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THE POLLINATION VALUE OF HONEYBEES TO THE BUMBLEBEE PLANT RHINANTHUS

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SUMMARY

During five seasons of observations on the pollination of Netherlands *Rhinanthus* species by bumblebees, honeybees were nearly completely absent. In the sixth season (1979) honeybees were observed on *Rhinanthus serotinus* in a relatively large amount. The pollen and nectar collecting behaviour of these honeybees is described and related with some similar observations in the Alps. The pollination value of both honeybees and bumblebees is determined. If only the number of individuals is taken into account, the role of honeybees in pollination of *R. serotinus* may be overestimated, since their flower visiting speed was low. Specialization into pollen or nectar collecting individuals also reduced the amount of flowers really pollinated. Honeybees did not play a role in the hybridization of *R. serotinus* and *R. minor*, because they did not visit the latter.

1. INTRODUCTION

On the initiative of the late professor D. Bakker the study of the pollination ecology of large-flowered hemiparasitic Rhinanthoideae (Scrophulariaceae) was started in 1974. It forms part of a project with a wider scope, concerning the ecology, physiology and biosystematics of this group of plants (TER BORG 1972, KLAREN 1975, KWAK 1979b; see also TER BORG et al. 1980 and MASSELINK 1980). *Rhinanthus* receives particular attention. It is a mainly Eurasian genus with c. 25 species (VON SOÓ & WEBB 1972), two of which are common in the northern Netherlands, *R. serotinus* (Schönh.) Oborny and *R. minor* L. It was found that these are almost exclusively visited by bumblebees (*Bombus* spp.) which can pay nototribic and sternotribic visits (i.e. the essential parts of the flower contact the dorsal respectively the ventral side of the insect's body) or behave as primary or secondary thieves (KWAK 1977). Honeybees (*Apis mellifera* L.) were hardly ever observed during five seasons' observations in The Netherlands, but during three yearly visits to the Alps they were noticed on the flowers of several *Rhinanthus* species collecting pollen and nectar in 1976 and 1978. Neither MÜLLER (1881) nor MACLEOD (1891) or KNUTH (1899), reporting on pollination of alpine and Pyrenean species respectively, mentioned honeybees as visitors of *Rhinanthus*. MÜLLER (1881) described *R. alectrorolophus* Poll. as a flower with two openings: one for butterflies and one for bumblebees exclusively. Recent publications by FOSSEL (1974, 1977) showed that honeybees are common visitors of *Rhinanthus* in alpine meadows. Since we were interested to know more about the behaviour of honeybees and its effects, in 1977 bee hives were moved to a very dense population of *Rhinanthus*. Still honeybees were hardly found on the *Rhinanthus* flowers (KWAK 1979a). However, in 1979 honeybees appeared common visitors in this same area. This offered the opportunity for a further study of (i) the

behaviour of pollen and nectar collecting honeybees, (ii) the relative importance of honeybees and bumblebees for the pollination and (iii) the role of honeybees in the hybridization of *Rhinanthus serotinus* and *R. minor*. In this paper the behaviour of honeybees on *Rhinanthus* species in the Alps is related with the observations in The Netherlands.

2. MATERIALS AND METHODS

In July 1976, 1977 and 1978 trips were made to the Alps. By that time of the year most of the Alp meadows at lower altitudes have been already mown, but at higher altitudes *Rhinanthus* is in full flower. Populations of *Rhinanthus minor*, *R. aristatus*, *R. alectorolophus* as well as *R. antiquus* (nomenclature according to HARTL 1974) were visited in W. Austria and E. Switzerland. The behaviour of bumblebees and honeybees was noted and photographed. Working speed of nectar and pollen gatherers was determined by following the individuals, noting the number of flowers visited per foraging period.

In The Netherlands mixed populations of *Rhinanthus serotinus* and *R. minor* are situated in the State Nature Reserve 'Stroomdallandschap Drentsche A', south of Groningen. In one of these meadows bee counts on *Rhinanthus* were made during a standard walk every half hour on June 21 in 1979, an exceptionally fine day. During this walk 90 m² were observed (*fig. 1*). Within this area we estimated to be present about 55,400 flowers of *R. serotinus* and 11,900 flowers of *R. minor*, i.e. all together an average of c. 750 flowers/m². The temperature was registered by a thermograph placed permanently in the vegetation.

Pollen and nectar collecting behaviour of bumblebees has been reported in previous papers (KWAK 1977, 1979a).

3. OBSERVATIONS

3.1. Honeybees foraging on *Rhinanthus*

3.1.1. The nectar collecting behaviour

Honeybees were observed to collect nectar on *Rhinanthus* in three different ways. Firstly, they collected nectar as secondary thieves, using the holes made by bumblebees (*fig. 2*). Sitting in this way outside the flower there was no deposition of pollen on the bee's body and no contact with the stigma.

Secondly, they collected nectar by forcing their body between calyx and corolla. In this position they probably pushed loose the corolla along a naturally present division mark, particularly in older flowers. This way of behaviour was rather time consuming. Pollination of the visited flower was unlikely, since there was hardly pollen deposition nor contact with the stigma.

Thirdly, the honeybees collected nectar on buds and young, not fully expanded flowers, entering upright. In the young flowers only one theca was ripe and nectar was present. Pollen was deposited mainly on the thorax of the bee. It was visible as a light yellow spot (*fig. 3*). These honeybees, specialized in nectar collecting, did not groom together the pollen grains into the pollen baskets. The

stigma contacted the bee's body at the site dusted with pollen (nototribically). The stigma is already receptive in this phase of anthesis (KWAK 1979a), and therefore this mode of nectar collecting may result in pollination. The selection of flowers in the correct stage took a rather long time.

All three ways of foraging were observed in alpine populations of *R. alectorolophus* and *R. aristatus*. These two *Rhinanthus* species, both with flower sizes similar to that of *R. serotinus*, showed few holes in the calyces, compared to *R. serotinus* in The Netherlands (fig. 2). Neither in The Netherlands nor in the Alps I did observe honeybees on *R. minor*, a species with relatively small flowers. The same holds for *R. antiquus*; elevation or weather conditions during our short visit may have effected the bees' absence on this species.

The first times we observed honeybees visiting *R. serotinus* in The Netherlands, they foraged in the second way but soon afterwards all nectar collecting honeybees behaved as secondary thieves.

3.1.2. The pollen collecting behaviour

Honeybees were seen to collect pollen on *Rhinanthus* in only a single mode. They hang upside down on the upper lip, pushing their tongue and sometimes their front legs between the teeth of the flower, and between the thecae. If ripe pollen was present it fell down on the head and the ventral side of the bee's body (figs. 4-6). There was no distinct part of head or venter that was dusted. The stigma contacted various sites of the body depending on the bee's position.

3.2. The relative importance of honeybees and bumblebees

Results of the bee counts are summarized in fig. 7. Data are averaged for each hour. Observations started at 5.00 a.m. The first bumblebee was seen at 6.00 a.m., outside the area observed during the standard walk. The first honeybees were observed at 10.00 a.m. During the warmest period of the day bumblebees were completely absent while honeybees continued foraging, with maximal frequency in the late afternoon.

Most honeybees (89%) collected pollen; few (11%) collected nectar (fig. 7). Of the bumblebees 19% collected pollen as sternotribic visitors (mainly *Bombus terrestris* and *B. lucorum*, few *B. pratorum*, *B. lapidarius* and *B. hypnorum*), 35% collected nectar as nototribic visitors (mainly *B. pascuorum* and one individual of *B. hortorum*). On the daily total of observed individuals visiting *Rhinanthus* 65% came to honeybees and 35% to bumblebees. However, in relation to pollination only the number of pollinating visits (in general only the pollen collecting visits) per time unit is important. In *R. serotinus* 18, 15 and 11 flowers are visited per minute by *B. hortorum*, *B. pascuorum* and sternotribically pollinating bumblebees (see KWAK 1979b). For honeybees this value was 5 flowers per minute for pollen collecting. Although there were nearly twice as many honeybees as bumblebees present throughout the day and 89% of the honeybees could bring about pollination against only 65% of the bumblebees, the visiting speed has such an influence that on this particular day honeybees and bumblebees were equally important in pollinating *R. serotinus* flowers: 36% of the flowers were pollinated

by honeybees and 39% by bumblebees (table 1).

More *R. serotinus* flowers were visited than reported in table 1 but for pollination the nectar thieving individuals of both honeybees and bumblebees were not important. Both *R. minor* and *R. serotinus* contained nectar; the mean values present per flower were 240 and 760 nl respectively. Honeybees collected mainly pollen and bumblebees were interested in nectar too. 19% of the *R. serotinus* flowers were perforated, i.e. 10,530 flowers. Nectar collecting thieving honeybees have visited only 3,060 flowers: 29% of the perforated flowers or only 5.5% of all *R. serotinus* flowers present. *R. minor* flowers were not perforated.

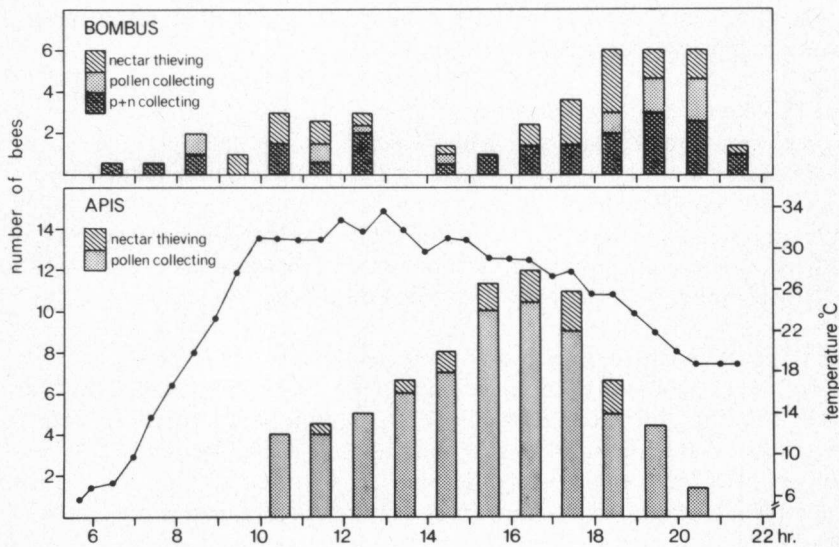


Fig. 7. Changes in numbers of bumblebees and bees on *Rhinanthus* flowers and temperature on 21 June 1979.

Fig. 1. In June flowering *Rhinanthus* population in the State Nature Reserve "Stroomdallandschap Drentsche A"; in the centre the path followed during the standard walk.

Fig. 2. A *Bombus* worker pollinating a *Rhinanthus aristatus* with proboscis fully inserted into the corolla tube. Left arrow indicates point of stigmatic contact, right arrow indicates a perforation in the calyx of the opposite flower.

Fig. 3. A honeybee collecting nectar on a young flower of *R. aristatus* (method 3); making contact and pollinating the stigma with residual pollen on the thorax (arrow).

Fig. 4. A honeybee collecting pollen on *R. alectorolophus*, proboscis inserted into the galea between the teeth.

Figs. 5, 6. A honeybee collecting pollen on *R. serotinus* proboscis inserted into the galea between the teeth; arrow indicates point of stigmatic contact with pollinator.

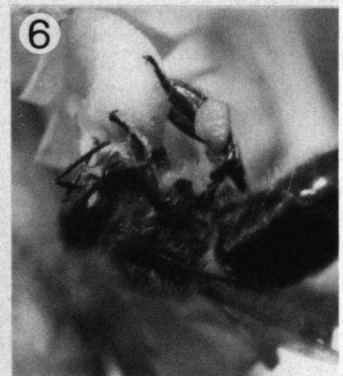


Table 1. Nototribic and sternotribic visits of *Bombus* and pollen collecting visits of *Apis* individuals to *Rhinanthus* flowers in the observation area on 21 June, 1979.

	flowers present	visited by <i>Bombus</i>	%	visited by <i>Apis</i>	%	total % visited
<i>R. minor</i>	11,900	450	3.8	0	0	3.8
<i>R. serotinus</i>	55,400	21,450	38.7	19,950	36.0	74.7

3.3. The role of honeybees in the hybridization of *R. minor* and *R. serotinus*

Honeybees were not observed on *R. minor*, although this plant species contains pollen and nectar in large amounts. A single individual of *B. pascuorum* foraged on *R. minor* visiting only 4% of the *R. minor* flowers present (table 1).

4. DISCUSSION

Although sometimes honeybees visit *R. serotinus*, *R. alectorolophus* and *R. aristatus* for pollen and nectar, the flowers are more suitable to be visited and pollinated by bumblebees. In Alp meadows at higher altitudes, where honeybees are often absent, bumblebees are the only pollinators. The question arises on which occasions honeybees will visit *Rhinanthus* species. The moving of honeybee hives to a very dense stand of *Rhinanthus* did not result in honeybee visits in 1977 (KWAK 1979a). The availability of other pollen and nectar providing plants may have had a great influence.

We observed that honeybees collected nectar in three different ways. FOSSEL (1974, 1977) mentioned only the first two methods. According to this author it is clear that due to the way of nectar collecting only small amounts of *Rhinanthus* pollen grains will be found in the honey, so the amount of *Rhinanthus* nectar will be underestimated when methods of pollen analysis of honey are used.

Nectar is available during the whole day (nectar characteristics will be reported in a later paper) and collected by both *Bombus* and *Apis* individuals. However, most honeybees collected pollen, only a small proportion was observed to collect nectar (fig. 7). The nectar thieving honeybees are dependent on the perforating activity of bumblebees, but since only 29% of the perforated flowers was visited by nectar collecting honeybees, this was not the limiting factor for the small proportion nectar collecting honeybees.

By comparing the relative importance of honeybees and bumblebees during the day, it is demonstrated that honeybees can play a role in the pollination of *Rhinanthus*, but their role is easily overestimated if the number of individuals is taken into account. In fact, the number of flowers visited per minute is low compared to bumblebees. Also the foraging time of honeybees during the day is limited. Bumblebees may forage from sunrise to sunset or even longer. A peak is often reached by mid morning, and in hot weather there may be a noticeable decline during the middle of the day (LØKEN 1949); this decline is also visible in fig. 7. HOLMES (1964) also observed a decline in numbers of bumblebees and a

simultaneous increase of honeybees. He believed that, although honeybees and bumblebees were not responding similarly to the environmental influences that were operative, bumblebees were absent for quite other reasons, such as increased crowding of insects on the flowers.

A similar lack of crowding may be the reason of the abundance of honeybees on *Rhinanthus* in 1979. An extremely hard winter and a late spring possibly were the cause of low numbers of bumblebees in June. The decreased interspecific competition may have offered the honeybees the exceptional opportunity to forage on *Rhinanthus*.

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