

Predation on black flies (Diptera: Simuliidae) by the carnivorous plant *Pinguicula vulgaris* (Lentibulariaceae) in northern Sweden

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Adult black flies represented nearly 85% of 915 arthropods captured by the carnivorous plant *Pinguicula vulgaris* L. along a stream in northern Sweden. Two species, *Cnephia eremites* Shewell and *Cnephia pallipes* (Fries), accounted for more than 97% of the total number of captured black flies. By virtue of their large populations, site fidelity at lake outfalls, and concentrated activity near the ground, these flies provide a predictable supply of prey that could affect the fitness of streamside carnivorous plants.

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1. Introduction

The boreal region encompasses a circumpolar area of about 11% of the Earth's land surface (Bonan & Shugart 1989). Within this region, the immature stages of black flies typically dominate the aquatic ecosystem, with populations of some species reaching densities of 600,000 larvae/m² (Wotton *et al.* 1998). A significant part of this massive secondary production is transferred to the terrestrial environment as winged adults. The impacts of adult black flies on the terrestrial ecosystem have been interpreted largely in terms of the nuisance and biting habits of the females, which derive from the need for homeothermic blood to mature the eggs, and the transmission of blood-borne agents of disease. Poorly explored in the terrestrial ecosystem is the role of adult black flies as plant pollinators and insectivore prey

(Malmqvist *et al.* 2004). Nonetheless, lengthy lists of predators on black flies, both immatures and adults, have been compiled (e.g., Davies 1981, 1991; Werner & Pont 2003), with some studies documenting black flies as the dominant dietary item of certain birds and fish (Gíslason 1985, Yoerg 1994, Robert & Cloutier 2001). However, we have found only one reference to a carnivorous plant capturing black flies: about 0.8% of the total prey in one population of the Nearctic pitcher plant *Sarracenia purpurea* L. consisted of black flies (Cresswell 1991).

A common group of carnivorous plants in the boreal environment is the genus *Pinguicula*, consisting of three species in northern Scandinavia. The plants are perennial geophytes with one or a few flower stalks and a basal rosette usually of 2–8 leaves, each 2–5 cm long, bearing an upper glandular surface capable of capturing and di-



Figure 1. *Pinguicula vulgaris* in northern Sweden, 15 June 2003, with adult black flies stuck to the adhesive surface of the leaves; the majority of black flies are beneath the curled leaf margins.

gesting arthropods (Karlsson *et al.* 1996). Prey, typically small arthropods, contribute significant amounts of nitrogen and phosphorous to *Pinguicula* and increase plant-nutrient uptake from the soil, enhancing fitness characters such as seed production and survival (Karlsson *et al.* 1996). Plants can obtain nearly all of the necessary nitrogen and phosphorous from their prey (Karlsson *et al.* 1994). Here we document the first report of black flies captured by carnivorous plants (*Pinguicula vulgaris* L.) in the boreal region.

2. Material and methods

We recorded the arthropods captured by *P. vulgaris* beside a stream (Skattån) ca. 600 m below its origin from a natural lake (Skatträsket) in Sweden (Swedish grid reference [x y]: 16622 72556) on 15 June 2003. Plants were sampled along an approximately 90-m stretch of stream bank, within 1.2–2.1 m of the stream margin. We removed all macroscopic arthropods, by hand, from five groups of five plants each, for a total of 25 plants, each plant with 4–9 (mean 5.9 ± 0.34 S. E.) leaves but without flowers. Mites were not sampled because some of them might inhabit the leaves (Karlsson *et al.* 1994). At the time of sampling, air temperature was 12.0° C, water temper-

ature 13.2° C, conductivity 17 μ S/cm, pH 6.85, and stream width 2.5 m. We also collected larval black flies from the stream adjacent to the plants. All black flies were identified to the lowest taxonomic level, typically the species, whereas nonsimuliid taxa were identified to family. Voucher specimens of adult black flies are deposited in the Clemson University Arthropod Collection, Clemson, South Carolina.

3. Results and discussion

From 25 plants, we collected 915 arthropods representing 22 families (Table 1). The majority (96.9%) of these arthropods were winged. Although our study was limited in space and time, a clear pattern emerged: captured prey were dominated by nematoceros Diptera (94.6%), particularly the family Simuliidae (84.7%). Our data agree with those of previous reports from northern Sweden that show a preponderance of nematoceros Diptera captured by *P. vulgaris*. However, our data do not mirror the high percentage of Collembola previously reported (Karlsson *et al.* 1994). Diptera also are the dominant prey captured by additional species of *Pinguicula* in other regions of the world (Zamora 1990, Antor & Garcia 1994, Alcalá & Domínguez 2003).

Nearly 98% of the captured black flies in our

Table 1. Arthropods ($n = 915$) captured by *Pinguicula vulgaris* beside a stream (Skattån) in northern Sweden, 15 June 2003, listed alphabetically by order and within order.

Taxon	Larvae	Males	Females	Unknown	% of total
Araneae					
Linyphiidae	–	3	–	–	0.3
Coleoptera					
Staphylinidae	1	–	–	–	0.1
Collembola					
Entomobryidae	–	–	–	6	0.7
Hypogastruridae	–	–	–	1	0.1
Isotomidae	–	–	–	11	1.2
Diptera					
Ceratopogonidae	–	–	2	–	0.2
Chironomidae	–	4	19	–	2.5
Chloropidae	–	–	1	–	0.1
Empididae	–	–	1	–	0.1
Phoridae	–	–	1	–	0.1
Sciaridae	–	29	40	–	7.5
Simuliidae	–	647	128	–	84.7
Hemiptera					
Aphididae	–	–	1	–	0.1
Cicadellidae	7	–	–	–	0.7
Psyllidae	–	1	–	–	0.1
Hymenoptera					
Braconidae	–	1	–	–	0.1
Ceraphronidae	–	1	–	–	0.1
Formicidae	–	–	2 (workers)	–	0.2
Scelionidae	–	3	–	–	0.3
Lepidoptera					
Coleophoridae	–	1	–	–	0.1
Plecoptera					
Nemouridae	–	1	–	–	0.1
Trichoptera					
Hydroptilidae	–	–	3	–	0.3

study consisted of two species in the genus *Cnephia*, viz. *C. eremites* Shewell and *C. pallipes* (Fries). These species also were dominant (88.1%) among larval black flies in the adjacent stream. Each cluster of five plants had a mean of 155 (± 25.4 S. E.) black flies, with as many as 24 individuals per leaf. The preponderance of the genus *Cnephia* among the captured arthropods reflects the bionomics of these flies. Both species of *Cnephia* are common in the boreal regions of the world, where they breed in large populations at the outfalls of natural lakes and artificial impoundments. After emerging from the pupae, they concentrate their activities at the natal site. Females are obligatorily autogenous (i.e., the mouthparts are not adapted for blood feeding); they, therefore, do not need to disperse from the

natal sites for blood meals, but instead remain near the stream, searching for oviposition sites, although flights for sugar meals might occur. Of 124 captured females, 8 carried chorionated eggs, 13 had immature eggs, and the remainder were devoid of eggs, suggesting that they had deposited their eggs before capture or that the immature eggs and fat body had been digested by the plants. Males search for and couple with females on the ground, rather than in the more typical aerial mating swarms (Adler *et al.* 2004). A population of *Cnephia* has developed in the Skattån stream since at least 1993; the adults emerge during June when *P. vulgaris* is actively growing. We do not know, however, the influence of *Pinguicula* predation, if any, on the population of the two species of *Cnephia*.

Table 2. Simuliid adults (males and females) captured by streamside *Pinguicula vulgaris*, plus simuliid larvae collected in the adjacent stream (Skattån) in northern Sweden, 15 June 2003; species are listed alphabetically.

Species ^A	Males	Females	Larvae
<i>Cnephia eremites</i> Shewell	635	x ^B	110
<i>Cnephia pallipes</i> (Fries)	3	x ^B	46
<i>Simulium paramorsitans</i> Rubtsov	5	1	17
<i>Simulium truncatum</i> (Lundström)	1	2	1
<i>Simulium vernalis</i> Macquart	0	0	3
<i>Stegopterna trigonum</i> (Lundström)	3	1	0

^A One male and two females of the genus *Cnephia* were infected with mermitiid nematodes.

^B Species-level characters are not available to identify the 124 females of *Cnephia*.

Other than two ant workers and one stonefly adult, black flies were the largest organisms captured by the plants in our study. These black flies are nearly the same size as *Drosophila* flies that have been fed experimentally to *P. vulgaris*. Nitrogen from captured *Drosophila* is allocated to plant reproductive organs and winter buds and also increases the uptake of nitrogen from the soil; however, only about 29–42% of the nitrogen in *Drosophila* is exploited, which is less than the stimulated root uptake from the soil (Hanslin & Karlsson 1996). Hanslin and Karlsson (1996) speculated that prey smaller than *Drosophila* might allow more complete digestion and assimilation of prey. Too many prey, however, could negatively affect photosynthetic abilities (Karlsson *et al.* 1996) or perhaps provide substrate for bacterial and fungal growth harmful to the plant. Studies are needed to determine the nutritive value of black flies, measured as an increase in plant fitness, and the possible costs associated with increased numbers of prey.

The male-biased sex ratio (5:1) of the captured *Cnephia* might reflect (1) the possibility that males are more active than females on stream banks and, therefore, more likely to be captured, (2) a characteristic sex ratio of the species, as in

the obligatorily autogenous Nearctic *Cnephia dacotensis* (Dyar & Shannon) in which mating occurs on the ground and males outnumber females by more than 3 to 1 (Back & Harper 1979), (3) a greater probability of escape by females, as recorded for spider-web captures of some Nearctic black flies (Adler *et al.* 1983), or (4) a temporal sampling bias; most black flies are protandrous (i.e., males emerge before females), and we might have collected the flies before the peak of female emergence.

The flow of organisms and energy between aquatic and terrestrial systems, represented here by the interactions of terrestrial carnivorous plants and their aquatic-derived prey, provide a model system in landscape ecology (cf. Nakano & Murakami 2001). The capture of black flies by *P. vulgaris*, although presumably opportunistic, further illustrates the breadth of possible interactions between black flies and other biota of the boreal region.

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