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The feeding ecology of a carnivorous plant (*Pinguicula nevadense*): prey analysis and capture constraints

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Summary. The taxonomic composition and size of arthropods captured by *Pinguicula nevadense*, an endemic carnivorous plant of the high-mountain zone of the Sierra Nevada (southern Spain), are analysed. The actual prey of *P. nevadense* and the available arthropods trapped by "mimic-traps" are compared, in order to identify the capture constraints of the plant. The results show that *P. nevadense* captures various arthropod taxa. Winged insects, especially Nematocera, make up the main component of the diet. The range of prey sizes in all *P. nevadense* populations studied is similar. The taxonomic composition of arthropods trapped by the mimic-traps is similar to that of the actual prey of *P. nevadense*. However, the plant captures prey only below a specific size threshold. These size constraints appear to be the principal factor determining the actual prey of this carnivorous plant.

Key words: *Pinguicula* – Prey analysis – Spatial variability – "Mimic-traps" – Capture constraints

Carnivorous plants are a group of organisms that reverse the usual trophic relationship in nature: the plant is the predator, and the animal is the prey (Thompson 1981). Although the peculiarity of this interaction has attracted the attention of investigators for a long time (e.g. Darwin 1875), the majority of studies have focused on the cytohistologic description of the capture mechanism, and the analysis of the physiological processes related to digestion and nutrient assimilation (e.g. Pate and Dixon 1978; Green et al. 1979; Heslop-Harrison and Heslop-Harrison 1980; Aldenius et al. 1983; Karlsson and Carlsson 1984). As a result, the feeding ecology of most species is unknown today, or only anecdotal information is available, often obtained away from the natural habitat of the plant (see Juniper et al. 1989, Ch. 7). Furthermore, almost the only data available is the taxonomical identity of the prey, even in the case of the species that have received more attention (e.g. *Drosera* sp.: Achtenberg 1973; Dixon et al. 1980; Watson et al. 1982; Thum 1986).

In this paper, I analyse the prey of *Pinguicula nevadense* (Lindl.) Casper, a carnivorous plant endemic to southern Spain. In the *Pinguicula* genus, the capture mechanism is an "adhesive trap" (sensu Juniper et al. 1989). The prey are captured by means of the adhesive action of a mucilage segregated by special glands situated on the surface of the leaf (Heslop-Harrison and Knox 1971).

The specific objectives are the following:
1) To analyse the taxonomic composition and prey size distribution of the arthropods captured by *P. nevadense*.
2) To compare the characteristics of the actual prey with the arthropods trapped by "mimic-traps".

Study area and methods

Notes on the natural history of the plants

P. nevadense is endemic to the Sierra Nevada. The typical annual vegetative growth form is a flat, basal rosette of 6–8 rounded leaves, almost as wide as long, 1–3 cm in length. The growth period is very brief, completing the annual biological cycle in approximately 2 months.

P. nevadense grows exclusively on acid substrates in the high-mountain zone which remains humid throughout the summer. The plant community found in this habitat is composed of a great number of species, many of them endemic (Molero and Perez 1987). The specific composition of the community changes along a humidity gradient, and it is possible to distinguish relatively "dry" and "humid" sectors, each with its characteristic species. *P. nevadense* appears throughout this gradient, next to *Carex nigra* in the more humid microhabitat, and *Nardus stricta* and *Vaccinium uliginosum* subsp. *microphyllum* in the dryer microhabitat (see Fernandez Casas 1974 for a more detailed description).

Numerous populations are found in the high-mountain zone between 2100 and 3100 m, but only near certain streams and springs. The size of the local populations varies between a hundred and a million individuals.

Sampling of arthropods captured by P. nevadense

Captured prey was sampled in three populations situated at 2160 m, 2460 m, and 3100 m (hereafter Piornal, San Juan, and Troposfera, respectively). The first and the last population are located at the lower and upper distribution limits of *P. nevadense*, respectively, and the largest population in both area and number of individuals is San Juan which is situated between them. It was possible to distinguish three subpopulations of the San Juan population according to the degree of humidity of the substrate: "dry", "humid", and "wet". The three microhabitats chosen, located at the same altitude 15 m apart, define a gradient of humidity over which the carnivorous plant can grow and reproduce.

The leaves of *P. nevadense* usually curve inwards, which makes it difficult to identify the prey in the field. For this reason, the sampling procedure consisted in cutting a leaf from each rosette for later prey identification and measurement in the laboratory by means of a binocular microscope with micrometer. Prey size was determined by measuring the length of the body from the end of the head to the end of the abdomen, excluding the appendages.

Leaves were collected in each population from the moment that the flower buds appeared at the beginning of rosette growth until the end of the flowering period. The sampling dates for each population were as follows: Piornal, 27 May to 19 June; San Juan, 22 June to 10 August; Troposfera, 16 July to 10 August. In 1989 samples were taken at San Juan and Troposfera only over the same period. At each sampling session 15–20 functional leaves of the same age were collected in each population, each leaf from a different individual. In the case of San Juan, each subpopulation was sampled independently. Sampling was carried out weekly. The total number of individuals sampled in each population or subpopulations varied between 70 and 100.

Sampling of prey availability

The availability of arthropods in the microhabitats where *P. nevadense* is found was determined by using traps made out of adhesive granular plastic paper, similar to the original plant in size, shape, and colouring. These "mimic-traps" were coated with a glue (made by Rata-Stop) which did not discolor, smell, or dry out. They were placed in the study area next to *P. nevadense* individuals during the same sampling period. The experiment was conducted in the dry and humid subpopulations of San Juan in 1988 and 1989. At each sample date 40 mimic-traps (20 in each subpopulation) were placed, left for 4 days, and then collected in order to identify and measure the arthropods in the laboratory. The comparison between the prey actually captured by *P. nevadense* and the arthropods captured by the mimic traps should allow us to identify the capture constraints of the plant, since the glue used has a great adhesive capacity. Since *P. nevadense* and the "mimic-traps" act as passive traps, the prey captured by plant and mimic trap can be considered as independent. Thus, statistical comparisons can be made.

Results

The diet of *P. nevadense* comprises various arthropod taxa (Table 1). Most of the prey are winged forms. Nematocera are the most abundant, approximately 50% of the total prey captured, followed by, in order of quantitative importance, Acarina, Diptera excluding Nematocera, and Collembola. The remaining groups are poorly represented. The populations at different altitudes

Table 1. Taxonomic composition of prey captured in the Piornal and Troposfera populations of *Pinguicula nevadense*, and in the Dry, Humid, and Wet microhabitats of the San Juan population, together with the taxonomic composition of the arthropods trapped by the mimic-traps in the Dry and Humid microhabitats. The relative abundance of each taxon (%), the sample size *n*, and the proportion of winged and non-winged individuals are also shown

Taxonomic groups	Prey of *P. nevadense*												Arthropods trapped by the mimic-trap					
	Piornal		Dry		Humid		Wet		Troposfera		Total		Dry		Humid		Total	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Nematocera	266	50.1	303	62.1	327	48.0	199	29.3	660	61.6	1755	50.8	306	47.8	216	27.7	522	36.5
Diptera non Nematocera	25	4.7	76	15.6	152	22.3	55	8.1	87	8.1	395	11.4	191	29.8	330	42.4	521	36.5
Acarina	44	8.3	25	5.1	73	10.7	297	43.7	153	14.3	592	17.1	27	4.2	50	6.4	77	5.4
Collembola	110	20.7	7	1.4	29	4.3	52	7.6	62	5.8	262	7.6	7	1.1	32	4.1	38	2.7
Hymenoptera non Formicidae	9	1.7	24	4.9	26	3.8	23	3.4	40	3.7	122	3.5	35	5.5	31	3.9	76	5.3
Tisanoptera	27	5.1	15	3.1	8	1.2	3	0.4	21	1.9	74	2.1	5	0.8	3	0.4	8	0.6
Aphidae	24	4.5	13	2.7	18	2.6	13	1.9	18	1.7	86	2.5	5	0.8	4	0.5	9	0.6
Homoptera non Aphidae	10	1.9	4	0.8	24	3.5	10	1.5	5	0.5	53	1.5	2	0.3	26	3.3	28	1.9
Coleoptera	5	0.9	10	2.0	8	1.2	4	0.6	9	0.8	32	0.9	11	1.7	13	1.7	24	1.7
Araneae	10	1.9	8	1.6	4	0.6	16	2.3	5	0.5	43	1.2	8	1.2	14	1.8	22	1.5
Lepidoptera	–	–	3	0.6	9	1.3	8	1.2	4	0.4	24	0.7	10	1.6	4	0.5	14	1.0
Hemiptera	1	0.2	–		–		–		–		1	0.03	–		–		–	
Plecoptera	–		–		3	0.4	–		1	0.1	4	0.1	33	5.1	55	7.1	88	6.2
Formicidae	–		–		–		–		7	0.6	7	0.2	–		–		–	
Orthoptera	–		–		–		–		–		–		–		1	0.1	1	0.1
Σ	531		488		681		680		1072		3450		640		779		1428	
% Winged	69.1		91.8		84.4		46.3		78.8		73.8		93.4		87.7		90.4	
% Non-winged	30.9		8.2		15.6		53.5		21.2		26.2		6.6		12.3		9.6	

have practically the same taxonomic range of prey, as do the Dry, Humid, and Wet subpopulations situated at the same altitude but in different microhabitats. Nematocera is the most abundant group in the Dry and Humid subpopulations, whereas in the Wet one Acarina dominate, and Nematocera is the next in order of quantitative importance. The number of Acarina and Collembola stuck to the leaves increases progressively along the Dry-Humid-Wet gradient.

Most of the arthropods found in the traps are also winged forms (Table 1). Nematocera and Diptera excluding Nematocera are the most abundant taxa, making up 70% of the total. Of the 13 groups represented, 12 are also found on the leaves of *P. nevadense* and only one, Orthoptera, is found exclusively on the mimic-traps. Despite this noticeable taxonomical similarity, some taxa are more abundant on the mimic-trap (e.g. Diptera and Plecoptera) than on the actual plant (Nematocera). These differences in relative abundance are significantly different between the Humid subpopulation of plants and their corresponding mimic-traps ($G=182$, $df=12$, $P<0.001$, G-test), but not between the plants belonging to the Dry subpopulation and the corresponding mimic-traps ($G=8$, $df=11$, n.s.).

P. nevadense shows a similar range of prey sizes in all populations (Fig. 1), although the size class distribution differs significantly between populations ($G=700$, $df=28$, $P \ll 0.001$). More than 80% of the captured prey are less than or equal to 2 mm in size, rarely larger than 3.5 mm. The biggest prey found was a small lepidopteran, 7 mm long.

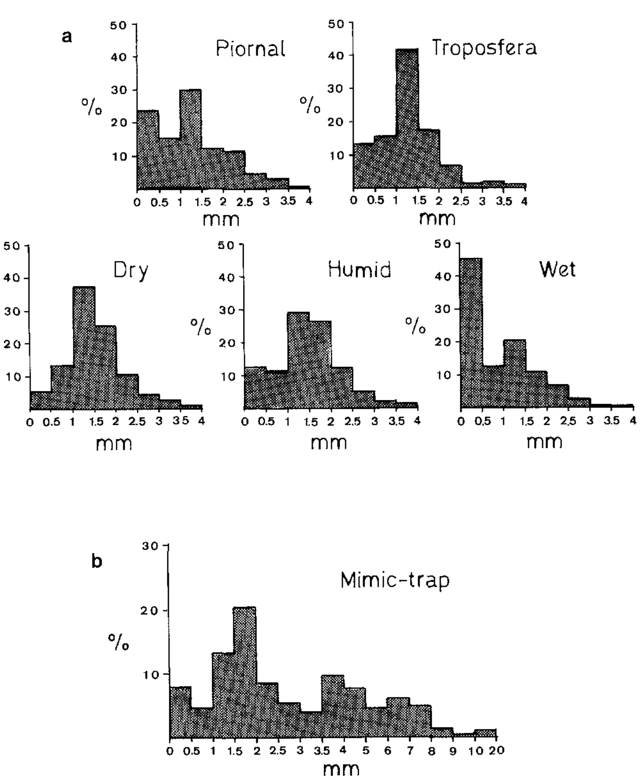

Fig. 1. a Size class distribution of prey captured in the Piornal and Troposfera population of *Pinguicula nevadense*, and in the Dry, Humid, and Wet microhabitats of the San Juan population. **b** Size class distribution of the arthropods trapped by the mimic-traps. The data from the Dry and Humid microhabitats are combined. See Table 1 for sample sizes

The size range of arthropods captured on the traps is also shown in Fig. 1. Nearly 30% of the individuals captured in the Dry subpopulation are bigger than 3.5 mm, and this value increases in the Humid subpopulation to 40%. The biggest arthropod captured in the trap was an orthopteran 20 mm in size. The mimic-traps capture a greater range of sizes than *P. nevadense*, and the size distributions are significantly different (Dry versus corresponding mimic-trap: $D=0.338$, $P \ll 0.001$ Kolmogorov-Smirnov test); Humid versus corresponding mimic-traps: $D=0.436$, $P \ll 0.001$). A comparison of the size of Nematocera and Diptera excluding Nematocera, the two dominant taxa in both the plant and the mimic-trap, shows that Nematocera do not differ statistically in size distribution between the plant and the mimic-trap ($D=0.105$, $P<0.1$), whereas dramatic differences appear in the case of Diptera excluding Nematocera ($D=0.879$, $P \ll 0.0001$).

Discussion

The results of this study show that *P. nevadense* captures prey of various insect and arachnid orders. This taxonomical diversity is a common characteristic of the majority of carnivorous plants studied to date (Juniper et al. 1989). Winged insects, especially Nematocera, are the main components of the diet of *P. nevadense*. These results differ from those of the studies carried out by Karlsson et al. (1987) with *Pinguicula villosa*, *P. alpina* and *P. vulgaris*, species which occupy a habitat in the tundra similar to that of *P. nevadense* in the Sierra Nevada and in whose diet Acarina and Collembola appear as the dominant groups. Winged insects, especially Nematocera, are also the principal prey captured by *Pinguicula vallisneriifolia* (Zamora, unpublished), another endemic plant of the Iberian Peninsula.

The attraction, retention, and capture of prey are the initial phases in the feeding process for carnivorous plants, which ends in absorption and assimilation of nutrients derived from the digestion of prey (the "carnivorous syndrome", sensu Juniper et al. 1989). Given its passive method of capturing prey, *Pinguicula* does not select its prey, strictly speaking, although there may be mechanisms of visual attraction which increase the probability of capture of certain taxa (Joel et al. 1985). In *Pinguicula* the capture mechanism is a mucilaginous compound, secreted by stalk glands on the surface of the leaf. The diversity of the diet, both in taxonomic composition and size, will depend on the retention capacity of the plant. The comparison between the prey actually captured by *P. nevadense* and the arthropods captured on the mimic-trap can allow us to examine the possible constraints of the capture mechanism. The results obtained show that the taxonomic composition of prey attached to leaves is nearly the same as that of the mimic-trap. Therefore, there does not seem to be a taxonomical selection in the diet. The filter appears to be related to prey size, since *P. nevadense* only captures prey from the lower end of the available size range. The sticky mucilage is not capable of retaining big arthropods that pass over its leaves, though they are frequently trapped by the mimic-trap. This is especially clear in the case of Diptera excluding Nematocera. Despite the difference in the size distribution (Fig. 1), the capture threshold is practically the same in all cases. The probability of capture of the arthropods whose size is close to this threshold is fundamentally related to its escape ability, as well as the "capture surface" of the prey with respect to the leaf. Some terrestial arthropods, such as ants, are capable of escaping from the leaf (Zamora, in press); this rarely occurs in other species of the same size with a greater "capture surface", such as long-winged and -legged individuals (e.g. small nocturnal Lepidoptera and large Nematocera). This differential response by potential prey of the same size but with different behaviour and/or morphological characteristics is somewhat similar to the escape-behaviour observed in insects with respect to a spider web (Nentwig 1982).

In conclusion, the comparison between the actual prey of the plant and the arthropods trapped by the mimic-traps shows that the principal factor determining the diet of *P. nevadense* is the retention capacity of the trapping mechanism. The arthropods that became prey were always below a specific size threshold. This size constraint may also be found in the diet of other carnivorous plants species using an adhesive trap (e.g. Watson et al. 1982). For this reason, further studies on the feeding ecology of this peculiar group of organisms should consider the "prey size" factor in relation to the adhesive capacity of the trapping mechanism as a prime object of study.

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