08$, with continuity correction). Among the snails which had eaten *Stachys*, significantly more had eaten a mixed diet than among the other snails ($\chi^2 = 4{\cdot}61$, $P = 0{\cdot}03$). For *Circaea* and *Senecio*, this analysis could not be done because of low expected values in one cell

| | Pure diet | Mixed diet |
|---|---|---|
| *Adenostyles* present | 33 | 14 |
| *Adenostyles* absent | 81 * | 15 |
| *Stachys* present | 9 | 7 |
| *Stachys* absent | 105 * | 22 |

* Pure diet of one of the 13 other plant species detected in the faeces.

### CONSUMPTION OF PURE DIETS

The consumption of pure diets of *Adenostyles*, *Circaea*, *Stachys* and *Senecio* is shown in Fig. 2. The median consumption of the pure *Adenostyles* diet decreased significantly over time in experiments nos. 1 and 2, while it was constant in experiment no. 3 (Spearman rank correlation coefficient; experiment 1: $\rho = -0{\cdot}28$, $P < 0{\cdot}003$; experiment 2: $\rho = -0{\cdot}28$, $P < 0{\cdot}002$; experiment 3: $P > 0{\cdot}1$). The median consumption of *Circaea* decreased significantly over the experiment and equaled zero on day 4 (Spearman rank correlation coefficient; $\rho = -0{\cdot}36$, $P < 0{\cdot}0001$). The consumption of *Stachys* did not increase or decrease significantly over time (Spearman rank correlation coefficient; $P > 0{\cdot}3$). However, it was significantly heterogeneous among days (Kruskal–Wallis test, $P < 0{\cdot}01$). The consumption of *Senecio* increased significantly over time (Spearman rank correlation coefficient, $\rho = 0{\cdot}24$, $P < 0{\cdot}03$).

The consumption of *Circaea* was approximately 100 times lower on average than the consumption of *Adenostyles* (Mann–Whitney *U*-tests; $P < 0{\cdot}001$ on all days). Similarly, the consumption of *Stachys* was also much lower than the consumption of *Adenostyles* on all days (Mann–Whitney *U*-tests; $P < 0{\cdot}001$ on days 1 and 2, $P < 0{\cdot}01$ on days 3 and 4). The consumption of *Senecio* was similar to that of *Adenostyles* on days 1–3, but significantly higher on day 4 (Mann–Whitney *U*-tests; $P > 0{\cdot}3$ on days 1–3, $P < 0{\cdot}01$ on day 4). When comparing the consumption of different food plant species, nitrogen uptake might be a better measure than fresh weight eaten. We have therefore transformed all data into mg total nitrogen eaten. Relative to *Adenostyles,* the consumption of *Circaea, Stachys* and *Senecio* was slightly increased when expressed in mg nitrogen, but the qualitative pattern of differences between plant species remained unchanged (data not shown).

### COMPARISON OF PURE AND MIXED DIETS

Pure and sequentially mixed diets are compared in Fig. 3. The values for *Adenostyles* consumption are given on the left-hand side. More *Adenostyles* was eaten by snails previously kept on *Circaea* than by those previously fed *Adenostyles* (Mann–Whitney *U*-tests, $P < 0{\cdot}01$ on day 3, $P < 0{\cdot}02$ on day 4). On day 3, the sequentially mixed diet was eaten 10 times more than the pure diet, and on day 4 it was eaten six times

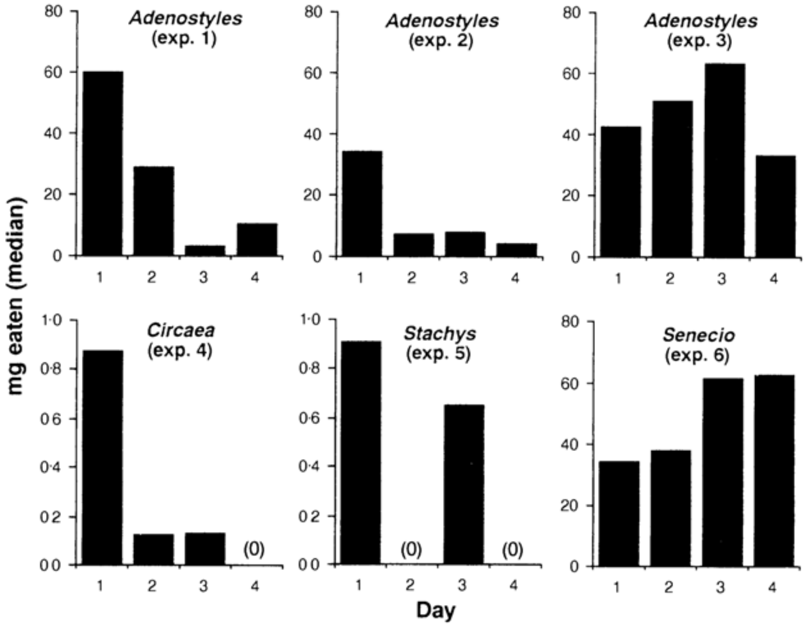

**Fig. 2.** The median consumption of pure diets of *Adenostyles*, *Circaea*, *Stachys* and *Senecio* on 4 consecutive days. The values are adjusted for snail size. Note that the consumption of *Adenostyles* and *Senecio* is plotted with a different scale than the consumption of *Circaea* or *Stachys*.

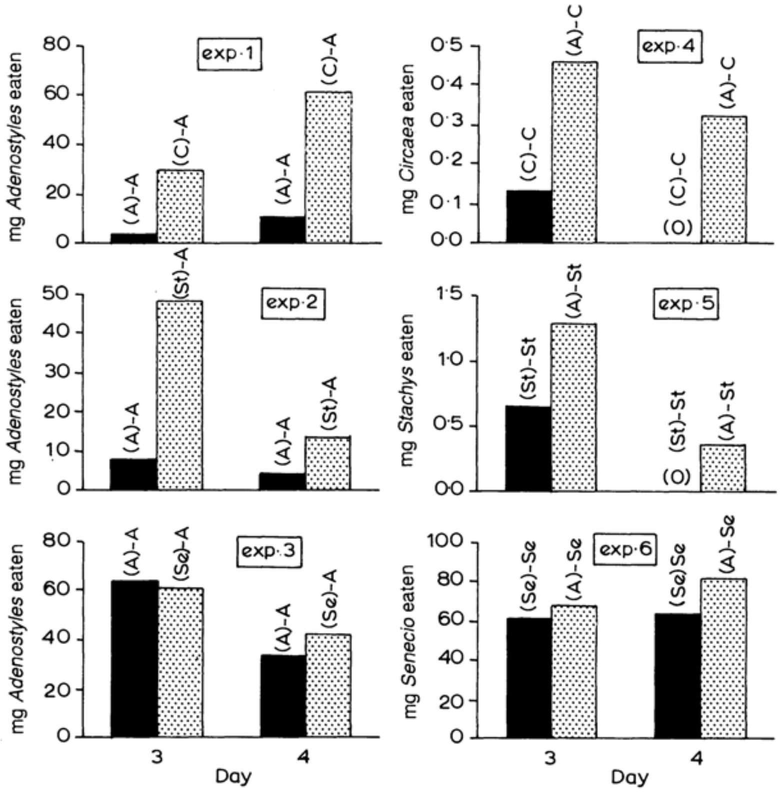

**Fig. 3.** Consumption of *Adenostyles*, *Circaea*, *Stachys* or *Senecio* as a function of the preceding diet. Values for the pure diet group (■); values for the sequentially mixed diet group (▨). The food regime is indicated above each bar as in Table 1, but the food given on the first 2 days is in brackets because its consumption is not shown. Reciprocal experiments are drawn side by side.

more. Similarly, snails previously kept on *Stachys* ate more *Adenostyles* than those previously fed *Adenostyles* (Mann–Whitney *U*-tests, $P < 0{\cdot}003$ on day 3, $P < 0{\cdot}002$ on day 4). On day 3, the sequentially mixed diet was eaten six times more than the pure diet and on day 4, it was eaten three times more. By contrast, there was no difference in *Adenostyles* consumption by snails which had been kept on *Senecio* and snails which had been kept on *Adenostyles* (Mann–Whitney *U*-tests, $P > 0{\cdot}8$ on day 3, $P > 0{\cdot}3$ on day 4).

The consumption of *Circaea*, *Stachys* and *Senecio* in pure and sequentially mixed diets is compared on the right half of Fig. 3. More *Circaea* was eaten after 2 days on *Adenostyles* than after 2 days on *Circaea* (Mann–Whitney *U*-tests, $P < 0{\cdot}006$ on day 3, $P < 0{\cdot}008$ on day 4). On day 3, the sequentially mixed diet was eaten 3·5 times more than the pure diet. On day 4, median pure *Circaea* consumption was zero and the ratio could not be calculated. Similarly, snails which were previously fed *Adenostyles* ate more *Stachys* than snails previously kept on *Stachys*. However, the trends were not significant in this experiment (Mann–Whitney *U*-tests, $P > 0{\cdot}2$ on day 3, $P > 0{\cdot}3$ on day 4). On day 3, the sequentially mixed diet was eaten two times more than the pure diet, while on day 4, the ratio could not be calculated. By contrast, there was no difference in *Senecio* consumption by snails which had been kept on *Adenostyles* and those which were fed *Senecio* (Mann–Whitney *U*-tests, $P > 0{\cdot}9$ on day 3, $P > 0{\cdot}1$ on day 4).

## Discussion

The faeces examination indicates that the snails usually consume a sequentially mixed diet in the field. Within the estimated period of 1–3 days, the great majority of all snails had eaten more than one food item. Further, this does not seem to be the result of random feeding, but rather reflects active selection of certain food types by the snails. First, most plants are not completely eaten after they are encountered by the snails. Both field and laboratory observations suggest that individual meals consist of 0·1–4 $\text{cm}^2$ leaf area on average and that snails often change food plants between meals. Secondly, many food items are not eaten in proportion to their availability. In particular, a walking snail is constantly confronted with leaf litter which covers the whole forest floor, yet this is only a minor component of the diet (Speiser & Rowell-Rahier 1991). Thirdly, certain combinations of food items are eaten more often than others. Indeed, among the snails that had eaten *Adenostyles* or *Stachys* more had eaten a mixed diet than among the other snails. *Stachys* may seem to be largely avoided by the snails

(Table 2). However, *Stachys* is rare at the investigated site and its consumption is over-proportional to its availability (Speiser & Rowell-Rahier 1991). Furthermore, snails that had eaten several green (= presumed toxic) plant species had eaten a larger number of brown plants (= presumed less toxic because of degradation) than snails that had eaten only one green plant species (B. Speiser, unpublished data). Thus, our experimental approach reflects the snails' natural feeding behaviour.

Two of the plants used in the feeding experiments (*Adenostyles* and *Senecio*) were acceptable to the snails, while the other two (*Circaea* and *Stachys*) were mostly unacceptable. When given the pure diet, consumption of all plants except *Senecio* decreased over time. Whether this reflects the toxic effects of secondary compounds or nutrient unsuitability cannot be determined with these data. Both secondary compounds and nutrients can influence the amounts of a given food eaten (e.g. Raubenheimer & Simpson 1990). Although we shall try to discriminate between these two causes below, it should be stressed that nutrients and secondary compounds interact in many ways during feeding and digestion (e.g. Brattsten 1988; Creswell, Merritt & Martin 1992; Slansky & Wheeler 1992).

The feeding experiments clearly support the hypothesis that the snails eat more of sequentially mixed than of pure diets. Further, we predicted that the effect of the food plant change in the sequentially mixed diet group should be most pronounced on the first day after the change (i.e. day 3), because the snail gut contains more of the first plant on day 3 than on day 4. This is supported by the data. In the field, the frequency of food plant changes is higher than in our experiments and therefore the effects of mixed diets are probably more pronounced.

Different factors may cause animals to eat mixed diets.

**1.** Mixed diets may be favoured because they keep the levels of the individual toxins from different plant species low (Freeland & Janzen 1974). To our knowledge, the existence of this mechanism has not been shown experimentally for any animal species. A related explanation is the idea that different secondary compounds not only dilute each other, but rather interact antagonistically with each other. Tannins may bind to saponins in the gut, and a mixed diet of tannins and saponins in the right proportions is less toxic for mice than a pure diet of either saponin or tannin only (Freeland, Calcott & Anderson 1985). For other secondary plant chemicals, such effects have not been demonstrated to our knowledge.

**2.** In general, plants contain different proportions of nutrients. A mixed diet can be composed to provide all nutrients in optimal proportions, while a pure diet may be deficient in some nutrient. Nutrient complementation in mixed diets has been documented for several herbivore species (Cohen *et al.* 1987; Schiff, Waldbauer & Friedman 1988, 1989; Simpson *et al.* 1990; Bernays & Bright 1991). In some cases, nutrients do not directly complement each other, but the presence of one type of food increases the digestibility of another food type (Bjorndal 1991 and references therein).

**3.** New food plants may become available at any time of the season, and the chemical composition of the plants may change over time. Under these circumstances, herbivores have to sample all available plants constantly in order to be able to choose the best foods. This explanation is given for mixed diets of leaf cutter ants (Rockwood 1976), beavers (Jenkins 1978) and ungulates (Owen-Smith & Novellie 1981). In many cases, several of these mechanisms may operate simultaneously to cause animals to eat mixed diets (e.g. Clark 1982).

Our experiments were designed primarily to test whether snails eat more of a given plant in a sequentially mixed diet, rather than to investigate the underlying mechanisms. Nevertheless, circumstantial evidence favours the mechanism of secondary compound dilution. The snails ate more of a sequentially mixed than of a pure diet, if the mixed diet was composed of two plants from different families (which contained completely different secondary compounds). By contrast, if the mixed diet was composed of the two chemically similar Senecioneae *Adenostyles* and *Senecio*, it was consumed in similar amounts as the pure diet. Additional evidence favouring the secondary compound dilution mechanism comes from the faeces examination: no single snail had eaten both *Senecio* and *Adenostyles*. Secondary compounds were found to be important for the feeding decisions of *Arianta* in the wild, while nitrogen was not important in that study (Speiser & Rowell-Rahier 1991).

Whether nutrient complementation caused the snails to eat more of the sequentially mixed diets cannot be determined with these experiments. Nitrogen content of the leaves (an important nutrient for many herbivores) does not explain the observed feeding behaviour of the snails: *Adenostyles* and *Senecio* are the two most dissimilar plants with respect to nitrogen content, yet they are the only plant pair tested in which the sequentially mixed diet was eaten in similar quantities as the pure diet. However, the nutritional requirements of snails are very poorly understood and other substances may also be important.

In our experiments, there were no other foods for the snails to sample. However, snail behaviour has evolved to meet the conditions in the field and not those of our experiments, thus sampling cannot be ruled out as an additional factor causing the snails to eat more of sequentially mixed diets.

The 'hunger' level of the snails may also have influenced their food consumption. Snails which were given either *Circaea* or *Stachys* during the first 2 days ingested approximately 30–100 times less food (and were therefore probably more hungry on day 3) than snails which were given *Adenostyles* or *Senecio*. In experiments 1 and 2, the snails from the sequentially mixed diet group were thus probably more deprived than those from the pure diet group. In these two experiments the difference between the two treatment groups was most pronounced. By contrast, in experiments 4 and 5 the snails from the sequentially mixed diet group were probably less deprived than those from the pure diet group. In these two experiments the difference between the two treatment groups was less pronounced than in experiments 1 and 2, but still clearly detectable. Thus it seems that a greater hunger level caused the snails to eat more food, but to a lesser extent than did a sequentially mixed diet. However, a greater hunger level does not necessarily lead to higher consumption in all species (S. Simpson, personal communication), and for *Arianta*, the feeding in response to hunger has not yet been determined.

Any food plant change is associated with metabolic costs of movement, time loss, risks of starvation and the hazards of travelling. Herbivorous mammals are well adapted to these problems: they are highly mobile and they have good vision and highly developed brains to locate new food plants and to remember good food sources. By contrast, snails and slugs are much less mobile, and locomotion is extremely costly for them: up to 35% of total energy expenditure may be used for locomotion (Denny 1980). If travelling snails run out of water, they cannot produce a mucus trail; they are stuck and incur high risks of predation or crushing (Baur & Baur 1990). Nevertheless, the advantages of mixed diets seem to be sufficient to offset the costs and risks of additional food plant changes even for these animals.

## Acknowledgements

We warmly thank S. Simpson, H. Rowell and A. Baur for their comments on the manuscript and the Schweizerischer Nationalfonds for financial support (grant no. 31-26263·89 to MRR).

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