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The trapping success of a carnivorous plant, Pinguicula vallisneriifolia: the cumulative effects of availability, attraction, retention and robbery of prey

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Factors determining the trapping success of *Pinguicula vallisneriifolia*, a carnivorous plant of southern Spain which grows in limestone rock walls are examined. Several ecological aspects are considered jointly, such as the abiotic environment in relation to spatio-temporal prey abundance, behaviour of prey and kleptoparasites, and plant traits that directly determine trapping efficiency, such as the amount and retention capacity of the mucilage under contrasting ecological conditions. Observations are combined with field experiments in four *P. vallisneriifolia* microhabitats differing in radiation and substrate wetness.

The abundance of flying insects and the mucilage-retention capacity mainly determined differential prey captures between habitats, while kleptoparasitism had a similar quantitative effect in all habitats. Irradiance intensity and insect availability correlated negatively, i.e. in sunny, dry places, flying insects were scarce, whereas in shady, wet places, insects were abundant. Plant mucilage secretion also depended on light availability, and the adhesiveness of the droplets correlated negatively with insect availability (that is, more mucilage adhesiveness in the sunny and wall habitats, with fewer insects available, and vice versa in the shady habitat). As a result, plants growing at the extremes of the abiotic gradient (sunniest and shadiest habitats) trapped less animal biomass. This fact poses a schizophrenic problem for *P. vallisneriifolia*, which, as a green plant, needs both water and light for photosynthesis, and, as a carnivorous one, animal prey for nutrients.

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The capture success of a carnivorous plant, like sit-and-wait animal predators, depends mainly on the ecological and behavioural characteristics of its mobile prey. Firstly, capture success depends both on the quantity and quality of invertebrates available in the microhabitats where the plants grow. Secondly, potential prey may contact the leaves at random, or be actively attracted by visual and/or olfactory mechanisms (Joel et al. 1985, Juniper et al. 1989). In the latter case the trapped prey would be a non-random sampling of the insects available. Thirdly, because of the sessile life style, capture success may be determined by the density of other carnivorous plants growing in the same patch, and thus facilitation and/or competition for prey may occur (Gibson 1991a). Finally, the time span required for prey digestion invites kleptoparasitic and commensal interactions with opportunistic animals (Zamora 1990a). In this way, the trapping success of a carnivorous plant is the result of a complex process where the abundance, spatio-temporal distribution and behaviour of the prey and kleptoparasites strongly determine the quantity of animal biomass that can be trapped and ultimately digested by the plant.

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Nevertheless, trapping success in carnivorous plants is not exclusively a matter of animal ecology (i.e. abundance and behaviour of potential prey and kleptoparasite pressure), but also depends on the performance of the trapping mechanisms (Givnish 1988). In the *Pinguicula* genus, the capture mechanism is an adhesive trap (sensu Juniper et al. 1989). The prey are captured on adhesive mucilage secreted by stalked glands situated on the upper surface of the leaf (Heslop-Harrison and Knox 1971). Despite the importance of trapping performance, very few studies consider the adhesive capacity of the trapping mechanisms to be a factor determining trapping success (but see Zamora 1990a, Gibson 1991b), and there is no information available on the relationship between the retention capacity of the leaf and the ecological conditions where the plant grows (Givnish 1988).

No study has so far analysed the trapping success of a carnivorous plant, considering all the ecological, behavioural and physiological factors above mentioned. At best, some studies deal with specific questions, such as prey analysis (e.g. Watson et al. 1982, Thum 1986, Zamora 1990b, Cresswell 1991, Antor and García 1994), capture rate (Karlsson et al. 1987, 1994, Cresswell 1991), capture constraints (Zamora 1990b, Gibson 1991b), density-dependence of capture rate (Cresswell 1991, Gibson 1991b) and kleptoparasitic interactions (Zamora 1990a). Furthermore, studies analysing the significance of carnivory for plant growth and reproduction under natural conditions have quantified only the final stage of trapping (i.e. the number of prey and/or animal biomass trapped; Thum 1988a, b, De Ridder and Dhont 1992), without considering the multifactorial nature of the prey-capture process. To understand the ecological factors determining trapping success in different habitats, and the evolutionary explanations for the pathway towards carnivory, it is necessary to analyse the importance of the previously mentioned factors acting in succession, as well as their possible interaction.

In this study, I analyse the entire sequence of cumulative effects, from insect availability to the trapped and finally digested prey on the leaves. I consider a combination of ecological aspects, such as the abiotic environment in relation to prey abundance, prey and kleptoparasite behaviour, and physiological plant traits that directly determine trapping efficiency, such as the amount and retention capacity of the mucilage under contrasting ecological conditions.

The analysis of the cumulative steps determining capture success (i.e., availability, attraction, retention and robbery of prey), which is the main goal of this article, can be split into consecutive objectives: 1) To analyse the composition, size, abundance and spatio-temporal distribution of actual and potential prey in relation to abiotic factors, and to evaluate the fit between potential and actual prey and capture rate in different habitats. 2) To analyse the possible facilitation of and/or competition for prey due to plant aggregation. 3) To identify possible attraction mechanisms. 4) To quantify the mucilage secretion of the leaves, and to evaluate the mucilage retention capacity. 5) To quantify experimentally the rate of kleptoparasitism. 6) To integrate all the foregoing factors to analyse trapping success in different ecological scenarios.

These objectives have been tested by means of simple, comprehensive field experiments, complemented with observations and censuses.

Plant natural history

Pinguicula vallisneriifolia is an endemic plant of southeastern Spain, typically found on wet rock walls and cliffs of the limestone mountains in the Sierra de Cazorla y Segura (Jaen province). As opposed to the characteristic growth pattern of the genus *Pinguicula* (i.e. a compact rosette of leaves lying flat on the ground; Juniper et al. 1989), this species presents two leaf types during its vegetative growth period. The first 5–7 leaves, developing in spring (April–May, "spring leaves") form a rosette which lies flat against the wall; later, the leaves change in morphology and spatial distribution, becoming larger, much longer than wide, and overhanging the wall perpendicular to the basal rosette. During the June–August period, each plant develops about 4 to 10 distal leaves ("summer leaves"), coinciding with the senescence of the basal leaves. Distal leaves are 10 to 30 cm in length, and usually curve downwards. Distal leaves senesce at the beginning of September with the formation of the winter bud. Both basal and distal leaves are glandular, and secrete mucilage. *P. vallisneriifolia* reproduces sexually (May–June) as well as asexually, by means of stolons (July–August), and axillary buds (September).

Methods

The field work was carried out in a 2000-ha reserve in the Sierra de Cazorla y Segura. The study site, Covacho del Aire (1250 m a.s.l.), at the headwaters of a small spring surrounded by a limestone wall (ca 50 m high and 150 m long), which is part of several adjacent vertical cliffs in an orographically complex area. The Covacho del Aire study area is situated in the centre of the geographical distribution area of *P. vallisneriifolia*, and harbours one of the largest populations of this endemic plant species.

Four main habitat types were differentiated on the basis of solar radiation levels; these habitats define the distribution gradient for *P. vallisneriifolia*.

1) Sunny habitat, where plants grow on an east-facing section of wall; these plants receive ca 6 h of direct afternoon and evening sunlight (from 14.30 to 20.30). Consequently, the rock substrate is dry, and represents the distribution limit for *P. vallisneriifolia*.

2) Shaded wall habitat, situated in the central part of

the north-facing wall, where plants receive no direct sunlight, and represents the typical habitat of *P. vallisneriifolia*. The spatial distribution of *P. vallisneriifolia* plants on the shaded wall is patchy, with asexual reproduction leading to frequent dense aggregations, where neighbouring plants could interfere with prey capture, whereas isolated individuals appear in recently colonized areas. This heterogeneous distribution allows a more detailed analysis regarding the role of plant aggregation and substrate wetness as factors influencing capture success. Thus, in the sampling of the shaded wall habitat, I have differentiated: 1) aggregation level (solitary vs crowded plants, solitary meaning no other *Pinguicula* within a 1-m radius), and 2) wetness level of the wall surrounding the plant within a 1-m radius (the dry sector, where plants are rooted in small wet crevices in an otherwise dry wall versus the wet sector, where the water soaks the entire rocky surface). Sampling followed a two factor design: aggregation level and substrate wetness. To quantify plant density in the wet and dry sectors with plant aggregations, I counted the number of individual plants (excluding seedlings and stolons) within a 800-cm^2 quadrat randomly placed 20 times per sector. I also quantified the level of substrate wetness around the plants estimating the percentage of wet and/or dry rock surface within the 800-cm^2 quadrat.

3) Shaded ground habitat. Plants grow on the travertine deposits on the ground at the base of the shaded wall habitat, free from competition. Plants receive no direct sunlight, and the travertine substrate was wet from continuously flowing water.

4) Deep shade habitat, where the plants grow on a slope within a small cave situated at the bottom of the north-facing wall. The ceiling of the cave strongly limits radiation, providing a shadier environment than the others and representing the distribution limit of *P. vallisneriifolia* in shady places. The rock substrates of the shady habitat were rather wet.

The four habitats are located at the same altitude; the Shaded wall habitat (hereafter wall), Shaded ground (hereafter ground) and Deep shade (hereafter shady) habitats are ca 10 m from each other, and these are ca 50 m from the Sunny habitat (hereafter sunny).

Abiotic measurements

Total radiation was measured using a Li-Cor LI-200 sz Pyranometer sensor connected to a Li-1000 data logger (Li-Cor Inc., Lincoln, Nebraska); air temperature and air humidity were taken using a Rotronic YA-100 (Rotronic AG, Zürich) temperature and humidity combined sensor. Samples were collected in the four habitats, consistently using the same recording point (i.e. the centre of the patch in each habitat). Sensors were placed near the tip of the distal leaves (i.e. 15 cm from the wall or the ground). I collected samples from the abiotic environment at the beginning, middle, and end of the prey-capture study (end of June, end of July and middle of August, respectively). Abiotic data were registered at 1-h intervals from sunrise to sunset in the four habitats. The pyranometer sensor surface was held horizontally, thus irradiance measurements refer to the horizontal plane. Night temperature and humidity values were also recorded.

Prey characteristics and capture rate

A preliminary sampling in 1991 indicated that summer is the main capture period for *P. vallisneriifolia,* as spring basal leaves captured few prey. For this reason, distal leaves were collected in each habitat from the end of June, when the first distal leaves are fully functional, and the basal leaves beginning to senesce, to the middle of August of 1992, before distal leaves senesce. Sampling was carried out for 6 weeks, collecting 10 leaves per sampling and habitat, for a total of 60 leaves (from 60 plants) from the sunny, ground and shady habitats. A total of 120 leaves (120 plants) were collected from the wall habitat, to evaluate the prey-capture importance of aggregation and wetness (30 leaves from aggregated wet plants, 30 from aggregated dry plants, 30 from solitary wet plants, and 30 from solitary dry plants).

In each of six sampling sessions, functional, recently developed distal leaves of different reproductive plants were labelled in each habitat, and all prey items removed from the leaves. The time frame was the following: the leaves were labelled at sunrise, and counted in 12-h periods (09.00 to 21.00, diurnal period, and 21.00 to 09.00, nocturnal period), for two d, totalling two diurnal and two nocturnal periods of prey samplings. At the end of each 12-h period, all prey attached to the leaves were identified and measured in the field using a hand microscope (10×) equipped with a micrometer. Prey size was defined as body length from the tip of the head to the end of the abdomen, excluding the appendages. Afterwards, all prey were removed from the leaves to begin a new 12-h capture period. Ten prey taxa could be identified (Table 2) under field conditions.

After the diurnal/nocturnal sampling, the labelled leaves were allowed to trap prey for 5 d without removing them. Thus, the overall sampling design was: two d of 12-h sampling periods divided between night and day, and a sampling period of 5 additional d, totalling 7 d of sampling. This time period is shorter than the total time that distal leaves remain functional, being able to capture insects for 2 to 3 weeks. At the end of this 7-d period, the labelled leaves were collected for later prey identification and measurement in the laboratory by means of a binocular microscope equipped with a micrometer. In order to evaluate the possible dependence of capture rate on leaf position, the number of prey adhering to the basal (from the base to the middle of the leaf) and distal zones were counted separately (from the middle to the apex). These two leaf zones were estimated by tracing the outline of the leaf on a sheet of clear plastic for subsequent leaf-area

determination using a scanner (Macintosh One Scanner) in connection with an image analyser program (Canvas 3.02, Deneba Systems, Inc.).

The biomass of each prey taxon was estimated by means of regression equations that account for the allometric relationship between body length and dry body weight (Hódar, unpubl). For the larger prey, such as Diptera and Hymenoptera, the dry weight (0.01 mg) was obtained by weighing several specimens of each group. For the remaining groups, dry weight was obtained by weighing several specimens belonging to the same size class, obtaining a minimum of 10 size classes per taxa. The R^2 values obtained for each taxon were: Nematocera, $R^2 = 0.97$, $n = 10$; Diptera non Nematocera, $R^2 = 0.95$, $n = 26$; Hymenoptera, $R^2 = 0.84$, $n = 24$; Thysanoptera, $R^2 = 0.91$, $n = 6$; Aphidae, $R^2 = 0.59$, $n = 6$; Homoptera non Aphidae = 0.68, $n = 12$; Coleoptera, $R^2 = 0.88$, $n = 16$; Araneae, $R^2 = 0.89$, $n = 20$; Heterocera, $R^2 = 0.97$, $n = 10$.

Arthropod availability

Arthropod availability was determined using passive traps made of small wooden sticks, 25 cm in length and 8 mm in width. The central 15 cm of the sticks (37 cm^2 of trap surface per stick) were coated with odourless glue (Tanglefoot). For handling, the top was left adhesive-free, as was the bottom, which was fixed to the wall with plastiline (in dry areas) or nails and wire (in wet areas).

Traps were designed to mimic *Pinguicula* distal leaves not only in size and shape, but also in threedimensional position. Thus, the trap was intended to catch insects from the same vantage point as that of the plant. Arthropod availability was sampled in the same four habitats as in the case of plant prey capture. Placed at the same time as leaves were labelled, and close to the labelled plants, traps were checked within the same time frame as that of leaf sampling: two d with 12-h periods of counting (but not removing) prey, and 5 additional d for 7 d in all. Afterwards, the traps were collected to identify and measure the items in the laboratory.

Sampling was carried out during the first (end of June), third (middle of July) and last (middle of August) week of prey capture, placing 10 traps per habitat and sampling week – a total of 30 traps from the sunny, ground and shady habitats, and 60 from the wall habitat, following the same bifactorial design previously described for plant prey analysis.

For an accurate comparison of available prey vs trapped prey, it is necessary to consider exclusively the fraction of arthropods adhering to the traps that the plants are able to capture. In the genus *Pinguicula*, the arthropod prey were always below a specific size threshold, because of the limited retention capacity of the mucilage (Zamora 1990b, Gibson 1991b). A preliminary sampling indicated that 64% ($n = 140$) of prey larger than 5 mm adhered to the leaves exclusively by their appendages (legs and wings), only a few making contact also with the body. The fact that larger prey hung by their appendages hampers prey digestion by the plant because the leaf is unable to produce a "temporary stomach" (Darwin 1875). For these reasons, I have restricted the consideration of "prey" to any insect which the plant is able to trap (adhesive capacity) and digest (body in contact with the leaf), and this applies to insects of 5 mm or less in length. Furthermore, the exclusion of the few larger insects from the statistical analysis significantly reduced the skewed degree of the prey-size distributions, providing the normal distribution required by parametric tests.

On the other hand, *P. vallisneriifolia* has two commensal arthropods which take advantage of prey on the leaves: mites (*Oriobatula* sp., Oribatulidae, Acarina), less than 0.6 mm in length, and *Dicyphus* sp. (Miridae, Hemiptera), 4 mm in length. Both species are able to crawl on the leaves without being trapped – the mites because of their small size can crawl between the stalked glands, avoiding the adhesive droplets, and the *Dicyphus*, because of its extraordinary strength, can walk on the glandular surface. As neither species is prey, but rather commensal, they have been excluded from the prey counts. Thus, I have considered any available insect smaller than 5 mm and captured by the traps (excluding commensal mites) to be suitable prey for *P. vallisneriifolia*, whereas insects larger than 5 mm were considered unsuitable (see also Gibson 1991b).

Evaluation of possible attraction mechanisms

To investigate the leaf colour as a potential visual attraction, I used life-size colour photographs of a typical reproductive *P. vallisneriifolia* individual, covered with glue. Picture-traps were placed on a piece of cardboard hanging from the wall near the true plants in the wall habitat. As controls, I used paper cut-outs identical to the photo in size and shape, also covered by glue, but brown in colour (i.e., imitating the colour of the rock). Each piece of cardboard had one picture-trap, and one control cut-out (both covered by glue). At each sampling date (end of June and middle of July) 8 picture-traps and 8 cut-outs were placed, left for 7 d, and then collected to identify and measure the arthropods in the laboratory.

For a direct evaluation of the attractiveness of *P. vallisneriifolia* to insects, the rate of insects landing on leaves of this species was compared with the insect landing rate on other plant species in the same patch: *Potentilla petrophylla*, the only plant neighbour of *P. vallisneriifolia* in the wall habitat; and *Brachypodium sylvaticum* (grass hereafter), growing in the ground habitat adjacent to the wall. Censuses were carried out by means of observations of flying insects approaching the leaves. Landing rates were quantified by monitoring between 5 and 12 leaves at a time, and noting the number of flying insects landing on leaves in a 2-min period. The leaf areas of the three plant species were estimated by tracing the outline of the leaf (20 leaves per species) on a sheet of clear plastic for leaf

area determination. Landing rate was expressed as number of insects landed/time/leaf area.

Landing censuses were carried out at the end of July, and the results were grouped into the following periods: morning (from sunrise, ca 08.00 to 11.00), midday (from 12.00 to 16.00) and evening (from 17.00 to sunset, ca 21.00). The number of censuses was the same for all plant species and time periods – 90 censuses per plant species (*P. vallisneriifolia*, *Potentilla* and grass, respectively) and per habitat (wall or ground).

Due to the high number of censuses where no insect was seen landing on leaves, for the statistical analysis I have grouped (in blocks of 10 censuses) the censuses carried out within the same period. The resulting sample size is 9 blocks of censuses per habitat (wall and ground) and plant species (*P. vallisneriifolia*, *Potentilla* and grass), 3 blocks per period of time (morning, midday and evening).

Mucilage retention capacity

To quantify both the density of the stalked glands situated on the leaf surface and the diameter of the mucilage droplet produced at the top of the stalked gland, I used a binocular microscope equipped with a graticule in one eye piece, and a micrometer in the other (for counting the glands and measuring the diameter of the spherical secretion droplets, respectively). Both mucilage-droplet size and stalked-gland density were determined in 20 functional leaves from different plants in each habitat (sunny, wall, ground and shady, 80 leaves in total) immediately after leaf collection, in order to avoid any damage to the mucilage droplets produced by handling and/or time. I measured the mucilage droplet diameter of 40 randomly selected stalked glands, and counted the number of stalked glands in ten 1-mm^2 quadrats per leaf, avoiding the midrib and the margin of the leaf. An estimation of the volume of mucilage secreted by each leaf was obtained by multiplying the volume of the spherical droplets by the number of stalked glands per unit of leaf surface.

Retention capacity of leaves was directly measured by placing living flies on functional leaves. Fly size was divided into three categories: small (*Drosophila melanogaster*, wild race, 2.2 mm), medium (*Drosophila melanogaster*, virilis race, 3.3 mm), and large (native flies of 5 mm collected in the surrounding vegetation). The experiment was carried out using 10 plants per habitat (one leaf per plant) in the sunny, wall, ground, and shady habitats. Seven flies were placed on each leaf: 3 small, 3 medium, and 1 large fly. Flies were handled delicately and placed in a natural landing position on the leaf (i.e. placing the six legs in contact with the glandular surface). Any fly damaged by handling was discarded from the experiment. If the insect remained fixed for more than 1 h, it was considered "trapped".

Robbing rate and kleptoparasitic animals

Kleptoparasitism was tested by diurnal and nocturnal observations of animals searching for food near the plants growing in the four habitats. The robbing rate was experimentally evaluated using leaves belonging to different plants in the four habitats, placing three flies (*Drosophila melanogaster* wild race) per leaf: one in each of the basal, central and distal positions. These plants were located at the same site where plant prey were sampled.

Once the flies were placed, always at sunrise, I conducted periodic sampling at 12-h intervals to test diurnal and nocturnal differences in robbing rate, following the sampling design previously described for prey captures: two d with 12-h periods of counting and 5 additional d, for a total of 7 d. In each sampling, I noted the number of flies remaining on the leaf, and their positions.

The robbing rate was quantified three times, corresponding to the beginning, medium, and end (end of June, middle of July and middle of August, respectively) of the overall sampling period, totalling 3 sampling weeks, 10 leaves per habitat and sampling session (i.e., a total of 30 leaves from the sunny, wall, ground, and shady habitats).

Because the plants were protected from rain by the rock wall in all habitats, prey loss was attributed to kleptoparasitic animals.

Statistical analysis

A χ^2 test was used to analyse differences in taxonomic composition of prey and insects captured by the traps. I checked the expected values obtained by analysing the original data. Since all distributions had at least one expected value of less than one, and some distributions had more than 20% of the expected values less than 5, I combined the rarer taxa to perform the goodness-of-fit test (Zar 1984). The distributions of all variables were checked before statistical analysis. Prey size, prey biomass and capture rate variables were log-transformed, to improve normality.

The ANOVAs were carried out using a type III sum of squares, due to the unbalanced nature of the data (Dowdy and Wearden 1985). Throughout this paper, means are expressed ± standard error. Statistical analyses were performed using the computer software StatView 4 (Feldman et al. 1991) and SuperANOVA (Gagnon et al. 1989) for Macintosh.

Results

Abiotic conditions

The four habitats differed markedly in mean irradiance because of the differences in exposure and/or level of cliff coverage. For example, the sunny and shady habitats

Table 1. Abiotic conditions in the sunny, wall, ground and shady habitats. Data obtained in an open area near the study site (100 m apart, the same altitude) represent a control of the climatic conditions without the microclimatic effect produced by the cliff. Data (mean ± SE) correspond to the average total irradiance, air temperature and humidity values from sunrise (08.00) to sunset (21.00) during a typical, sunny day in the middle of the sampling period (30 July 1992). Abiotic data collected at the beginning (end of June) and the end (middle of August) of the sampling period follow the same pattern. The results of the statistical comparison are the following: Irradiance: $F = 21.6$, $df = 4,61$, $p = 0.0001$; Air temperature, $F = 1.61$, $df = 4,61$, $p = 0.1822$; Relative humidity, $F = 5.0$, $df = 4,61$, $p = 0.0015$. Means followed by different superscript letters are significantly different at $p < 0.05$ by Scheffe's t-test.

Abiotic conditions	Habitats				
	Sunny	Wall	Ground	Shady	Open area
Irradiance (W/m^2)	176.7 ± 48.9^a	34.1 ± 4.4^b	29.5 ± 4.5^b	6.4 ± 0.9^c	284.0 ± 100.8^a
Air temperature (°C)	30.2 ± 1.4^a	27.3 ± 0.6^a	28.2 ± 1.1^a	26.6 ± 0.8^a	28.8 ± 1.1^a
Relative humidity (%)	38.6 ± 2.5^a	45.7 ± 1.3^a	45.6 ± 2.3^a	51.2 ± 2.0^b	41.0 ± 3.2^a

differ in irradiance by almost two orders of magnitude (see Table 1 for statistical comparisons). Differences between habitats in radiation were larger than differences in temperature and air humidity. The sunny habitat was the warmest and driest (36°C maximum, 22% humidity minimum), whereas the shady habitat was the coolest and wettest (Table 1). Thus, radiation differences generated a gradient of abiotic conditions, the sunny and shady sites being the extremes, while the wall and ground habitats were intermediate. Temperature and humidity data registered at night indicated that the sunny habitat was the warmest and driest also at night. (24 h, 30 July 92: Sunny, T = 24°C, H = 49.2%; Wall, T = 23°C, H = 56%; Ground, T = 23.2°C, H = 57.1%; Shady, T = 22,8°C, H = 55.4%).

Spatio-temporal distribution of prey and available arthropods

Taxon and size

The diet of *P. vallisneriifolia* included various arthropod taxa (Table 2). Almost all prey were winged insects, with Nematocera the most abundant (63.9%), followed in decreasing order of importance by Diptera non-Nematocera, Hymenoptera, Aphidae and Thysanoptera. Other groups were very scarce.

Plants growing in different habitats had a similar taxonomic composition of prey, although the relative abundance of the various taxa differed significantly between habitats ($\chi^2 = 752.9$, $df = 18$, $p = 0.0001$). Nematocera was the dominant prey in all habitats, although its quantitative importance varied between 58.6% on the ground to 83.4% in the shady habitat. Other groups also showed strong quantitative differences, such as Diptera non-Nematocera (from 0.8% in the sunny habitat to 33.4% on the ground), whereas Thysanoptera and Aphidae were more abundant in the sunny places (Table 2).

Nematocera, Diptera non-Nematocera and Hymenoptera were the most abundant taxa found in the woody traps, making up 94.2% of the total (Table 3). The relative abundance of the various taxa found in the traps differed significantly between habitats ($\chi^2 = 987.2$, $df = 18$, $p = 0.0001$). The 10 groups represented are also found on the leaves of *P. vallisneriifolia* (Table 2). Despite this

Table 2. Taxonomic composition of prey captured by *P. vallisneriifolia* in the sunny, wall, ground and shady habitats. To facilitate between-habitat comparisons, as well as plant capture – trap capture comparisons, prey abundance values (capture rate) have been standardized by expressing the number of individual prey captured per 10 cm^2 of leaves per 7 d. 10 cm^2 correspond to the average area of a typical leaf. The relative abundance of each taxon (%) and the total sample size (N) are also shown. Coleoptera, Araneae and Heterocera were combined to the Others category in order to perform the statistical comparisons in the sunny, wall and ground habitats, whereas in the shady habitat Aphidae and Homoptera non-Aphidae were also combined.

Taxa	Sunny		Wall		Ground		Shady		Total	
	Capture rate	%	Capture rate	%	Capture rate	%	Capture rate	%	Capture rate	%
Nematocera	3.30	61.60	3.48	63.42	8.69	58.59	7.15	83.37	5.65	63.88
Diptera non-Nematocera	0.04	0.76	0.66	12.15	4.95	33.37	0.47	5.48	1.53	20.43
Hymenoptera	0.28	5.32	0.56	10.22	0.58	3.89	0.90	10.55	0.58	6.85
Thysanoptera	0.80	14.83	0.17	3.11	0.04	0.31	0	0	0.25	2.22
Aphidae	0.60	11.03	0.19	3.61	0.41	2.78	0.02	0.20	0.30	3.29
Homoptera non-Aphidae	0.16	3.04	0.14	2.60	0.09	0.62	0	0	0.10	1.30
Others	0.18	3.42	0.27	5.0	0.06	0.43	0.03	0.4	0.14	2.01
Σ	5.36		5.47		14.82		8.57		8.55	
N	263		998		1618		493		3372	

Table 3. Taxonomic composition of arthropods captured by woody traps in sunny, wall, ground and shady habitats. Arthropod capture rate is expressed as the number of items captured per 10 cm^2 of trap surface per 7 d. The relative abundance of each taxon (%) and the sample size (N) are also shown. Coleoptera, Araneae and Heterocera were combined to the Others category in order to perform the statistical comparisons in the sunny, wall and ground habitats, whereas in the shady habitat Aphidae and Homoptera non-Aphidae were also combined.

Taxa	Sunny		Wall		Ground		Shady		Total	
	Capture rate	%	Capture rate	%	Capture rate	%	Capture rate	%	Capture rate	%
Nematocera	1.83	40.13	2.45	47.97	9.29	48.84	5.11	42.56	4.57	46.13
Diptera non-Nematocera	0.36	8.07	1.20	28.05	7.37	38.75	3.48	29.01	3.10	31.21
Hymenoptera	1.14	25.11	0.61	14.35	1.95	10.27	3.16	26.36	1.72	16.87
Thysanoptera	0.67	14.8	0.05	1.28	0.03	0.19	0	0	0.19	1.68
Aphidae	0.02	0.45	0.02	0.43	0.16	0.84	0.06	0.52	0.06	0.63
Homoptera non-Aphidae	0.07	1.57	0.09	2.14	0.05	0.28	0.04	0.37	0.06	0.78
Others	0.45	9.87	0.24	5.78	0.16	0.79	0.14	1.18	0.15	2.69
Σ	4.55		4.26		19.01		12.0		9.85	
N	446		934		2152		1358		4890	

taxonomical similarity, some taxa, as Nematocera and Aphidae, were proportionally more abundant on leaves than on traps, whereas the reverse situation occurred for Diptera non-Nematocera and Hymenoptera. As a result of these differences, the relative abundance of actual plant prey differed statistically from the arthropods captured by the woody traps in each habitat: sunny habitat, $\chi^2 = 122$, df = 6, p = 0.0001; wall habitat, $\chi^2 = 121.7$, df = 6, p = 0.0001; ground habitat, $\chi^2 = 100$, df = 6, p = 0.0001; shady habitat, $\chi^2 = 246.2$, df = 3, p = 0.0001.

P. vallisneriifolia prey size differed statistically between habitats (F = 128.5, df = 3, 3358, p < 0.0001). More than 90% of the prey captured were less than 3 mm, whereas nearly 12% of the individuals captured by the traps were over 5 mm in length. The traps captured a greater range of sizes than *P. vallisneriifolia* in all habitats (Fig. 1), and there were also statistical differences between habitats in the size distribution of available insects (F = 123.6, df = 3, 4886, p = 0.0001). The smaller insects captured both by plants and traps appeared in the sunny habitat, whereas in other habitats, insects over 3 mm in length were more common on traps than might be inferred from the actual prey of the plant (Fig. 1). Thus, *P. vallisneriifolia* captures prey from only the lower end of the available size range, because of the limited retention capacity of the mucilage in comparison with the glue used in the traps. A comparison between the size of the actual prey and the size of the available arthropods shows statistical differences in all habitats (Sunny, F = 18.6, df = 1, 707, p = 0.0001; Shady, F = 91.9, df = 1, 1849, p = 0.0001; Wall, F = 115.4, df = 1, 1930, p = 0.0001; Ground, F = 18.9, df = 1, 3768, p = 0.0001).

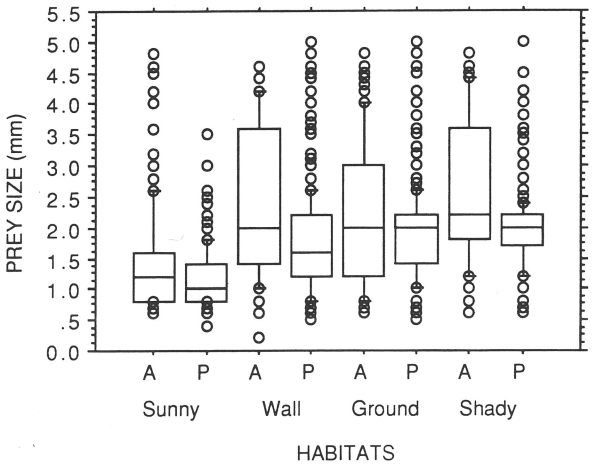

Fig. 1. Size distribution (box plots) of actual plant prey (P) and available arthropods (A) captured by traps in the four habitats. In the box plots, the top of a box represents the 75th percentile and the bottom the 25th percentile, and a box contains the middle 50% of the values. The line in the box represents the median. The top whisker ranges from the 25th to the 10th percentile. The circles represent outliers.

Capture rate

Spatial and temporal differences in prey capture rates were analysed with a two-way ANOVA using habitat and

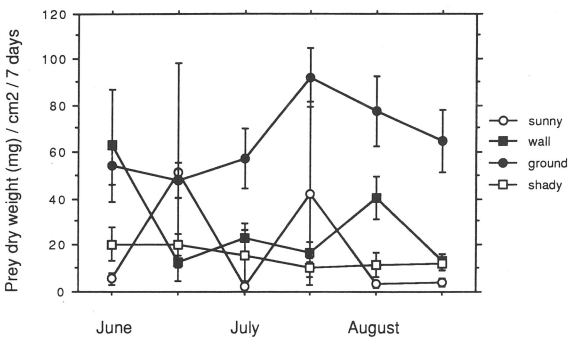

Fig. 2. Distribution of prey captures over the season in the four habitats. Each point represent the mean ± SE of dry weight/leaf area/7 d.

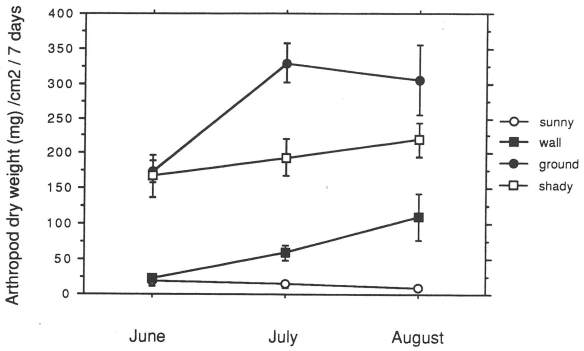

Fig. 3. Distribution of arthropod availability over the season in the four habitats. Each point represent the mean ± SE of dry weight/trap area/7 d.

sampling period as factors (Fig. 2). There were statistical differences between habitats in plant capture rate ($F = 21.6$, $df = 3, 285$, $p < 0.0001$ for number of prey cm^2 7 d^{-1}, and $F = 61.0$, $df = 3, 285$, $p < 0.0001$ for prey biomass cm^{-2} 7 d^{-1}), the temporal differences being smaller ($F = 4.2$, $df = 2, 285$, $p = 0.001$ for number of prey cm^{-2}, and $F = 4.1$, $df = 2, 285$, $p = 0.02$, for prey biomass cm^{-2}), and there was no statistical interaction between spatial and temporal factors ($F = 1.27$, $df = 6, 285$, $p = 0.272$, and $F = 1.86$, $df = 6, 285$, $p = 0.08$, respectively). These results are in good agreement with those obtained using the woody traps, because the habitat factor also accounts for most differences in prey capture (Fig. 3), both in the number of arthropod as well in the arthropod biomass cm^{-2} 7 d^{-1} trapped by the woody traps ($F = 106.9$, $df = 3, 132$, $p < 0.0001$, and $F = 57.6$, $df = 3, 132$, $p < 0.0001$, respectively). The wall, ground and shady habitats have more available prey during August than during June, whereas the sunny habitat shows the opposite trend (Fig. 3). Moreover, temporal differences in capture rate are smaller than spatial ones ($F = 8.5$, $df = 2, 132$, $p = 0.0003$, for number of arthropod cm^{-2}, and $F = 7.2$, $df = 2, 132$, $p = 0.001$, for arthropod biomass cm^{-2}), and there was statistical interaction between habitat and sampling week factors ($F = 6.2$, $df = 6, 132$, $p = 0.0001$ for number of arthropod cm^{-2}, and $F = 2.23$, $df = 6, 132$, $p = 0.04$ for arthropod biomass cm^{-2}). Woody traps captured more prey cm^{-2} 7 d^{-1} than plants on the ground ($F = 32.2$, $df = 1, 88$, $p < 0.0001$) and shady ($F = 20.5$, $df = 1, 88$, $p < 0.0001$) habitats, where most of the available prey appeared (Tables 2 and 3). On the contrary, plants and traps had a similar capture rate in the sunny habitat ($F = 0.05$, $df = 1, 87$, $p = 0.823$), the average of plant captures being greater than for traps in the wall habitat ($F = 6.4$, $df = 1, 175$, $p = 0.012$). On the other hand, insect biomass captured by woody traps was invariably greater than plant prey biomass captures in every habitat (sunny, $F = 14.6$, $df = 1, 87$, $p = 0.0003$; wall, $F = 17.3$, $df = 1, 175$, $p = 0.0001$, especially in the shady ($F = 127.9$, $df = 1, 88$, $p = 0.0001$) and ground ($F = 102.3$, $df = 1, 88$, $p = 0.0001$) habitats.

Day-night captures

P. vallisneriifolia captures similar taxa during the day and the night as a whole, although in different proportions ($\chi^2 = 137.9$, $df = 4$, $p = 0.0001$). Some taxa are more frequently trapped during the day, such as Diptera non-Nematocera, Hymenoptera and Aphidae, whereas the reverse situation occurs with Nematocera, especially in the sunny habitat. Despite these differences in relative abundance, neither prey size nor prey biomass differed statistically between diurnal and nocturnal samples ($F = 1.40$, $df = 1, 711$, $p = 0.239$, and $F = 1.03$, $df = 1, 711$, $p = 0.310$, respectively).

Diurnal and nocturnal capture rates were also very similar ($F = 1.67$, $df = 1, 599$, $p = 0.196$). These results are in good agreement with the capture rate of the diurnal

Table 4. Taxonomic composition of the captures og aggregated and solitary plants of the wall habitat, expressed as number of prey per 10 cm^2 of leaves per 7 d, together with the corresponding number of insects captured by traps (aggregated traps = placed intermingled with the plants; solitary traps = placed 1 m from the nearest plant), expressed as the number of items captured per 10 cm^2 of trap surface per 7 d. The relative abundance of each taxon (%) and the total sample size are shown. Thysanoptera, Aphidae and Homopterta non-Aphidae, have been combined with the Others category for the statistical comparisons.

Taxa	Plants				Traps			
	Aggregated		Solitary		Aggregated		Solitary	
	Capture rate	%	Capture rate	%	Capture rate	%	Capture rate	%
Nematocera	2.08	56.17	5.72	66.40	1.40	40.83	2.75	53.02
Diptera non-Nematocera	0.53	14.47	0.95	10.99	0.86	25.32	1.55	29.98
Hymenoptera	0.52	14.04	0.65	7.61	0.76	22.22	0.45	8.77
Thysanoptera	0.16	4.25	0.20	2.32	0.03	1.03	0.07	1.46
Aphidae	0.08	2.34	0.45	5.28	0.03	1.03	0.0	0
Homoptera non-Aphidae	0.11	2.98	0.22	2.53	0.09	2.58	0.09	1.83
Others	0.21	5.74	0.42	4.84	0.24	6.97	0.25	4.93
Σ	3.69		8.61		3.41		5.16	
N	500		498		387		547	

Table 5. Stalked-gland density and mucilage production per unit of leaf area in the four habitats. Mean followed by different superscript letters are significantly different at $p < 0.05$ by Scheffé t-test.

Stalked gland traits	Habitats			
	Sunny	Wall	Ground	Shady
Stalked glands/mm^2	16.92 ± 0.53^a	15.39 ± 0.36^a	13.78 ± 0.36^b	14.73 ± 0.32^b
Volume of mucilage (μl/cm^2)	1.56 ± 0.18^a	1.22 ± 0.09^a	2.20 ± 0.18^b	0.76 ± 0.11^c

and nocturnal woody traps, where there were no statistical differences between the number of insects trapped during the day and the night by the traps ($F = 0.22$, $df = 1, 299$, $p = 0.636$).

Proximate factors determining capture success

Substrate wetness and plant aggregation

Plants growing in wet and dry patches of the wall habitat caught prey of similar taxonomic composition ($\chi^2 = 8.2$, $df = 6$, $p = 0.223$), size ($F = 0.12$, $df = 1, 837$, $p = 0.789$) and biomass ($F = 0.1$, $df = 1, 1837$, $p = 0.881$). A two-way ANOVA (substrate wetness and plant aggregation as factors) indicated that capture rates were also very similar irrespective of the wetness level of the rocky substrate were the plants grew ($F = 1.70$, $df = 1, 115$, $p = 0.194$), and there was no statistical interaction between substrate wetness and the level of plant aggregation ($F = 0.02$, $df = 1, 115$, $p = 0.891$). Only the level of plant aggregation (average plant density of aggregated plants = 138.7 ± 8.6 plants m^{-2}) influenced the prey-capture rate ($F = 83.4$, $df = 1, 115$, $p = 0.0001$). In fact, aggregated plants had less than half the capture rate of solitary plants (Table 4).

Furthermore, plants growing in aggregations differed statistically from those living alone with regard to prey taxonomic composition ($\chi^2 = 65$, $df = 6$, $p = 0.0001$, see Table 4). Nematocera were more abundant in solitary than in aggregated plants, and were also more frequently captured by traps placed outside, rather than within the plant aggregations. Overall, plants and traps showed similar qualitative and quantitative capture patterns (Table 4).

Aggregated and solitary plants also differed in prey size ($F = 18.9$, $df = 1, 837$, $p = 0.0001$) and prey biomass ($F = 39.8$, $df = 1, 837$, $p = 0.0001$), the average prey biomass of aggregated plants being twice (mean = 55.22 ± 6.5 μg) that of solitary plants (mean = 25.61 ± 3.20 μg). As a consequence, the total biomass trapped per unit of leaf area was the same in both aggregated and solitary plants ($F = 0.001$, $df = 1, 117$, $p = 0.976$), because prey-biomass differences (larger prey on aggregated plants) counterbalanced the numeric differences in prey captured (more prey on solitary plants).

Leaf sector

The number of insects adhering to the tip sector of the leaf (i.e. from the middle of the leaf to the apex) was greater than that of the basal sector (i.e. from the middle to the base of the leaf) in all habitats ($p < 0.0001$ in all comparisons using one-way ANOVA). The tip and basal capture rates of the aggregated and solitary plants of the wall habitat were: aggregated plants, mean basal sector = 1.7 ± 2.1 prey 10 cm^{-2} 7 d^{-1}, mean tip sector = 4.9 ± 4.2; solitary plants, mean basal sector = 6.6 ± 0.7 prey 10 cm^{-2} 7 d^{-1}, mean tip sector = 9.5 ± 0.8. The leaf density of aggregated plants limits the access of flying insects to the basal parts of the leaves and, for this reason, the leaf basal sector of aggregated plants captures a lower proportion of prey than does the corresponding basal sector of solitary plants.

Attraction

Both colour pictures and control drawings had similar captures with respect to taxon diversity ($\chi^2 = 11.2$, $df = 6$, $p = 0.08$) and prey size ($F = 2.68$, $df = 1,466$, $p = 0.102$). Nevertheless, the capture rate of colour pictures was double that of controls (mean = 21.0 ± 1.64 and $8.2. \pm 1.0$ per 10 cm^2, respectively, $F = 44,2$, $df = 1,30$, $p = 0.0001$). This result indicates that leaf colour is one factor attracting insects to the traps.

A total of 245 insects were counted landing on *Pinguicula* and neighbouring plants. Most were small Diptera representing potential prey for *P. vallisneriifolia.* Census results indicated that *Pinguicula* leaves were used as perches by flying insects with the same frequency as for *Potentilla petrophylla* leaves in the wall habitats (no. of insects per census landing on both *P. vallisneriifolia* and *P. petrophylla* leaves = 0.008 ± 0.003 per 10 cm^2, $F = 0.0009$, $df = 1, 17$, $p = 0.93$). On the other hand, small insects perched more on grass leaves than on the glandular leaves of *Pinguicula* in the ground habitat (no. of insects per census landing on both grass and *P. vallisneriifolia* leaves = 0.22 ± 0.008 per 10 cm^{-2} and 0.04 ± 0.008 per 10 cm^{-2}, respectively, $F = 67.6$, $df = 1, 17$, $p = 0.0001$), despite the fact that the two species grow intermingled, and their leaves therefore have many points of contact. Thus, no obvious *P. vallisneriifolia* attraction mechanisms emerge from these results, and flying insects prefer to perch on smooth (e.g. grass) rather than on glandular leaves (*Pinguicula*) and/or pubescent ones (*Potentilla*).

Table 6. Fly escape behaviour as a function of insect body size. The number of flies initially placed on the leaf within each fly size category (in brackets), and the number of flies that remained at the end of one hour in each habitat are shown. The χ^2 test compares the number of flies initially placed on the leaf with the number of flies that remain at the end of one hour. *: $p = 0.005$; **: $p = 0.0001$.

Fly size	Habitats			
	Sunny	Wall	Ground	Shady
Small (30)	30	30	28	24
Medium (30)	30	30	24	19
Large (10)	9	9	4	2
χ^2 values	0.1 ns	0.1 ns	10.6*	39.9**

Retention

Plants growing in different habitats varied both in stalked gland density ($F = 10.5$, $df = 3, 76$, $p < 0.0001$) as well as in the volume of mucilage per droplet ($F = 11.7$, $df = 3, 76$, $p < 0.0001$). As a result, leaves from different habitats produced differing quantities of mucilage per unit of leaf surface ($F = 18.9$, $df = 3, 76$, $p < 0.0001$, see Table 5); plants growing in shady conditions secreted less mucilage than did plants growing in the other habitats.

The experimental placement of wild flies on leaves indicated that plants growing in ground and, above all, in shady habitats, have less retention capacity than plants growing on wall and sunny habitats (Table 6). All flies of 2.2 and 3.3 mm in body size remained trapped in wall and sunny habitats, whereas the largest flies, 5 mm in size, and several intermediate sizes, tended to escape from plants growing in the ground and the shady habitats. Thus, there is no exact correspondence between the mucilage volume and the retention capacity, probably because mucilage viscosity (quality) does not correspond precisely to mucilage quantity. For example, plants growing in the sunny habitats produce less mucilage, but of greater retention capacity, than plants growing in the ground habitat.

Robbery

A slug, *Deroceras hilbrandi* (Agriolimacidae), is the main kleptoparasite of *P. vallisneriifolia* in the wet habitats and those with filtered sun – that is, shady, ground and wall – whereas a lizard, *Algyroides marchi* (Lacertidae) is the main kleptoparasite in the sunny and dry places – such as the sunny habitat. The slugs were able to crawl on the glandular surface of the leaves without being trapped. Slugs are mainly kleptoparasites, but sometimes they are also herbivores of *P. vallisneriifolia*. Lizards searching for prey in the sunny places, frequently stopped at a *P. vallisneriifolia* plant, and if they found a suitable trapped prey, they would take it. Slugs robbed predominantly at sunset, in the early morning and at sunrise. In contrast, the lizards stole prey mainly at midday and in the evening, when the sunlight fell directly on the rocky substrates.

There were no statistical differences in the robbing rates between the three periods ($\chi^2 = 1.4$, $df = 8$, $p = 0.993$). The feeding experiments showed that only around 2% to 5% of the flies initially placed were robbed in the first 24 h, whereas on the other 7 d, the proportion of robbed flies was between 18% and 36% (Table 7).

As can be seen in Table 7, robbing data and prey-capture data are pooled for a more quantitative evaluation of the robbing rate as a percentage of the capture rate. Despite the fact that plants growing in the ground habitat have the greatest kleptoparasitic pressure, this robbing rate represents only a small fraction of the total trapped prey, because of the large capture rate of ground plants. In contrast, sunny plants lost a quarter of the total prey capture to lizards.

Table 7. Results of the feeding experiments to evaluate robbing rate. There are no statistical differences between the initial number of flies placed and the nocturnal/diurnal robbing rate, thus only the number of flies initially placed, and the number of flies and percentage (within brackets) that remain at the end of seven d are shown. The prey captured/leaf column corresponds to the average number of prey captured per leaf per 7 d in each habitat, and the prey robbed/leaf column corresponds to the average number of flies robbed per leaf per 7 d. The last column (prey captured minus prey robbed) shows the differences between the average number of prey captured minus robbed flies per leaf; also, robbed prey is expressed as a percentage against the initial average number of the captured prey (in brackets). The χ^2 test compares the number of flies initially placed on the leaf and the number of flies that remain at the end of 7 d. *: $p = 0.0002$; **: $p = 0.0001$.

Number of flies placed in each habitat	Number of remaining flies			Prey capture minus prey robbed		
	1–7 July	20–27 July	6–13 August	prey captured/leaf	prey robbed/leaf	prey captured/robbed
Sunny (30)	22 (73.3)	24 (80)	16 (53.3)	4.2	0.93	3.27 (22.1)
Wall (30)	21 (70)	24 (80)	20 (66.7)	6.6	0.83	5.77 (12.6)
Ground (30)	16 (53.3)	22 (73.3)	14 (46.7)	20	1.27	18.73 (6.3)
Shady (30)	25 (83.3)	27 (90)	25 (83.3)	6.4	0.43	5.97 (6.7)
Σ (120)	109 (72.7)	123 (82)	96 (64)	8.8	0.81	7.99 (11.3)
χ^2 test values	20*	6.2 n.s.	36.5**			

Discussion

Random sampling versus prey attraction

Large differences in arthropod availability between habitats a few metres apart was caused by different abiotic conditions (Table 1). These abiotic differences encourage most flying insects to be concentrated in the wet, shaded places, avoiding the generally warm and dry ones (sunny habitat). For this reason, plants and traps captured many insects throughout the summer in the shadiest and wettest places (see Figs 2 and 3). Flying insects showed a similar pattern of habitat selection during the night, perhaps implying that wetness and temperature differences between habitats, although smaller than radiation differences during the day, are also important factors (Unwin and Corbet 1991). Thus, prey availability strongly depended on the abiotic context where the plant grew. A similar situation has been described for *P. nevadense* (Zamora 1990b), a carnivorous plant that obtains different prey along a gradient of soil wetness, in the same solar environment, at high altitudes in the Sierra Nevada.

Plants and traps followed a similar spatial and temporal pattern of insect capture, indicating a random sampling of prey (i.e. with more insects available, plants captured more prey, and vice versa, see Tables 2 and 3). In addition, plants captured the same quantity of animal prey (expressed both in number of prey and biomass/leaf area) during the day as during the night, and the traps showed exactly the same pattern. This fact is not in good agreement with the idea of visual attraction by the plant, because it is difficult to imagine a visual mechanism such as the reflection and absorption of UV light of digestive secretions (Joel et al. 1985) acting in the same way both day and night.

Although both plants and woody traps caught the same taxa, some groups, such as Nematocera and Aphidae, were more abundant captures of the plant than of the traps (Tables 2 and 3). These differences could be interpreted as evidence that some taxa are slightly attracted by the leaves. Alternatively, differences in the retention capacity of the trap glue and leaf mucilage may cause these differences. Small prey, mainly Nematocera and Aphidae (1.4–1.6 mm), were more common on leaves, while large Diptera non-Nematocera and Hymenoptera (1.8–2.5 mm) were more abundant on traps. In fact, a comparison of the size of Nematocera and Diptera non-Nematocera, the two dominant taxa in both the plants and the traps, shows that Nematocera did not differ statistically in size between plants and the traps, whereas strong differences appeared in the case of Diptera non-Nematocera ($p < 0.0001$ for plant-trap comparisons in all four habitats, one-way ANOVA). Bearing in mind that woody traps mimic distal leaves in size, shape and three-dimensional position, differences in density and relative abundance of taxa with respect to those captured by traps may be due to the combined results of limited attraction (e.g. Nematocera, see also Antor and García, 1994) and/or weak mucilage retention capacity (e.g. Diptera non-Nematocera) in comparison with the glue used in the traps (see Zamora 1990a for a similar case with *P. nevadense*).

If plants attract prey, the presence of a plant might increase the capture rate to another neighbouring plant at no cost to either (Rathcke, 1983). However, the results provided no proof, on a per plant basis, for any prey attraction by crowding because solitary plants capture even more prey than aggregated ones (see also Gibson 1991b, Thum 1988a). However, the total biomass trapped by aggregated and solitary plants was the same per unit of leaf surface, because the aggregated plants captured few but larger prey. The result: the same reward of animal biomass, irrespective of the level of plant aggregation.

The experiments with colour photographs indicated that the yellowish-green colour of the leaves is one factor which attracts flying insects to the traps (see also Karlsson et al. 1987). However, landing censuses indicated that insects perch with the same frequency on *P. vallisneriifolia* leaves as on *Potentilla caulescens* leaves on the rock wall, whereas grass leaves are strongly preferred to *Pinguicula* leaves in the ground habitat. Thus, there are no clear attraction differences between *P. vallisneriifolia* leaves and those of neighbouring plants (see Williams 1976, for *Drosera*). The only clear conclusion is that flying insects prefer to perch on glabrous (e.g. grass) rather than on glandular (*Pinguicula*) or pubescent (*Potentilla*) leaves. The main difference between *P. vallisneriifolia* leaves and the leaves of other plants is that *Pinguicula* can retain a fraction of the insects that perch on the glandular leaves.

In conclusion, no obvious mechanism of differential attraction by *P. vallisneriifolia* leaves resulted from my observations and experiments. Some herbivorous, mainly diurnal insects, such as Homoptera, visit the leaves of *Pinguicula*, attracted, as to any other plant, by the green colour, whereas Nematocera and related taxa associated with decomposition-like odours may be slightly attracted by the weak fungus-like odour exuded by glandular secretions. Also, the putrid odour of prey decomposition has been suspected of attracting certain prey types (Juniper et al. 1989). Furthermore, it is possible that some small floral visitors, like Thysanoptera, attracted by the flowers, are finally trapped by the leaves (Zamora, unpubl.). When considering only Nematocera and Aphidae, the total plant capture is almost double that of the traps; however, we should remember than Diptera non Nematocera and Hymenoptera showed exactly the opposite pattern (being more abundant in the traps than on the leaves).

Despite this limited attractiveness, the characteristics of the distal leaves – size, form and spatial distribution overhanging from the wall – increase the capture of flying insects (which appear to prefer landing on leaves rather than on the rocky surface). In this respect, the greater capture rate of the tip of the leaves in comparison with the basal sector clearly indicates that 15 to 20 cm away from the rocky surface is a better vantage point to

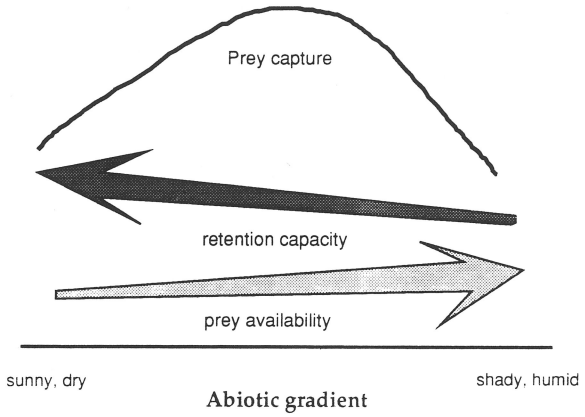

Fig. 4. Summary of the main factors determining trapping success. From the bottom to the top of the scheme: 1) gradient of abiotic conditions (from sunny, dry microhabitats to shady, humid ones); 2) gradient of prey availability (grey arrow); 3) gradient of retention capacity (black arrow); 4) plant prey capture along the abiotic gradient, with a minimum at each end of the gradient.

wait for flying insects than the microsite closer to the wall. Thus, leaf architecture, size and shape strongly determine the feeding ecology of *P. vallisneriifolia* (see also Thum 1986, Schulze and Schulze 1990, Antor and García 1994).

Testing the leaf retention capacity

The comparison between available insects (i.e. insects smaller than 5 mm captured by traps) and the actual prey indicated that, irrespective of taxonomic differences, *P. vallisneriifolia* captures prey only from the lower end of the available size range. The mucilage is not capable of retaining larger insects, though they are frequently caught by the traps. Thus, mucilage retention capacity is a major factor determining prey capture (see also Zamora 1990b and Gibson 1991b).

On the other hand, plants show a pattern of mucilage production related to the quantity of radiation available. Plants secreted very small quantities of mucilage in shady habitats, and were therefore unable to catch most of the insects that landed on the leaves; traps, however, caught many insects. Plants produced more mucilage with more radiation and water (i.e. ground habitat, Table 5); however, the retention capacity of these plants was weaker than in plants growing on drier substrates (wall and sunny habitats, Table 6), retaining more prey than did even the woody traps. A simple explanation for these differences could be that the smaller size of the mucilage droplet is a direct consequence of a higher water transpiration of the leaves in dry and sunny places. The resulting increase in solute concentration, and thus in mucilage viscosity, augments the experimentally tested retention capacity. Also, I attribute a large proportion of the retention loss of ground and shade plants to the damage to the mucilage droplets caused by the great number of larger insects available in these habitats that can land on the leaves, but escape. Thus, a leaf oversaturated by trapped prey and/or one damaged by large insects may have less capacity to retain prey than would the virgin leaf with undisturbed mucilage droplets (see also Wolfe 1981).

In conclusion, the percentage of insects which escape from *P. vallisneriifolia* leaves depends both on insect body size (the bigger the size, the greater the escape possibilities) and on mucilage viscosity, which is less in shady and very wet sites such as the ground habitat, and greater in drier sites such as the sunny and wall habitats.

Robbing rate

Once the insects were trapped by the plant, the last losses before prey digestion were due to opportunistic animals, with a spatial distribution related to the degree of radiation and substrate wetness. Slugs were restricted to the wet and shaded places (wall, ground and shady habitats), whereas the lizard, due to its thermal requirements, appeared exclusively in the sunny habitat. Despite these differences, the robbing rate, similar in all habitats, was not high, although, when values for prey theft are compared to those of prey capture, robbing pressure proved to be proportionally more important where the plants captured few prey (sunny habitat) than where the plants obtained the most successful captures (ground habitat). This limited robbing pressure was a direct consequence of the hanging-leaf plant architecture, which hindered any kleptoparasite from crawling to the leaf tip, the most successful leaf portion for prey capture. On the contrary, the robbing rate was greater on the basal portion of the distal leaves, the most accessible for any kleptoparasite (Zamora and Gómez, in press.).

Trapping success versus trapping efficiency: the importance of the abiotic scenery

Species belonging to the genus *Pinguicula*, like most carnivorous plants, are restricted to infertile soils in sunny, humid places (Givnish 1988). However, the dry Mediterranean climate divorces sunny places (synonymous with dry places) from wet places, (synonymous with shady ones). This duality poses a schizophrenic problem for *P. vallisneriifolia*, which, as a green plant, needs both water and light for photosynthesis, and, as a carnivorous one, needs animal prey as a source of nutrients (Givnish 1988). The response possibilities are limited in *Pinguicula* because the leaves have the dual role of photosynthesis and nutrient absorption from prey, and both physiological activities may undergo trade-offs under sub-optimal ecological conditions. In fact, no habitat provided both unlimited solar radiation and prey to the plants under natural conditions. Radiation measurements

and insect samples indicated that light quantity correlated negatively with insect availability, generating two opposing resource gradients (Fig. 4). Plant mucilage secretion also correlated with light availability, and the retention capacity of the viscous droplets is higher in the sunny and wall habitats than in the shaded habitat. Other factors which affected the total prey biomass trapped by the leaves, such as the limited attraction for Nematocera, or kleptoparasitic pressure, have a similar quantitative effect in all habitats.

The analysis of the cumulative factors determining capture success indicated that, from a trapping efficiency standpoint, the plants trapped more prey in relation to availability where there were fewer insects available (i.e. the sunny and wall habitats, where the plants captured even more insects than in the traps), whereas the plants captured less prey in relation to availability where there were more insects available (i.e. the shady and ground habitats, where the plants captured only half the number of insects smaller than 5 mm captured by the traps). Nevertheless, from the perspective of trapping success (i.e., the total quantity of animal biomass trapped per unit of leaf surface), the plants obtained less animal biomass at both ends of the abiotic gradient (sunny and shady habitats, see Fig. 4), than in the ground habitat, where a moderate retention capacity is counterbalanced by the greater insect availability. As a result, plants growing in the ground habitat obtained nearly four times more insect biomass than did shady and sunny plants.

Thus, all cumulative factors considered, trapping success was determined by the abiotic microsite where the plants grow, which determined both insect availability and physiological retention capacity of the plants. Contrasting habitats could lead to the selection of two distinct strategies: plants on walls and in the sunny places must maximize trapping efficiency of the few flying insects available by means of a more viscous mucilage (in fact, sunny and wall plants captured more insects than the traps). On the other hand, shady plants (despite their low retention capacity), have high capture possibilities due to the greater insect availability. As a consequence, shaded plants obtained a cheap reward in terms of animal biomass per unit of carnivory investment in comparison with plants growing in the other habitats, secreting one third of the mucilage of sunny and wall plants and obtaining similar captures.

These results clearly indicate the need for investigating the interplay between physiological mechanisms and the ecological scenario where the plants grow, in order to understand not only multi-factorial processes such as trapping success, but also the ecophysiology of carnivory investment, and thus the evolutionary pathway towards carnivory in plants.

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