

POLLINATION ECOLOGY OF FIVE HEMIPARASITIC, LARGE-FLOWERED RHINANTHOIDEAE WITH SPECIAL REFERENCE TO THE POLLINATION BEHAVIOUR OF NECTAR-THIEVING, SHORT- TONGUED BUMBLEBEES

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SUMMARY

Operation of the pollination mechanisms of *Rhinanthus serotinus* (Schönh.) Oborny, *R. minor* L., *Pedicularis palustris* L., *P. sylvatica* L., and *Melampyrum pratense* L. by nectar and pollen-collecting bumblebees (*Bombus* Latr.) was studied. Pollination by bumblebees may be achieved in two ways:

1. Head-thorax pollination by nototribic long-tongued bumblebees. Long-tongued bumblebees forage upright for nectar, while the stigma nototribically contacts residual pollen in the head-thorax crevice; pollen not retained in this crevice is groomed from the body by a forward movement of the middle legs crossed over the dorsum and deposited in the corbiculae.
2. Venter pollination by sternotribic, short-tongued bumblebees (incl. nectar thieves). Nectar thieves obtain nectar by biting a hole in the long corolla tube close to the nectary. These short-tongued bumblebees usually collect pollen in an inverted position. They grasp the edge of the galea with their mandibles and tear it asunder. Their abdomen is curved under the pollen chamber formed by the galea enclosing the anthers. Pollen is vibrated loose by means of wing movements, which produce a hissing sound; pollen is deposited on the ventral side of the body of the bumblebee, particularly on the sternites and transported to the corbiculae. Both ways of pollen collecting result in deposit of large amounts of pollen on the bodies and in the corbiculae of the pollinating bumblebees.

1. INTRODUCTION

This paper forms part of a series on the flower biology and biosystematics of large-flowered *Rhinanthoideae* in the Netherlands: *Pedicularis palustris* L., *P. sylvatica* L., *Rhinanthus serotinus* (Schönh.) Oborny, *R. minor* L. and *Melampyrum pratense* L. It describes the behaviour of insects visiting these species.

Flower visiting insects are generally classified as normal visitors and primary or secondary nectar thieves (LØKEN 1962). A normal visitor introduces head and tongue into the corolla tube to secure nectar while stigma and style nototribically touch head and thorax. A primary nectar thief obtains nectar by biting a hole into the long corolla tube close to the nectary. Secondary nectar

thieves secure nectar by using holes bitten by primary nectar thieves. The thieves thus obtain nectar supplies without pollinating the flower (STAPEL 1933, FREE 1970, MACIOR 1973). Some authors consider the perforating behaviour of short-tongued bumblebees injurious (JANY 1950, EATON & STEWARD 1969).

Although many species of the genera *Pedicularis*, *Rhinanthus* and *Melampyrum* are present in Europe, especially in the Alps, usually only the normal way (head-thorax) of pollination is mentioned (MÜLLER 1881, VON KIRCHNER 1911, SCHOENIGEN 1922, OLBERG 1951, FAEGRI & VAN DER PIJL 1966, KUGLER 1970, PROCTOR & YEO 1973, HEGI 1974).

Many authors mention nectar thieves, especially several *Bombus* species, visiting the five hemiparasites concerned (MÜLLER 1881, HEINSIUS 1890, SCHULZ 1890, HEUKELS 1910, MEIDELL 1944, EBERLE 1951, WERTH 1955, TER BORG 1972, HEGI 1974).

MÜLLER (1881) saw a *Bombus terrestris* queen on *Pedicularis sylvatica*, chewing on the upper lip. HEINSIUS (1890) saw *B. Scrimshiranus* (= *B. jonellus*), a nectar foraging worker, on a flower of *P. sylvatica* pulling one of the anthers out of the galea with its mandibles and eating pollen from it. After this visit the anther was hanging out of the galea. Neither author associated the observed behaviour with pollination.

In America the genus *Pedicularis*, which possesses a great degree of variation in floral forms, received much attention. SPRAGUE (1962) studied seven species of *Pedicularis* in the context of pollination and evolution. Although numerous bumblebees were observed visiting the flowers the pollination mechanisms of some species remained an enigma even after two seasons' observation. Cinematographic studies by MACIOR (1968, 1970, 1973) of pollinating insect behaviour (*Bombus* species) on *Pedicularis* clarified the operation of the mechanisms. Close coadaptations between some flowers and their pollinators do exist (MACIOR 1971).

A pollen collecting behaviour different from the normal way resulting in pollination of European species is mentioned by MEIDELL (1944) for bees and bumblebees on *Melampyrum pratense*, by FAEGRI & VAN DER PIJL (1966) for bumblebees on *Pedicularis palustris*, and by KOEMAN-KWAK (1973) for bumblebees on *P. palustris*.

The present study was undertaken to extend our knowledge of the floral ecology of all the large-flowered *Rhinanthoideae* in the Netherlands, with special reference to the pollination behaviour of short-tongued bumblebees. In one of my following papers, I hope to deal with the effect of bumblebee visits on the seed set and hybridization.

2. MATERIALS AND METHODS

From May until September of 1974 and 1975 insects were observed visiting populations of *Pedicularis palustris*, *P. sylvatica*, *Rhinanthus serotinus*, *R. minor* and *Melampyrum pratense* in the North of the Netherlands including the West Frisian island of Schiermonnikoog. Observations were made from sun-

rise until sunset if the weather was favourable for bumblebee activity. Bumblebees were captured, anaesthetized by diethylether and identified (KRUSEMAN 1947, DEN BOER 1954). Foraging behaviour of insects in the field was recorded on 16 mm film at a recording speed of 64 frames per sec. and analyzed by single frame exposure.

3. OBSERVATIONS

3.1. Flower morphology

The zygomorphic flowers of members of the *Rhinanthoideae* are two-lipped. The lower lip forms a more or less flat landing platform in most species (*plate 1*). In *P. palustris* and *P. sylvatica* and less so in *R. minor* and *M. pratense* the lower lip is widely expanded; in *R. serotinus* it presses against the upper lip so that before introducing their heads into the corolla the visiting insects must push it away. In all species the upper lip forms a narrow, laterally flattened hood enclosing the four stamens. The two pairs of stamens face one another forming a pollen chamber in the galea. The pressure of the sides of the hood keeps them together thus preventing the escape of pollen. The powdery light yellow-beige pollen leaves the thecae via central longitudinal slits (*fig. 12*). The style just protrudes slightly from the underside of the hood near its tip (*P. palustris*, *P. sylvatica*, *R. serotinus*) or is enclosed by the hood (*R. minor*, *M. pratense*). Nectar is found at the base of the ovary.

3.2. Insect visitors

Insect visitors on the plant species studied were divided into two groups, viz., frequent visitors, collecting pollen and nectar (*Bombus* queens and workers) and occasional visitors (*Apoidea*, e.g. *Apis mellifica*, *Psithyrus* spp., *Lepidoptera* and *Syrphidae*). Thrips (*Thysanoptera*) were often present in the flowers.

3.2.1. Frequent visitors

Depending upon their behaviour on the flowers, two groups of bumblebees could be distinguished: nototribic pollinators and sternotribic pollinators.

3.2.1.1. Nototribic pollinators

Long-tongued bumblebees were seen to introduce their heads and tongues into the corolla tube to secure nectar, foraging upright in the normal way. The sides of the flower hood and the lower parts of the filaments were pressed apart by the tongue and head of the visiting bumblebee. The pollen dropped out of the pollen chamber mainly onto the head and thorax, while the stigma nototribically contacted residual pollen in the head-thorax crevice (*figs. 2, 3*). When introducing their heads, the bumblebees cross-pollinated the flower; when leaving the flower they may have brought about self-pollination. Pollen not retained in the head-thorax crevice was groomed from the body by a forward movement of the middle legs crossed over the dorsum and deposited in the corbiculae.

Bombus hortorum L., *B. pascuorum* Scop., *B. muscorum* L. (both queens and

workers) and *B. equestris* F., *B. ruderarius* Müll (queens) were seen to behave in this way only (table 1). Many *B. pascuorum* workers visited *R. serotinus* flowers in a more oblique-normal position. They entered the throat from the side of the flower. In their attempt to reach the nectar, the bumblebees completely turned their bodies so that pollen was first deposited on the thorax, then on the right or the left side of the body and finally on the venter of the bumblebee (figs. 5, 6).

3.2.1.2. Sternotribic pollinators

Pollen-collecting short-tongued bumblebees approached the flowers, landed upside-down on the upper lip, supported their inverted bodies by grasping the galea with their legs, and curved their abdomen under the pollen chamber. By grasping the edge of the galea with their mandibles and tearing it asunder, they opened the pollen chamber (figs. 9, 10, 11, 12). Wing vibrations, causing a hissing sound, released the pollen which was deposited on the venter (sternites) and on and between the legs of the bumblebees. Pollination was achieved when the stigma touched the pollen-covered venter of the inverted bumblebee. The bumblebees grasped the galea both on the left and the right side of the flower hood. (Left of the flower refers to that position when an observer views the flower from the point of the axis.) On the slightly twisted flower of *P. palustris* the bumblebees hung in an inverted position mainly on the left side (figs. 9, 10, 11). The whole process was carried out very quickly – all in all in about 1 to 3 seconds. After visiting one or several flowers the bumblebee groomed the pollen from the venter during the flight, and the pollen was transported to the corbiculae. Flowers visited by sternotribic pollinators often exhibited damage caused by the tearing and grasping of the insect's mandibles. Damage was visible, as brown spots on the upper lip, or as the absence of the distal part of the hood as in the case of *P. sylvestris* (figs. 2, 8).

B. lapidarius L., *B. hypnorum* L., *B. pratorum* L., *B. jonellus* Kirby and *B. terrestris* L. were sternotribic pollinators (table 1). (*B. terrestris* throughout

Plate 1.

Fig. 1. *Pedicularis sylvatica* flower; midway inside the corolla tube a thrips is present.

Fig. 2. *Melampyrum pratense* with a nototribic pollinating *Bombus hortorum* worker; the two lowest flowers have brown spots on the upper lips caused by sternotribic pollinators.

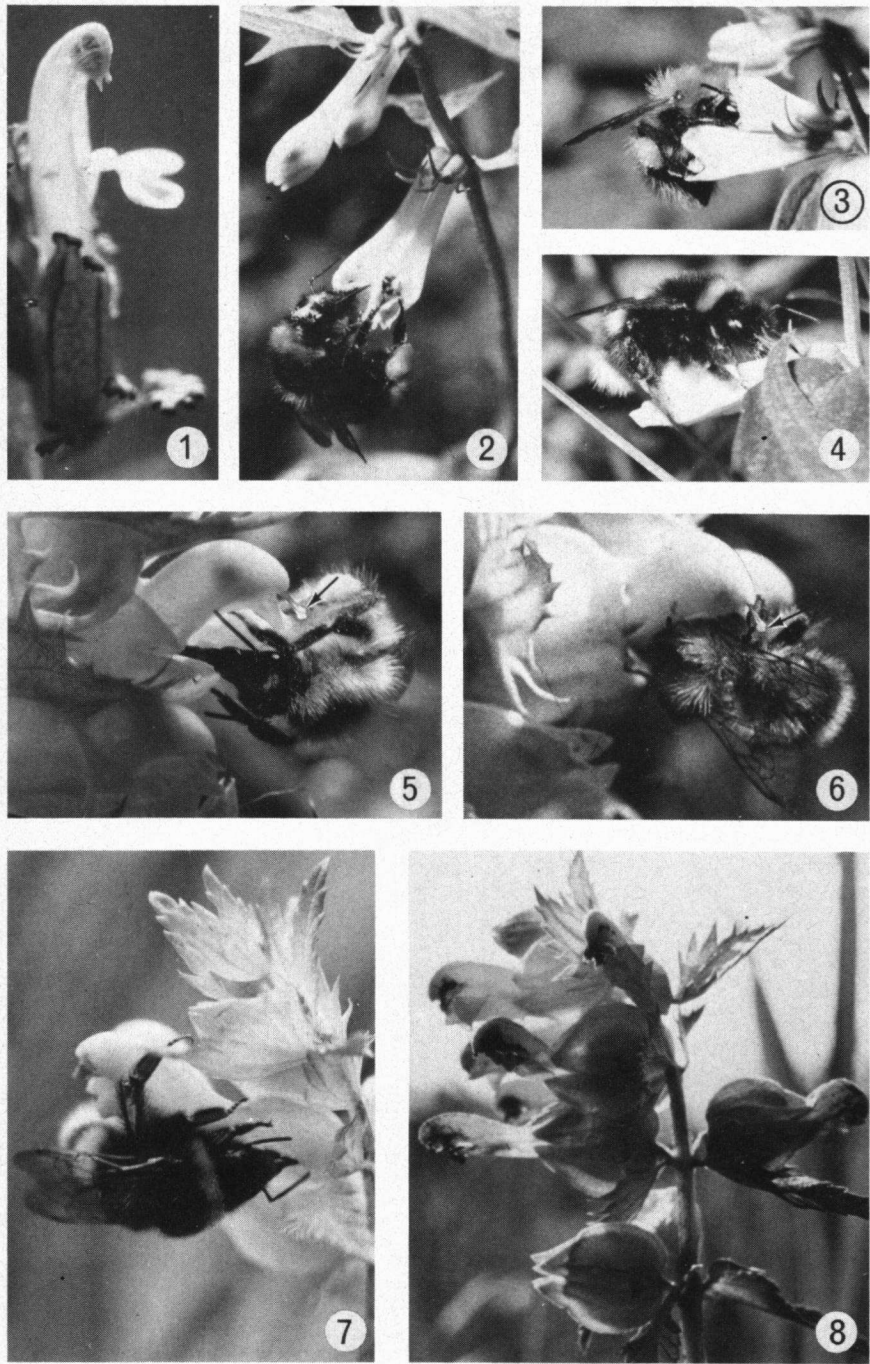
Fig. 3. *M. pratense* with a nototribic pollinating *B. pascuorum* worker.

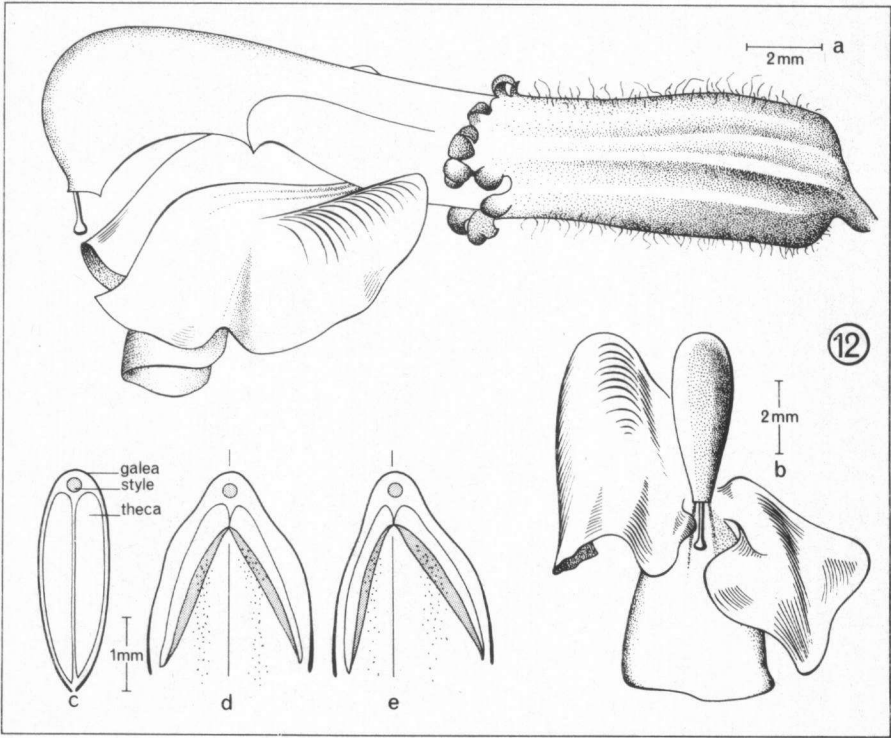
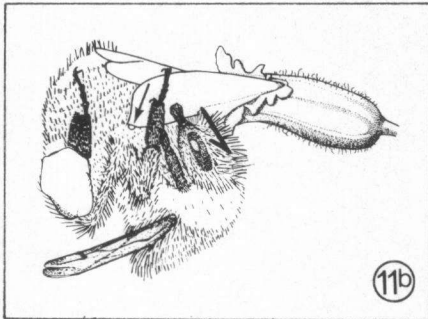
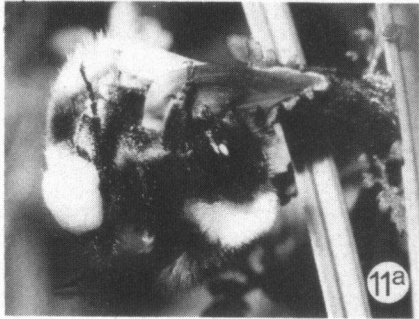
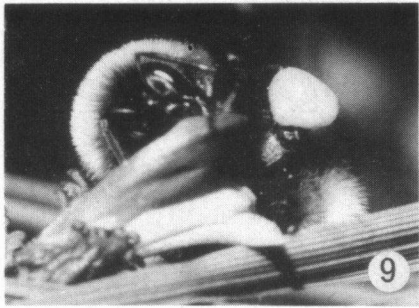
Fig. 4. *M. pratense* visited by a nectar-thieving *B. terrestris* worker.

Fig. 5, 6. *Rhinanthus serotinus* visited by a *B. pascuorum* worker, in an oblique normal position; arrow indicates point of stigmatic contact with pollinator.

Fig. 7. *R. serotinus* with a nectar-thieving *B. terrestris* worker.

Fig. 8. *R. serotinus* showing perforations on the calyx and brown spots on the upper lip.





this paper includes *B. lucorum* L. since the two species are not readily distinguishable in the field.)

The corolla tube of the plant species studied, and often the calyx (*R. serotinus* and *R. minor*), exhibited many perforations close to the nectary bitten by primary nectar thieves (*B. terrestris*, *B. jonellus*, fig. 8). Pollen transport from the body of the perforating bumblebee to the pistil is not to be expected (figs. 4, 7). Among the thieves three groups could be distinguished, viz., nectar collectors, pollen collectors and individuals collecting both on the same flower during one foraging trip. The latter always first collected pollen and then nectar through a perforation. *B. jonellus* and *B. terrestris* behaved as primary and secondary nectar thieves. *B. lapidarius*, *B. hypnorum*, *B. pratorum* and some workers of *B. muscorum* (on *P. palustris*) were secondary thieves. Other upright visiting bumblebees were never seen using the perforations. Sometimes queens and workers of *B. lapidarius*, *B. pratorum* or *B. terrestris* visited a *R. serotinus* or a *R. minor* flower upright (head-thorax pollination). *B. pratorum* and *B. terrestris* visited flowers of *M. pratense* also in an upright position, without inserting their tongues. They introduced their heads and vibrated with their wings. In this position pollen was mainly deposited on the clypeus and between the eyes. These bumblebees collected nectar through perforations.

3.2.2. Occasional visitors

Cuckoo bees (*Psithyrus*) secured nectar through holes as secondary thieves. Several species of butterflies, particularly *Plusia gamma* L., visited the flowers for nectar.

Now and then syrphids ate pollen from the under lip where it had fallen from visits of bumblebees. There is little chance that these occasional visitors released pollen or touched the stigma. The role of thrips in pollination is also doubtful (fig. 1). Rarely, small bees (e.g. *Halictus* spp.) spent a lot of time on one flower hanging on the upper lip and releasing pollen. Their visits were not very successful with regard to pollination due to their small body sizes. The corbiculae of one honeybee, however, contained *P. palustris* pollen only.

Plate 2.

Fig. 9, 10. A sternotribic pollinating *B. terrestris* worker on *Pedicularis palustris*.

Fig. 11a, b. A sternotribic pollinating *B. terrestris* worker on *P. palustris*; the mandibles grasping the edge of the galea are visible; arrow indicates point of stigmatic contact with pollinator.

Fig. 12a. *Pedicularis palustris* flower. b. front view of the asymmetric *P. palustris* flower. c. cross section through the galea; showing the position of the thecae in the galea. d. cross section through the galea when a nototribic pollinator enters the flower; the pollen chamber opens when the bumblebee introduces her head. e. cross section through the galea when a sternotribic pollinator visits the flower; by grasping the edge of the galea with her mandibles and tearing it asunder (right on the drawing) the pollen chamber is opened asymmetrically.

Table 1. Foraging positions of bumblebees on five species of *Rhinanthoideae*; plant species arranged according to decreasing corolla tube length; *Bombus* species of queen tongue lengths in order of sizes from long to short as given by Brian (1954).

		Pedicularis sylvatica	Melampyrum pratense	Pedicularis palustris	Rhinanthus serotinus	Rhinanthus minor
B. hortorum	Q U	U	U	U	U	U
	W U	U	U	U	U	U
B. muscorum	Q -	-	U	U	U	U
	W -	-	U(Ths)	U	-	-
B. equestris	Q -	-	U	U	-	-
B. lapidarius	Q U	-	-	I(U)	I(U)	I(U)
	W -	I	I/Ths	I(U)	I/Ths (U)	I/Ths (U)
B. pascuorum	Q U	-	U	U	U	U
	W U	U	U	Uobl.	U	U
B. ruderarius	Q -	-	-	(U)	-	-
	W -	-	-	(I)	-	-
B. hypnorum	Q -	-	-	(Ths)	-	-
	W -	I	I/Ths	I(U)	I	I
B. pratorum	Q -	(U)	(U)	-	(U)	(U)
	W I	I/Ths(U)	I/Ths	I/Ths(U)	I/Ths(U)	I/Ths(U)
B. jonellus	W I	-	I/Th	I	-	-
B. terrestris	Q -	-	I	I(Th, U)	I(Th, U)	I(Th, U)
	W I/Th	I/Ths(U)	I/Th	I/Th(U)	I/Th(U)	I/Th(U)

Q = queen

W = worker

U = upright, nototribic

Uobl. = upright, oblique normal

I = inverted, sternotribic

Th = nectar thief, both primary and secondary

Ths = secondary nectar thief

() = few observations

- = no observations

4. DISCUSSION

Whatever position an insect takes while collecting pollen on a flower of one of the *Rhinanthoideae*, the pressure of the hood to open the pollen chamber must be released (*fig. 12*). Most frequent visitors are bumblebees effecting nototribic or sternotribic pollination. Nototribic pollinators release the pressure rather passively by inserting their heads into the corolla to secure nectar while foraging upright. Sternotribic pollinators do so by tearing and grasping the galea with their mandibles while vibrating their wings. Both procedures result in touching the stigma and in releasing large amounts of pollen on the bodies of the bumblebees and in the corbiculae. In the nectar-robbing position, no pollen is released and the stigma is not touched. Although each plant species has its own floral morphology the principle of the pollination mechanisms is essentially the same for all species.

In general, the foraging position for pollen, whether upright or inverted,

appears directly related to the length of the forager's tongue (*table 1*, MACIOR 1975). Strictly speaking, tongue length should only influence the nectar-foraging position and not the pollen-foraging position.

MEIDELL (1944) thought the larger individuals on *Melampyrum* were visiting normally, and the smaller ones, because of their shorter tongues, were stealing. MACIOR (1974) concluded that perforating behaviour is associated with shortness of tongues in nectar foraging insects but that shortness of tongues is not necessarily associated with perforation behaviour. This is confirmed by my data (*table 1*). However, there are several exceptions to the rule; individual variations may exist within species, since in *B. terrestris* some queens and workers visited *R. serotinus* or *R. minor* upright and others visited these flowers inverted for pollen and perforated for nectar. Individual behaviour may vary also, because workers of *B. pratorum* and *B. terrestris* were spotted visiting different *R. serotinus* flowers both upright and inverted during one foraging trip.

Bumblebees need nectar to pack the dry pollen in the corbiculae, for their energetics, and for their brood. The impression exists that nectar supplies in flowers of *Rhinanthus* are not sufficient during the intensive foraging period of worker bumblebees. This deficit could be made up in various ways. *B. pascuorum* was often seen on buds of *R. serotinus* (only nectar available) and sometimes on *Trifolium repens* (nectar and pollen available). During one foraging trip, *B. lapidarius* frequently visited *R. serotinus* (inverted) for pollen only, and *T. repens* for both.

All these observations suggest that not only tongue length but also other factors determine the foraging position on flowers, their constancy in behaviour and their constancy in visiting flower species.

In some details, my observations on the position of the pollinating bumblebees differ from those of other workers. MEIDELL (1944), and BRIAN (1957) corroborated this, described a pollen-collecting behaviour of bumblebees and other bees on *M. pratense*. According to them, the bumblebees place themselves on the edge of the upper lip, stretch their hind legs across the flower's mouth, and vibrate their wings rapidly. This results in pollen being showered onto their legs ('leg pollination'). The gastrilegic bee *Megachile willoughbiella* (MEIDELL 1944) places herself on the top of the flower, turns swiftly around to the underside of the flower with her head downwards so that the venter nearly shuts the opening of the flower, and whirs her wings two or three times. The pollen is showered out and dusted on the venter. Concerning the position of the bee's abdomen in relation to the flower, my observations on bumblebees agree with MEIDELL's observations on *Megachile*. MEIDELL, however, neither mentions nor illustrates damage to the hood of the flower caused by the tearing and grasping of the mandibles of the (bumble)bees. *Megachile willoughbiella* occurs in the Netherlands (BENNO 1969) but was not seen on *M. pratense* or any other member of the *Rhinanthoideae*.

FAEGRI & VAN DER PIJL (1966) describe the behaviour of bumblebees visiting *P. palustris*. Two things differ with my observations: the entering of the head

in the galea and the absence of wing vibrations. The honeybee, as I observed on *P. palustris*, indeed forced her tongue between the thecae, but the use of mandibles or wing vibrations while collecting pollen was not seen.

Differences also exist with my previous observations (KOEMAN-KWAK 1973); hovering in the air and pushing against the upperlip. It is not possible to conclude whether the bumblebees in 1972 indeed behaved in a different way. There are no cinematographic records to clear up this matter.

MACIOR noted the use of the front legs to scrape pollen from the anthers of *P. lanceolata* (1969), *P. bracteosa* and *P. rainierensis* (1973) without wing vibrations. On *P. contorta* and *P. racemosa* (1973) and *P. labradorica* (1975) pollen is released by wing vibrations; the use of the front legs is omitted. But on *P. capitata*, *P. kanei* and *P. langsdorfii* (1975) the method of foraging for pollen by wing vibrations was combined with scraping of the front legs. On the five hemiparasites studied, the use of the front legs was not observed yet.

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