Carnivorous Plant-Slug Interaction: A Trip from Herbivory to Kleptoparasitism

Regino Zamora, Jose M. Gomez

Journal of Animal Ecology, Volume 65, Issue 2 (Mar., 1996), 154-160.

Stable URL:
http://links.jstor.org/sici?sici=0021-8790%28199603%2965%3A2%3C154%3ACPIATF%3E2.0.CO%3B2-I

Journal of Animal Ecology 1996, **65**, 154–160

Carnivorous plant–slug interaction: a trip from herbivory to kleptoparasitism

REGINO ZAMORA and JOSÉ M. GÓMEZ

Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

Summary

1. In this paper, we study the trophic ecology of *Deroceras hilbrandi*, a slug feeding on the prey captured by *Pinguicula vallisneriifolia*, a carnivorous plant.
2. We analyse slug abundance, foraging behaviour on *P. vallisneriifolia* plants and robbing rate in the field.
3. In the laboratory we experimentally test both the trophic preferences and the level of prey selection by the slug.
4. *Deroceras hilbrandi*, being more carnivorous than herbivorous, feeds on animal carcasses trapped by *P. vallisneriifolia*.
5. The laboratory experiments indicate that the slug is hardly selective regarding carcass size or degree of degradation.
6. Both mucilage secretion and the spatial distribution of the leaves strongly determine slug foraging behaviour on the plants. However, kleptoparasitic behaviour is risk-free because slugs are able to crawl on the leaves without being trapped.
7. As a result of this unusual animal–plant interaction, *D. hilbrandi* becomes a kleptoparasitic carnivorous slug.

Key-words: *Deroceras hilbrandi*, *Pinguicula vallisneriifolia*, kleptoparasitism, trophic habit change.

Journal of Animal Ecology (1996), **65**, 154–160

Introduction

Because of the low concentration of essential nutrients in plant tissues, herbivores face strong limitations in obtaining high-quality foods (Crawley 1983). A herbivore can use various strategies for obtaining a suitable meal, such as the selection of plant species and/or parts of the plants with a greater nutrient concentration, the selection of a mixed, balanced diet where different species provide diverse, complementary nutrients, and/or the choice of plants with a minimum concentration of toxic compounds (Stephen & Krebs 1986; Bernays & Chapman 1994). Another possibility is to change dramatically the herbivore trophic habit, by taking an animal meal when ecological conditions allow it (Crawley 1983). Animal tissues have a greater concentration of essential nutrients, such as nitrogen and phosphorus per unit of structural carbon, than do plant ones (Begon, Harper & Townsend 1990). For this reason, many herbivores, such as most granivorous and frugivorous birds (Newton 1985), several moth larvae (Crawley 1983) and dung beetles (Cambefort 1991), tend to feed on animal prey. Carnivory has been reported even for typical vertebrate herbivores, such as sheep and red deer (Bazely 1989). However, potential animal prey are usually mobile, and many herbivores have strong ecomorphological and/or behavioural limitations in capturing and handling them.

Carnivorous plants make large quantities of high-quality animal food items available to dietary opportunistic animals (Thum 1989; Zamora 1990). The long duration for which prey remain on the leaves encourages the development of kleptoparasitic interactions. Food-scrounging strategies open an access to a new resource (i.e. flying insects), otherwise impossible prey for a slow-moving invertebrate herbivore. In this paper, we analyse the trophic ecology of *Deroceras hilbrandi* Altena (Agriolimacidae), a species belonging to an animal group, the slugs, typically considered generalistic herbivores, which feed on the prey captured by *Pinguicula vallisneriifolia* Webb (Lentibulariaceae), a carnivorous plant. Specifically, we: (i) made field studies of the microhabitat use, trophic habit and the kleptoparasitic behaviour of *D. hilbrandi;* (ii) performed field experiments to test the slug's robbing rate of the prey trapped by the leaves of *P. vallisneriifolia;* (iii) performed laboratory experi-

ments to test both the trophic preferences and the level of prey selection by the slug.

NATURAL HISTORY OF THE SYSTEM

Species belonging to the genus *Deroceras* are generally herbivores, and some species are even regarded as an serious agricultural pests throughout the temperate world (Airey 1987, 1988; Kemp & Newell 1987; Bourne, Jones & Bowen 1990; Ferguson & Hanks 1990; Pakarinen, Niemelä & Tuomi 1990). On the Iberian Peninsula *D. hilbrandi* appears in wet mountain habitats (Castillejo 1990).

Pinguicula vallisneriifolia is an endemic plant of southern Spain, normally inhabiting wet rock walls and cliffs, characteristic of the limestone mountains of the Sierra de Cazorla y Segura. This species presents two morphological types of leaves during its foliar growth cycle. The first 5–7 leaves (April–May, spring leaves) form a rosette which lies flat against the wall; later, however, the leaves enlarge, becoming much longer than wide, and grow perpendicular to the basal rosette to overhang the wall (June–August, summer leaves). The growth of the distal leaves, coinciding with the senescence of the basal leaves, can reach 30 cm in length, and in turn senesce in September, with the formation of the winter bud. Both basal and distal leaves are glandular, and secrete mucilage. *P. vallisneriifolia* has mites (*Oribatula* sp.; Oribatulidae), which take advantage of prey on the leaves. The small size of these arthropods (less than 0·4 mm in length) allows them to crawl between the stalked glands without being trapped.

Methods

STUDY AREA

The field work was carried out in a 2500 ha reserve in the Sierra de Cazorla y Segura (southern Spain). The study zone, named Cobacho del Aire (1200 m a.s.l.) is the site of the headwaters of a small spring surrounded by a rocky wall (*c.* 50 m high and 150 m long). Plants grow on the wall (northern exposure) where no sunlight directly reaches the plants, but only diffuse radiation. This is the typical habitat where both *P. vallisneriifolia* and *D. hilbrandi* appear. The spatial distribution of the plants on the wall is patchy, some plants forming small clusters (hereafter aggregated plants), and others appearing isolated (hereafter solitary plants, i.e. considering a plant to be isolated when there are no other neighbouring *Pinguicula* within a 1-m radius). Also, some plants grow in dry rocks, rooting in small crevices, whereas other plants grow in wet cracks, where the water soaks the entire rocky surface. Thus, we have differentiated four sectors: wet solitary, wet aggregated, dry solitary and dry aggregated. Nearly 10% of the rocky wall was covered by *P. vallisneriifolia* plants, with a predominance of bare rocky sectors.

SLUG ABUNDANCE AND FORAGING BEHAVIOUR

We carried out censuses to determine the activity rhythm, abundance and microhabitat selection of the slugs in the study zone. We noted the slugs within a sector of the rocky wall (20 m in length and 2 m in height from the ground level) where the four sectors mentioned above alternate in similar proportions. Censuses were carried out from sunrise to sunset, at 2-hour intervals. During the censuses we noted the sector where the slug was found (four possibilities: wet aggregated, wet solitary, dry aggregated and dry solitary) and the plant species where the slug was seen, specifying the behaviour of the slug (i.e. movements and eating). Three plant species were available to the slug: *P. vallisneriifolia; Potentilla petrophylla* (Rosaceae), growing in the rocky wall intermingled with *P. vallisneriifolia*, and *Brachypodium sylvaticum* (Graminae), growing on the ground adjacent to the rocky wall, also intermingled with *P. vallisneriifolia*. Observations of slugs on basal leaves were recorded separately from those on distal leaves of *P. vallisneriifolia*. It was difficult to make detailed observations of the behaviour of the slugs during the night, and therefore at night we noted only whether the slugs were active or not.

SLUG MOVEMENTS ON LEAVES

To test whether the mucilage produced by the stalked glands hampers the movement of the slug on the leaves, we carried out a field experiment placing 15 slugs on the upper surface of 15 functional distal leaves. Once the slug was in place, we timed its movement over a standard distance (10 cm). Then, we timed the slug moving the same distance on the same leaf, but we removed the mucilage droplets manually by rubbing the index finger over the adhesive surface of the leaf. We used two replicates for each treatment (with and without mucilage), using average data per slug to avoid pseudoreplication. For analysing these data, we have used the nonparametric Wilcoxon pair-matched test (Martin & Bateson 1986).

HERBIVORE RATE

The herbivory rate by slugs on *P. vallisneriifolia* was determined in April 1992 by labelling 50 plants growing aggregated (25 in the wet sector and 25 in the dry one, both sectors belonging to the same wall where censuses and experiments were carried out). The herbivore rate was quantified as the percentage of leaf eaten in comparison with the total biomass of the labelled plant. Sampling was carried out in May, when the plants had only basal leaves; in July, when basal leaves

senesce, and only distal leaves remain functional; and November, after the senescence of the distal leaves, when the winter bud is already formed. We have occasionally observed a Tipulidae larvae feeding on the basal leaves of *P. vallisneriifolia*. This larva lives in the accumulations of organic matter surrounding the plants in the wet sites. We have used the mucus trail on the basal leaves to differentiate slug herbivory from Tipulidae herbivory.

SLUG ROBBING RATE

The kleptoparasitic behaviour of *P. hilbrandi* robbing prey from *P. vallisneriifolia* leaves was studied in the field by detailed observations of the slugs searching for food near the plants. The first observations and experimental determinations of the slug robbing rate in the field were carried out in June 1990. We selected 10 plants per sector (40 plants as a whole from the four sectors), and labelled in each one basal and one distal leaf. Then, we placed three specimens of *Drosophila melanogaster* (wild race) on each leaf (basal and distal), for a total of six flies per plant (240 flies over all). This fly species does not appear under natural conditions on the leaves of *P. vallisneriifolia*, so it cannot be confused with natural prey. After 48 hours, we noted the number of flies remaining on the leaves.

In 1991 and 1992, robbing rate was quantified following the same procedure previously described. To analyse the robbing probability in relation to fly position on both basal and distal leaves, we placed the three flies on a proximal, central, and distal position, respectively. Once the flies were placed, we conducted periodic sampling at 12-hour intervals using the following sampling design: 2 days with 12-hour periods of counting and 5 additional days, for a total of 7 days. On each sampling ocassion, we noted the number of flies remaining on the leaf, and their positions. We also verified the presence of mucus trails on the site where the flies were placed. In 1991 we studied the robbing rate twice in June and once at the beginning of July. In 1992 we analysed the phenological variability in robbing rate, repeating the experiment four times: May, when plants have only basal leaves; June, when plants have both functional basal and distal leaves; July and August, when only the distal leaves are functional, since basal leaves undergo senesce.

Statistical analysis of the factors determining the robbing rate was performed using a two-way ANOVA, considering two factors: the sector where the plant grows, with four levels (wet solitary, wet aggregated, dry solitary and dry aggregated), and leaf, with two levels (basal and distal). We have used June data for statistical analysis, when plants bear both basal and distal functional leaves. The ANOVAs were carried out using a type III sum of squares, due to the unbalanced nature of the data (Dowdy & Wearden 1985). Data were arcsin-transformed, to improve normality. In addition, we compared the cumulative curves of fly loss by slug robbery either between distal and basal leaf types or between microhabitats, using Wilcoxon tests, due to the censored nature of the data (Pyke & Thompson 1986).

LABORATORY EXPERIMENTS ON THE SLUG'S TROPHIC PREFERENCE

In June 1992, we collected nine slugs in a *P. vallisneriifolia* population of Sierra de Cazorla near the place where field observations and experiments were carried out. Freshly collected specimens of *D. hilbrandi* were stored in individual glass (Petri dishes) covered trays lined with damp filter paper maintained at 10 °C in the laboratory. The relative humidity was kept high with moist cotton wool. Slugs were classified according to three size categories: large (3–4 cm), medium (2–3 cm) and small (< 1·5 cm body length).

The slugs were starved for 38 hours before starting the laboratory trials. To simulate slug field foraging activity, the preference tests were performed from 21·00 h until 09·00 h (12 h, see below). Once the trials had finished, the slugs were returned to their place of origin. We cultivated *P. vallisneriifolia* plants and *Drosophila melanogaster* flies to carry out the following laboratory experiments.

1. *Experiment 1. Slug trophic preferences: herbivory vs. carnivory*. We placed two fresh, functional distal leaves of *P. vallisneriifolia*, one with 10 fresh fly carcasses (*Drosophila melanogaster*, wild race) and the other leaf without flies in each Petri dish. Both functional leaves came from the same plant. This test was replicated seven times per slug. One slug died after the conclusion of this first trial, and therefore the slug sample size for the following trials was 8.

2. *Experiment 2. Effect of fly carcass size*. We placed 10 fresh carcasses on a distal leaf: five small (wild race, body length = 2·2 mm) and five larger (virilis race, body length = 3·5 mm). This test was replicated five times per slug.

3. *Experiment 3. Effect of fly carcass age*. We placed 10 carcasses (wild race) on a distal leaf: five fresh and five 6 days old, taken from the leaves of *P. vallisneriifolia* cultivated in the lab. This test was replicated five times per slug.

4. *Experiment 4. Effect of leaf type*. We placed 10 fresh carcasses: five on basal and five on distal functional leaves. Both kinds of leaves were placed in the bottom of the Petri dish, being equally accessible to the slug. This test was replicated five times per each slug.

5. *Experiment 5. Effect of fly position*. We placed 10 fresh carcasses (wild race): five on a distal leaf and five on the bottom of the Petri disk. This test was replicated five times per slug.

6. *Experiment 6. Interaction with mites*. We placed two distal leaves per Petri dish: one leaf with five fresh fly carcasses (wild race), and five mites, and other with five fresh fly carcasses (wild race), but without mites.

At the end of the test we verified whether mites remained on the leaf where they were placed. This test was replicated five times per slug.

The results of the preference test were statistically analysed by means of nonparametric test (Martin & Bateson 1986). Prior to statistical analysis, the ingestion rate was averaged for each slug, to avoid pseudoreplication.

Results

SLUG ABUNDANCE AND FORAGING BEHAVIOUR

Slugs remain under stones and in wet crevices during the winter, being active only sporadically. In spring slugs start to be active, moving over the rocky substrates where *P. vallisneriifolia* grows. Slug abundance on the wall during spring was $1{\cdot}4 \pm 0{\cdot}53$ slugs per $40\,m^2$ (mean $\pm$ SE, range = 0–8 slugs per census). During the dry Mediterranean summer (June–August) the spring density doubled (3 slugs per $40\,m^2 \pm 0{\cdot}58$, range 0–12 slugs per census). *D. hilbrandi* begins its activity in the afternoon, remaining active all night until mid-morning, after which it becomes inactive (Fig. 1).

In 45·2% of censuses, slugs were observed on rocky substrates, and 54·8% on *P. vallisneriifolia* plants, where slugs were seen 60% of the time on basal leaves, and 40% on distal leaves. Slugs were not seen on neighbouring plant species, such as *Potentilla petrophylla* and *Brachypodium sylvaticum*. Slug activity was associated with the kind of substrate ($\chi^2 = 41{\cdot}7$, d.f. = $P = 0{\cdot}001$); that is, all slugs observed on rocky substrate were moving, whereas on leaves, slugs were frequently eating prey adhering to the leaves (on basal leaves the slugs were eating 49% of the time, and on distal leaves 64%).

Slugs on *P. vallisneriifolia* leaves fed on prey directly, without removing it. Slug klepto-activities were easily observed when prey were large, and overhung the leaf border. Slugs fed on these large prey beginning at the head, coiling round them in a snake-like way. A slug can devote up to 90 min to eating large prey, such as Tipulidae. Nevertheless, most *P. vallisneriifolia* prey are small-sized insects, such as Nematocera (body length < 3 mm, Zamora 1995), and these small prey remain immersed in the glandular surface of the leaves immediately after being trapped. For this reason, it was difficult to observe the slug eating this kind of small prey; the slug eats them as it passes over, often without pausing in its slow movement, the remaining legs and wings of the eaten prey being the damning evidence of the robbery. Mucus trails on the leaf surface and prey remains were consistently evident, and for this reason, we were able to differentiate the prey robbed by the slugs from the prey robbed by other kleptoparasites. We have seen spiders robbing prey very sporadically in the same microhabitats.

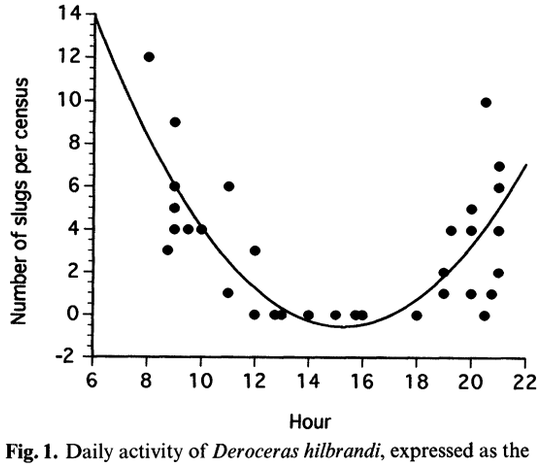

Fig. 1. Daily activity of *Deroceras hilbrandi*, expressed as the number of slugs per census depending on the hour of the day. Regression equation is y = Intercept $- 5{\cdot}05x + 0{\cdot}17x^2$ (both $P < 0{\cdot}0001$).

SLUG MOVEMENTS ON LEAVES

Mucilage droplets hamper slug movements on glandular, functional leaves, in comparison with hand-manipulated leaves without mucilage ($H = 7{\cdot}0$, $P = 0{\cdot}0001$; Kruskal–Wallis test). Slug velocity (mean $\pm$ SE) on distal leaves with intact mucilage droplets was $0{\cdot}52 \pm 0{\cdot}06\,mm\,s^{-1}$, whereas on distal leaves without mucilage it was $0{\cdot}90 \pm 0{\cdot}42\,mm\,s^{-1}$.

FIELD HERBIVORY RATE

Overall, slug herbivory was minor. During spring, plants growing in dry sectors suffered less herbivory (only one plant, with 5% of its biomass consumed, with respect to 25 labelled plants) than plants growing in wet sectors (three plants, with the 18% of the biomass eaten). During the summer, no leaves were consumed in both sectors. During winter, slugs consumed four winter buds in each sector (mucus trails were also evident on buds); 15% and 20% of the biomass were consumed in both sectors, respectively.

ROBBING RATE

The feeding experiments over 3 years in the field indicated that slugs preferentially robbed the flies placed on basal leaves. For example, in June 1990, the percentage of flies eaten by the slugs in 48 hours, with respect to the initial number of flies placed, was 27 on basal leaves and 1·9 on distal leaves. In June 1991, the percentage of flies eaten by the slugs during a week was 91·7% (basal leaves), and 21·3% (distal leaves). In June 1992, the percentage of flies eated by the slugs during a week was 75·8% (basal leaves), and 15·8% (distal leaves). For this reason, the cumulative fly losses from basal and distal leaves differed statistically

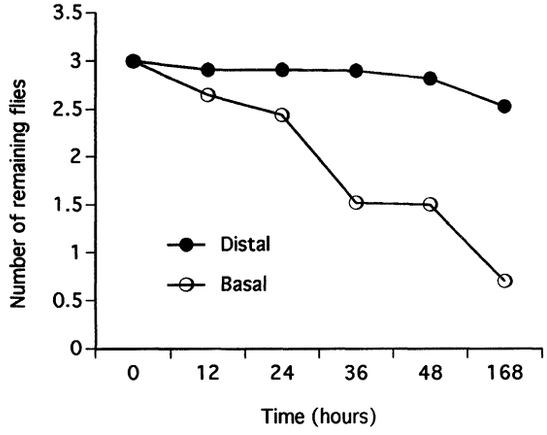

Fig. 2. Cumulative fly loss by slug robbery on basal and distal leaves in 1991.

($P < 0{\cdot}05$ each year, Wilcoxon rank test; see Fig. 2). On the other hand, the sector where the plants grew did not affect the robbing rate (Table 1).

Robbing probability on basal leaves was independent of the fly position on the leaf ($\chi^2 = 3{\cdot}9$, $P = 0{\cdot}14$), given that the slugs robbed 80%, 65% and 82·5% of the flies placed on the base, centre and tip of the leaf per week, respectively. In contrast, robbing probability depended on fly position on the distal leaves ($\chi^2 = 11{\cdot}6$, $P = 0{\cdot}003$), given that the slug robbed 32·5%, 12·5% and 5% of the flies placed on the base, centre and tip of the distal leaves per week, respectively (basal & distal robbing rate dates corresponding to 1991 & 1992 have been averaged because there were no statistical differences between the two years).

With respect to the seasonal variation in robbing rate, the slug hardly robbed during spring, when *P. vallisneriifolia* bears only basal leaves (in the wet sector 2·5% of the flies initially placed were robbed per week; in the dry sector, no fly was robbed during the same period). The slug's kleptoparasitic behaviour become progressively more evident during the summer. For example, the percentage of flies robbed at the end of June was 75·8 and 15·8 on basal and distal leaves per week, respectively. The percentage of flies robbed on distal leaves at the end of July and at the middle of August was 16·7, and 31·7, respectively (in these two last sampling periods, there were no functional basal leaves).

Table 1. Field robbing rate depending on wall sector (wet solitary, wet aggregate, dry solitary, dry aggregate) and leaf type (basal and distal)

Source of variation	df	SS	MS	*F*	*P*
1990					
Sector (A)	3	0·268	0·089	2·04	0·116
Leaf (B)	1	1·233	1·233	28·21	0·001
A*B	3	0·200	0·070	1·56	0·208
Error	64	2·788	0·036		
1991					
Sector (A)	3	0·228	0·076	1·23	0·305
Leaf (B)	1	12·272	12·272	198·81	0·001
A*B	3	0·117	0·039	0·63	0·598
Error	72	4·444	0·062		
1992					
Sector (A)	3	5·050	1·683	2·20	0·096
Leaf (B)	1	6·800	64·80	84·52	0·001
A*B	3	3·700	1·233	1·61	0·195
Error	72	55·20	0·767		

LABORATORY TEST OF TROPHIC PREFERENCES

Experiment 1. Slug trophic habit. Slugs fed almost exclusively on animal remains (2·25 ± 0·28 flies per slug and 12 h, range = 0–9 flies per slug and trial); only once did a slug eat a small portion of a *P. vallisneriifolia* leaf (5% of biomass). There was no statistical difference in the slug ingestion rate with respect to the trial ($H = 5{\cdot}0$, $P = 0{\cdot}60$, Kruskal–Wallis test). Nevertheless, there were statistical differences between slugs with respect to ingestion rate ($H = 23{\cdot}0$, $P = 0{\cdot}004$, Kruskal–Wallis test), and these differences were not due to slug size differences ($H = 3{\cdot}0$, $P = 0{\cdot}21$, Kruskal–Wallis test).

Experiment 2. Effect of fly carcass size. Fly size did not affect the slug's choice of carcass ($Z = -0{\cdot}26$, $P = 0{\cdot}79$, $n = 16$, Wilcoxon rank test). In fact, slugs ate 1·52 ± 0·34 small flies (mean ± SE) per slug and 12 h, and 1·65 ± 0·30 large flies per 12 h.

Experiment 3. Effect of fly carcass age. Slugs ate 2·15 ± 0·37 fresh carcasses and 1·42 ± 0·37 old ones per slug and 12 h, although this difference did not reach the threshold of statistical significance ($Z = -1{\cdot}16$, $P = 0{\cdot}24$, $n = 16$, Wilcoxon rank test).

Experiment 4. Effect of leaf type. The type of leaf (basal vs. distal) where the flies were placed did not affect slug robbing rate ($Z = -0{\cdot}88$, $P = 0{\cdot}38$, $n = 16$, Wilcoxon rank test), the number of eaten flies being 2·00 ± 0·29, and 1·52 ± 0·31 per slug and 12 h on basal and distal leaves, respectively.

Experiment 5. Effect of fly position. Slugs ate 1·57 ± 0·41 flies per slug and 12 h placed on the bottom of the Petri-dish, and 1·30 ± 0·26 flies placed on *Pinguicula* leaves. Thus, slugs feed on flies irrespective of the substrate where the carcasses were placed ($Z = -0{\cdot}28$, $P = 0{\cdot}77$, $n = 16$, Wilcoxon rank test).

Experiment 6. Interactions with mites. Mites did not affect slug foraging behaviour ($Z = -1{\cdot}61$, $P = 0{\cdot}10$, $n = 16$, Wilcoxon rank test), given that slugs ate a similar number of flies irrespective of the presence of mites (1·17 ± 0·17 flies with mites, and 1·15 ± 0·18 without mites). Slug ate no mites during the experiments.

Discussion

Field observations and lab experiments clearly show that *Deroceras hilbrandi* feeds on animal carcasses

trapped by *P. vallisneriifolia*, being more carnivorous than herbivorous and becoming a true kleptoparasite of this carnivorous plant species. In laboratory experiments the slug shows little selectivity regarding prey size and can feed upon the entire range of prey sizes found on the *P. vallisneriifolia* leaves, ignoring the mites, probably because of their small size (less than 0·4 mm) and/or because the mites, being mobile, are able to escape from the slug. The slug does not appear to select prey according to the degree of carcass degradation, although there is a tendency to consume the most recently dead prey. In fact, we have observed slugs in the field eating recently captured prey which were still alive.

Slug abundance in populations of *P. vallisneriifolia* appears to be low, although the surface-searching method used for assessing the slug population may underestimate slug numbers (Ferguson & Hanks 1990). Nevertheless, the relatively few slugs found in *P. vallisneriifolia* populations can have a high robbing rate per individual (up to 9 flies per 12 h), thus representing a potential negative effect on the plant. By stealing recently captured prey, instead of the dry carcasses, the slug is more injurious to the plant; that is, in losing fresh prey, the plant is deprived of nutrients at the beginning of its digestive processes, whereas the loss of dry carcasses occurs at the end of digestion when the nutrients have already been assimilated by the plant (Heslop-Harrison & Knox 1971). Therefore, there is probably a gradient from negative, when the slugs rob fresh carcasses (see also Zamora 1990), to neutral, when the slugs rob old ones, in the result of the interaction for the plant; this situation is invariably positive for the slug, although fresh prey would represent the best reward.

Slug feeding activities are concentrated in *P. vallisneriifolia* patches, probably because the wet microsites where the *P. vallisneriifolia* grows, and even the glandular leaves, are substrates with a high moisture content, a critical factor in regulating slug activity (Young & Port 1991). Furthermore, kleptoparasitic behaviour is risk-free because slugs are able to pass over the leaves without being trapped. The frequent robbery of the flies placed on the short, basal leaves is independent of fly position on the leaf, indicating that slugs can, without difficulty, reach every part of the basal leaves lying close to the wall. However, slugs selectively robbed flies placed on the proximal portion of the distal leaves, maintaining the same robbery behaviour in both years. The basal leaves and the proximal part of the distal leaves are the most accessible for any small animal crawling on the rocky wall, and this opportunistic behaviour is determined by the hanging-leaf architecture of the distal leaves as well as by the mucilage. In fact, in the laboratory, when we placed the same type of prey on functional basal and distal leaves, and when we equalized the accessibility of the two leaves by placing them on the soil in a Petri dish, the slugs consumed prey equally from the two types of leaves. Furthermore, field experiments demonstrated that mucilage secretion hampers the movements of the slug on the distal leaves, the velocity of the slug movement being reduced by half on leaves with mucilage in comparison with leaves without mucilage. As a result, the slug avoided crawling towards the tip of the distal leaves because of the greater distance to travel over the mucilage layer, despite the fact that the distal tip is the most succesful part for prey capture (Zamora 1995).

Slug kleptoparasitic behaviour appear to be an attempt to increase the quality of food consumed, preferring animal to plant tissue when both are equally available. This opportunistic behaviour allows *D. hilbrandi* to use a great amount of animal food, rich in essential nutrients and energy, which could not be obtained in any other way, since the slug cannot capture flying insects. In fact, food quality has enormous impact on growth, maturation rates, reproduction and longevity for some *Deroceras* species (Ramsell & Paul 1990; Rollo & Shibata 1991). Also, Pakarinen *et al.* (1990) found that several species belonging to the genus *Deroceras* selected plant food according to the N and P content. Furthermore, several studies even suggest that certain *Deroceras* species can change their trophic habit, to obtain an animal supplement for a herbivorous diet. For example, Airey (1987) found *Deroceras reticulatum* becoming cannibalistic, even preying on other slug species, and Mienis (1989) reported *Deroceras laeve* feeding on Florida wax scales. We believe that not only the possibility of obtaining a more profitable high-quality food item, but also the greater abundance of insects adhering to the leaves of *P. vallisneriifolia* throughout the summer have promoted the development of carnivory from herbivory in *D. hilbrandi* (see Camberfort 1991 for a similar case with dung beetles). In fact, during the winter, when there are no trapped insects available because *P. vallisnerifolia* has no functional leaves, *D. hilbrandi* sometimes feed on *P. vallisneriifolia* winter buds; buds represent a reservoir for *Pinguicula* where nutrients have a greater concentration than in fully developed leaves (Karlsson *et al.* 1991). During the spring, when there are few trapped insects on the basal leaves and few *D. hilbrandi* active, the slug slowly begins its kleptoparasitic behaviour, sporadically feeding both on prey and basal leaves. Slugs become exclusively carnivorous during the summer, just when plants reach maximum biomass and concomitantly have the greatest number of prey adhering to the leaves (Zamora 1995). In addition, *D. hilbrandi* was never seen feeding on neighbour plants of *P. vallisneriifolia*, such as *Potentilla* and *Brachypodium*. It is during the summer that the slug becomes most abundant in the habitat where *P. vallisneriifolia* grows, and shows an strong dependence on the numerous prey captured by *P. vallisneriifolia*.

The ecophysiological dependence of both *P. vallisneriifolia* and *D. hilbrandi* on the same wet habitats,

which are very scarce during the dry Mediterranean summer, promote the possibility of an interaction developing between these two species. By its opportunistic feeding behaviour, *D. hilbrandi* takes advantage of the prey trapped by *P. vallisneriifolia*, an abundant and predictable high-quality resource. The result is a kleptoparasitic carnivorous slug. In conclusion, hunger for essential nutrients appear to be the driving force behind this carnivorous plant–slug interaction. This result supports a recent hyphothesis (White 1993) on the role of nutrient limitation, such as nitrogen, as a major factor determining the ecology of organisms.

Acknowledgements

We thank the Agencia de Medio Ambiente for permission to work in the Parque Natural de Cazorla, Segura y Las Villas and for providing invaluable housing facilities, Carlos Herrera and Pedro Jordano for their encouragement from the beginning of this study, Isabel Fernández for helping us with the laboratory experiments, and María Rosario Alonso and Miguel Ibáñez for carrying out the slug determination. Three anonymous referees provided constructive suggestions. We also thank José A. Hódar for technical assistance. The English version of the text was looked over by David Nesbitt. This work was supported by a DGICYT grant PB90–0852. J.M.G. was supported by a PFPI grant from the Ministerio de Educación y Ciencia de España.

References

Airey, W.J. (1987) Laboratory studies on damage to potato tubers by slugs. *Journal of Molluscan Studies*, **53**, 97–104.

Airey, W.J. (1988) The influence of an alternative food on tuber damage by slugs. *Journal of Molluscan Studies*, **54**, 131–138.

Bazely, D.R. (1989) Carnivorous herbivores: mineral nutrition and the balanced diet. *Trends in Ecology and Evolution*, **4**, 155–156.

Begon, M., Harper, J.L. & Towsend, C.R. (1990) *Ecology. Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford.

Bernays, E.A. & Chapman, R.F. (1994) *Host-Plant Selection by Phytophagous Insects*. Chapman & Hall, New York.

Bourne, N.B., G.W. Jones & Bowen, I.D. (1990) Feeding behaviour and mortality of the slug, *Deroceras reticulatum* in relation to control with molluscicidal baits containing various combinations of metaldehyde with methiocarb. *Annals of Applied Biology*, **117**, 455–468.

Cambefort, Y. (1991) From saprophagy to coprophagy. *Dung Beetle Ecology* (eds I. Hanski & Y. Cambefort), pp. 22–35. Princeton University of Press, Princeton, NJ.

Castillejo, J. (1990) Babosas de la Península Ibérica. II. Los agriolimácidos. Catálogo crítico y mapas de distribución (Gastropoda, Pulmonata, Agriolimacidae). *Iberis*, **9**, 347–358.

Crawley, M. (1983) *Herbivory*. Blackwell Scientific Publications, Oxford.

Dowdy, S. & Wearden, S. (1985) *Statistics for Research*. John Wiley & Sons, New York, NY.

Ferguson, C.M. & Hanks, C.B. (1990) Evaluation of defined-area traping for estimating the density of the field slug *Deroceras reticulatum* (Müller). *Annals of Applied Biology*, **117**, 451–454.

Heslop-Harrison, Y. & Knox, R.B. (1971) A cytochemical study of the leaf-gland enzymes of insectivorous plants of the genus *Pinguicula*. *Planta*, **96**, 183–211.

Karlsson, P.S., Nordell, K.O., Carlsson, B.A. & Svensson, B.M. (1991) The effects of soil nutrients status on prey utilization in four carnivorous plants. *Oecologia*, **86**, 1–7.

Kemp, N.J. & Newell, P.F. (1987) Slug damage to the flag leaves of winter wheat. *Journal of Molluscan Studies*, **53**, 109–111.

Martin, P. & Bateson, P. (1986) *Measuring Behaviour: An Introductory Guide*. Cambridge University Press, Cambridge, UK.

Mienis, H.K. (1989) The marsh slug *Deroceras laeve* (Mollusca, Gastropoda) feeding on the Florida wax scales *Ceroplastes floridens* (Insecta, Rhynchota) in Israel. *Zeitschrift für Angewandte Zoologie*, **76**, 377–378.

Newton, A. (1985) *Finches*. Blackwell Scientific Publications, Oxford, UK.

Pakarinen, E., Niemelä, P. & Tuomi, J. (1990) Effect of fertilization, seaweed extracts and leaf-damage on palatability of lettuce to *Deroceras* slugs. *Acta Oecologica*, **11**, 113–119.

Pyke, D.A. & Thompson, J.N. (1986) Statistical analysis of survival and removal rate experiments. *Ecology*, **67**, 240–245.

Ramsell, J. & Paul, N.D. (1990) Preferential grazing by molluscs of plant infected by rust fungi. *Oikos*, **58**, 145–150.

Rollo., C.D. & Shibata, D.M. (1991) Resilience, robustness, and plasticity in a terrestrial slug, with particular reference to food quality. *Canadian Journal of Zoology*, **69**, 978–987.

Stephen, D.W. & Krebs, J.R. (1986) *Foraging Behaviour*. Princeton University of Press, Princeton, NJ.

Thum, M. (1989) The significance of opportunistic predators for the sympatric carnivorous plant species, *Drosera intermedia* and *Drosera rotundifolia*. *Oecologia*, **70**, 601–605.

White, T.C.R. (1993) *The Inadequate Environment. Nitrogen and the Abundance of Animals*. Springer Verlag, Berlin.

Young, A.G. & Port, G.R. (1991) The influence of soil moisture content on the activity of *Deroceras reticulatum* (Müller). *Journal of Molluscan Studies*, **57**, 138–140.

Zamora, R. (1990) Observational and experimental study of a carnivorous plant–ant kleptobiotic interaction. *Oikos*, **59**, 368–372.

Zamora, R. (1995) The trapping success of a carnivorous plant (*Pinguicula vallisneriifolia*): the cumulative effects of availability, attraction, retention and robbery of prey. *Oikos*, **73**, 309–322.

Received 29 November 1994; revision received 19 April 1995