

## THE POLLINATION OF *PEDICULARIS PALUSTRIS* BY NECTAR THIEVES (SHORT-TONGUED BUMBLEBEES)

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### SUMMARY

Operation of the pollination mechanisms of *Pedicularis palustris* L. by nectar and pollen foraging bumblebees (*Bombus* Latr.) was studied. It was found that pollination could be achieved in two ways:

1. by normal collectors, viz. long-tongued bumblebees;
2. by nectar thieves, viz. short-tongued bumblebees.

Normal collectors (*Bombus muscorum* L., *B. pascuorum floralis* Gmel. and *B. hortorum* L.) introduced their head and tongue into the 12 mm corolla tube to secure nectar, while stigma and style swept the forager's head and thorax. Nectar thieves (*Bombus jonellus* Kirby, *B. terrestris* L. and *B. lucorum* L.) obtained nectar through holes in the corolla tube made by the latter two species. Pollen collecting thieves pushed against the upper lip while hovering in the air. Thus pollen was released and dusted on venter and legs. This foraging behaviour was attended by a hissing sound, presumably caused by wing vibrations.

Both ways of pollination resulted in large-scale seed-setting, thus contradicting the common interpretation that nectar thieves do not effect pollination and seed production.

### 1. INTRODUCTION

Flower visiting insects are classified as normal collectors and primary and secondary nectar thieves (LØKEN 1962). Normal collectors introduce their head and tongue into the corolla tube to secure nectar; meanwhile stigma and style touch head and thorax. Primary nectar thieves obtain nectar by biting a hole into the long corolla tube close to the nectary. Secondary thieves secure nectar by using holes bitten by primary thieves. The thieves thus obtain nectar supplies without pollinating the flower (STAPEL 1933; MACIOR 1966; FREE 1970), with the exception of *Melampyrum* (MEIDELL 1944), as will be described below.

In *Pedicularis palustris* the role of normal collectors and nectar thieves was studied. In the genus *Pedicularis* (*Scrophulariaceae*) the structures of the flowers of most species appear to be adapted to bumblebee pollination. Some of them are pollinated by small bees, hummingbirds, butterflies and Syrphids. Self-pollination does not occur or to an insignificant extent (SPRAGUE 1960, 1962; MACIOR 1966, 1971; MACINNES 1972).

Upon examination of the pollination mechanisms of *Pedicularis palustris* it was found that nectar thieves may effect pollination. The behaviour observed was comparable to that described by MEIDELL (1944) for short-tongued

bumblebees visiting *Melampyrum pratense*. He did not consider the effectiveness of this mechanism, however.

This paper mainly deals with the pollination mechanisms of nectar thieves visiting *P. palustris* and a consideration of the effectiveness of such pollination.

## 2. MATERIALS AND METHODS

During June, July, and August of 1972 the insects visiting *P. palustris* populations were observed on Schiermonnikoog, a West Frisian island. Observations were made in four dune slacks, viz.: 1. Kapenglop (KAP), 2. Reddingsweg West (RWW), 3. Reddingsweg East (RWE), 4. area near the field station of the Free University of Amsterdam (VU). These areas were selected to investigate the influence of the different surrounding vegetation.

In the beginning of June plants in bud were caged to exclude insects, other plants nearby were individually marked. The blooming phenology and seed production of both groups of plants were recorded. Viability of the seeds was tested at 25°C, after stratification of the seeds for a period of two months. This treatment had been found to result in the highest germination percentage (KOEMAN-KWAK 1973).

Bumblebees were captured, anaesthetized by diaethylaether, identified (KRUSEMAN 1947; DEN BOER 1954) and individually marked with a waterproof paint. Observations were made from 07.00 a.m. till sunset if the weather was favourable. Individual bumblebees were followed during ten minutes or longer. Corbicular loads, if present, were taken and analyzed.

## 3. RESULTS

### 3.1. Nectar and pollen foraging of the pollinators

#### 3.1.1. Normal collectors

*Bombus muscorum* (Q, queen and W, worker), *B. pascuorum floralis* (Q, W), *B. hortorum* (W) were all captured on *P. palustris* foraging on the flowers as normal collectors. The tongue lengths of the queens are > 12 mm (BRIAN 1954). They introduced their head and tongue into the corolla tube to secure nectar, meanwhile receiving pollen on head and thorax which contacted the stigma of the next flower visited. The pollen was mainly deposited on the left side of the bee's head and thorax because the flower is slightly twisted (*fig. 1*). After the bumblebee had visited some flowers pollen was groomed from thorax and head by forward movements of the midlegs and transferred to the corbiculae.

#### 3.1.2. Nectar thieves, the nectar foraging behaviour

The only primary thief observed was *B. terrestris* (here applied as including *B. lucorum* since the two species are not readily distinguishable in the field). After probing the corolla surface with the antennae (which may give olfactory clues to



Fig. 1. *Bombus muscorum*, queen, foraging in normal position on a *Pedicularis palustris* flower.



Fig. 2. *Bombus terrestris*, worker, securing nectar through a hole in the corolla; the flower is completely covered.



Fig. 3. *Bombus jonellus*, worker, in nectar foraging position; the flower is visible.

the presence of nectar) both queen and worker made holes with their mandibles just on the margin of calyx and corolla; while biting they always sat on the upper lip parallel to the flower axis, thus covering the flower completely (fig. 2).

*Bombus* species which behaved as secondary thieves were *B. terrestris* (Q, W) and *B. jonellus* (W). Tongue lengths of the queens are  $<11$  mm (BRIAN 1954). *B. jonellus* was sitting sideways, perpendicular to the flower axis, so that the flower was visible (fig. 3).

### 3.1.3. Nectar thieves, the pollen foraging behaviour

*B. terrestris* and *B. jonellus* collected pollen on the *P. palustris* flower. The bumblebee:

1. approached the flower mostly from the right side (right of the flower refers to that position when an observer views the flower from the point of the axis);
2. hovered in the air beside the flower without alighting or supporting on flower parts;
3. pushed against the place on the upper lip behind which the anthers were enclosed. Thus pollen was released and dusted on the legs and venter of the bee from where it could be transported to the corbiculae. Grooming of the dorsum with the midlegs was not observed. Pushing was accompanied by a hissing sound, probably wing vibrations.

After pollen foraging the bee started pollen foraging on a second flower or

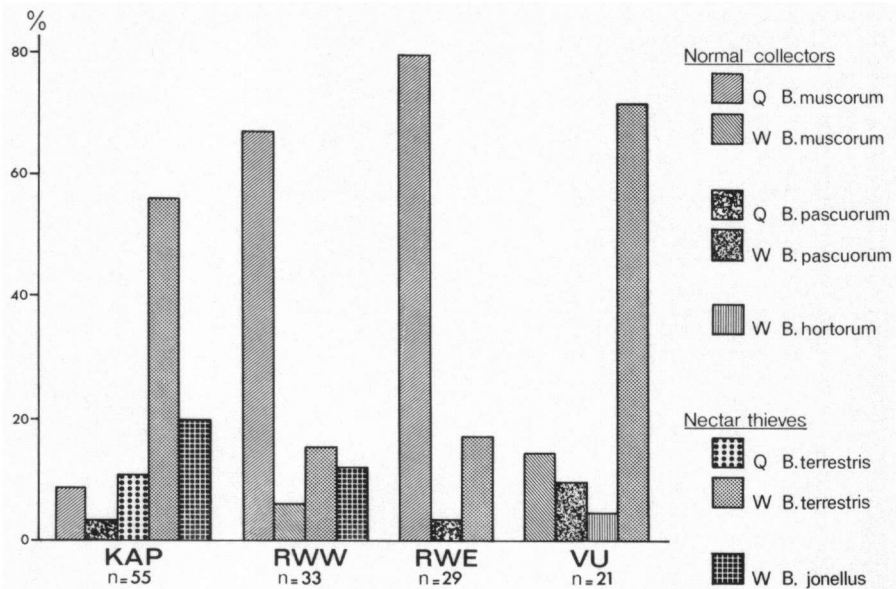


Fig. 4. The percentage contributed per *Bombus* species (see key) foraging on *Pedicularis palustris* to the total pollen loads collected per area.

nectar foraging on the same flower, as a primary (*B. terrestris*) or a secondary thief (*B. terrestris*, *B. jonellus*). When the same bee assumed a nectar foraging position the protruding stigma was touched and pollen transferred. Three groups could be distinguished: nectar collecting individuals, pollen collecting individuals, and individuals collecting both. It may be assumed that pollination was only achieved by the latter group.

### 3.2. *Bombus* species per area and their pollen loads

Five *Bombus* species regularly visited *P. palustris* but not all species were equally frequent in each area. Fig. 4 illustrates that many *B. terrestris* individuals were captured in KAP and VU. On the other hand many *B. muscorum* visited the flowers in RWW and RWE. Summarizing these differences between areas, KAP and VU show a predominance of "thief" visitation, whereas RWW and RWE show primarily "normal" visitation. Other *Bombus* species observed were *B. pascuorum*, *B. jonellus*, and *B. hortorum*.

Analysis of the loads showed that many consisted of only one pollen type, *P. palustris* (table 1). Mixed loads contained at most five pollen types. In total fourteen pollen types were distinguished in addition to *P. palustris*.

### 3.3. Self-pollination

Data on self-pollination potentials are summarized in table 2 and compared with the seed production in insect-pollinated plants in the immediate vicinity.

Table 1. Analysis of the loads of bumblebees foraging on *P. palustris* % pure *P. palustris* loads are given; in brackets total number of collected loads.

		KAP		RWW		RWE		VU	
<i>B. muscorum</i>	Q	60.0	(5)	86.3	(22)	82.6	(23)	—	—
	W	—	—	100	(2)	—	—	33.3	(3)
<i>B. pascuorum</i>	Q	100	(2)	—	—	100	(1)	—	—
	W	—	—	—	—	—	—	0	(2)
<i>B. terrestris</i>	Q	83.4	(6)	—	—	—	—	—	—
	W	90.3	(31)	80.0	(5)	100	(5)	66.7	(15)
<i>B. jonellus</i>	W	100	(11)	50.0	(4)	—	—	—	—
<i>B. hortorum</i>	W	—	—	—	—	—	—	100	(1)
Total		89.1	(55)	81.8	(33)	86.2	(29)	57.1	(21)

Table 2. Seed production: extreme values of the complete flowering period.

	Caged		Uncaged	
	seeds/capsule	% germination 25°C	seeds/capsule	% germination 25°C
KAP	0.0–0.7	0.0–21.7	11.6–15.8	86.0 (averages)
RWW	0.1–0.7	48.0–85.7	16.5–18.0	90.0
RWE	0.2–2.7	54.6–91.3	9.5–12.6	63.9

The seed output of uncaged plants was larger than that of caged ones. A difference exists between the number of seeds per capsule of pollinated plants of KAP (thieves) and RWW and RWE (normal collectors). KAP takes an intermediate position, which means that no essential difference occurs between the effectiveness of the methods of pollination.

The germination percentages of seeds of self-pollinated plants varied from one plant to another in the same way as the self-pollination potentials, but if seeds are developed, they also have germination capacity. The small number of seeds produced by caged plants may be partly due to side effects of the cage but it is clear that when large insects were excluded, seed-setting was decreased to a low level.

#### 4. DISCUSSION

A correlation appears to exist between the tongue length of the bumblebees and the way they visit the *P. palustris* flower. Species with a queen-tongue length exceeding 12 mm were observed to be normal visitors and shorter than 11 mm were thieves.

The areas studied showed a distinct difference with regard to the visiting *Bombus* species. The cause of this difference is possibly an ecological preference of the *Bombus* species; little is known about this subject (BRIAN 1957).

KAP was characterized by many thieves, *B. terrestris* individuals, and the Reddingsweg by normal collectors, *B. muscorum*. Analysis of the loads showed that *B. terrestris* and *B. ionellus* also functioned as real collectors of *P. palustris* pollen. Comparing these data with the results of table 2 showing that the seed production in KAP was not reduced, the conclusion is that pollination must have been effected by nectar thieves. The normal collectors in KAP also have effected pollination, but their contribution to the pollination of *P. palustris* was relatively small because of their number.

MEIDELL (1944) described one method by which short-tongued bumblebees effect cross-pollination of the related *Melampyrum pratense*. After the bee has robbed a flower of nectar, she places herself on the edge of the upper lip, stretching her hindlegs across its mouth and vibrates her wings rapidly. This results in pollen being showered on to her legs. When this same bee takes up her position on the next flower, her pollen-covered legs touch the projecting stigma, thus probably effecting pollination.

A nectar thief on *P. palustris* collected nectar after pollen foraging. The pollen collecting thief did not place herself on the upper lip, but hovered beside the flower. While nectar collecting, she was sitting on the upper lip parallel to the flower axis (*B. terrestris*), in the same position as the nectar collecting position on *Melampyrum pratense*, or sideways (*B. jonellus*).

Individuals collecting both pollen and nectar pollinated the *P. palustris* flower. The seed production of the flowers thus pollinated was comparable to that of flowers pollinated by normal collectors.

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