

POLLINATION OF *SERAPIAS VOMERACEA* BRIQ. (ORCHIDACEAE) BY IMITATION OF HOLES FOR SLEEPING SOLITARY MALE BEES (HYMENOPTERA)

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SUMMARY

In two locations in Israel, bees were found to be sleeping in flowers of *Serapias vomeracea* Briq. Of these bees, *Proposis* spp. and *Ceratina* spp. were too small to be pollinators, whereas *Eucera* spp., *Andrena* spp., *Osmia* spp. and *Tetralonia* spp., mostly males, pollinated.

Pollination occurs when in the afternoon hours the bees waver from flower to flower. The bees finally come to rest on a particular flower and remain there for the duration of the night. In the morning, the bees which slept in the flowers, are warmed up as a result of solar radiation which heats the flowers to 3°C above ambient temperature.

Since the males of many Hymenoptera sleep in holes, the hypothesis is that the flowers mimic such holes. The shortness of the flower tube can be held responsible for the observed frequent changes from flower to flower, which is so important for pollination efficiency.

1. INTRODUCTION

Serapias vomeracea Briq. is a Mediterranean species found in fertile meadows, heaths, and damp woods, from sea level up to 1000 m. altitude (DUPERREX 1965). In Israel, this species appears in damp open habitats all over the Mediterranean territory, mainly in dwarf shrub communities ("Batha") and in marsh fringes, without showing preferences to any particular soil (DAFNI 1979). Flowering season in Israel is from the end of March until the beginning of May.

Observation on *Serapias* pollination were made by GODFERY (1931), VAN DER PIJL & DODSON (1966), DANESCH & DANESCH (1969), and KUGLER (1977). Different *Serapias* species are pollinated by bees of the genera *Ceratina*, *Osmia*, *Anthidium* and *Eucera*, which were found sleeping in the flowers. The flowers offer no nectar or edible pollen and therefore, the floral rewards are unknown. In Israel, we studied the behaviour of the pollinating bees and made some measurements of the microclimate inside the flowers.

2. MATERIALS AND METHODS

The observations were carried out from 1973 to 1976 in Horshat Tal Orchid Reserve at Dan Valley (SHMIDA & DAFNI 1975) and during 1977 in the Neshet

Quarry (5 km NE. of Haifa). Flower visiting insects were collected from March 24th to April 25th in 1973 and 1974 at Horshat Tal, and from March 15th to March 30th 1977 in Neshar Quarry. To assess the occurrence of self-pollination, nine plants, with a total of 57 flowers, were covered by netting to exclude insects' visits. Temperature measurements were made with YSI, telethermometer, thermistor Probe type 400. On 14–15.4.1973 from 2 to 4 p.m., the behaviour of the bees was observed, using a glass cage, size 30 × 40 × 30 cm. at 24°C 70% humidity with artificial light. Male *Eucera* bees were collected from *Serapias* flowers the day before. In the first observation only the flowering plants of *Serapias vomeracea* were in the cage, together with two bees. During the second observation, the cage contained several flowering plants of *S. vomeracea* and of *Linum grandiflorum* Desf. together with five *Eucera* bees. Both observations were repeated 3 times.

3. RESULTS

The flower: The genus is characterised by the hood shape of the flower, which is produced by mutual adherence of the sepals and petals, together forming the galea. The labellum has two distinct parts. The basal part (hypochile) is rounded and its lateral lobes are bent upwards. The narrow distal part (epichile) points downwards. The column is long and terminates with a swordlike rostellum. A shiny paste-like fluid covers the stigma. The flower emits a light scent and does not contain any nectar, as was verified by using Fehlings reagent. All the flower parts are coloured deep-purple to reddish brown.

At noon and night-time, the internal flower temperature equals the external one, although in the morning, the flower temperature exceeds the ambient temperature up to 3°C between 9.30 and 11.30 a.m. (*table 1*).

Enclosed flowers produced only very few capsules by spontaneous autogamy, in comparison with flowers exposed to insects in the field (*table 2*). This proves the importance of pollinators for reproduction. A similar low spontaneous autogamy has been found for *S. vomeracea* (AVNI 1968) and for *S. lingua* (PAIS 1969). KUGLER (1977) described the disintegration of the pollinia and subsequent autogamy in the unvisited flowers of *S. parviflora* ssp. *parviflora*.

Table 1. Temperature (°C) just after the bee left a flower (between 9:30 a.m. to 1:00 p.m.).

Date	Inside the flower	Ambient air	Difference
Horshat Tal			
30.3.74	27.0	25.5	1.5
31.3.74	27.0	25.0	2.0
14.4.74	32.0	34.0	2.0
Neshar Quarry			
16.4.77	26.5	23.5	3.0
17.4.77	28.0	26.0	3.0
18.4.77	27.0	25.5	1.5

Table 2. Capsule production.

Location	Year	Number of plants	Number of flowers	Percentage of developing capsules
<i>Exposed flowers in the field</i>				
Horshat Tal	1973	33	229	63.8
Horshat Tal	1974	37	243	55.1
Nesher Quarry	1977	15	93	74.1
<i>Enclosed flowers</i>				
Nesher Quarry	1977	9	57	3.5

Pollinators and their behaviour: All insects collected from the flowers were found immobilised in the flower tube, a behaviour that we termed 'sleeping' (table 3). Because of their small size, *Prosopis* spp. and *Ceratina* spp. were found to be unable to remove pollinia, since there were no pollinia found on the thorax of the insects which had slept in the flowers. Pollination is carried out by the large, mostly male bees of the genera *Eucera*, *Andrena*, *Osmia* and *Tetralonia* (table 3). In general, these bees sit in the flowers in the afternoon and, only on cloudy days, at high noon. On sunny days between 9:00 a.m. and 1:00 p.m., the bees' most active hours, there were no bees seen in the flowers.

Bees were seen to enter flowers in the afternoon. The bees generally entered several flowers on the same plant. After each visit they were often loaded with additional pollinia. The number of pollinia observed most, was from 2 to 4 and could reach 22. This behaviour explains the high pollinating capacity of the bees.

Several minutes after introduction of the bees into the observation cage, activity started. In the cage with only *Serapias*, the bees entered the flowers several times. The length of time spent in a flower was from 4 seconds to 30 minutes. Often, between two visits, the bees groomed their heads, as if trying to remove the newly attached pollinia. In each of the three observations, after about 45 minutes, two of the five bees came to rest in a flower. In the cage where there were additional *Linum grandiflorum* flowers, the bees sucked nectar from these. Each

Table 3. Bees (general) sleeping in flowers of *Serapias vomeracea*.

Location:	Horshat Tal (5.4.74)			Nesher Quarry (20.3.77)			Total
	Male	Female	Unknown	Male	Female	Unknown	
<i>Eucera</i>	40	2	.	46	3	.	91
<i>Andrena</i>	.	.	1	4	.	1	6
<i>Osmia</i>	.	1	3	.	.	.	4
<i>Tetralonia</i>	.	.	.	1	.	1	2

visit lasted 30 to 40 seconds, and some of the flowers were revisited several times. However, the bees ignored the *Serapias* flowers, and only after 90 minutes did they enter a *Serapias* flower to rest.

4. DISCUSSION AND CONCLUSION

The females of these solitary bees (*table 3*) usually sleep in their holes in the ground. The hundred males which were found sleeping in a *Serapias* flower may indicate that to the bees, the flowers resemble their holes. Hymenoptera males of several species are known to sleep in nest-holes when they have an opportunity to do so. *Philanthus triangulum* F. males dig themselves small holes or make use of existing holes (THOMAS & PORTER 1972). BLÜTHGEN (1923) observed *Halictus* males entering nest-holes of their females, possibly in search of a partner for copulation. Also *Protoxaea gloriosa* Fox males show social sleeping behaviour and prefer holes over open flowers for sleeping. CAZIER & LINSLEY (1963) found these males sitting inside the empty tube-form pericarps of *Datura stramonium* L. Cazier remarks, 'A variety of other bees and wasps also use the dried pods of *Datura* for sleeping.'

The *Serapias* flower probably exploits a kind of 'entering behaviour' of bees and, because females have their own nests, it is mostly the males that enter the flowers. The flower acts as a nest replacement, which might explain the extremely dark pigmentation. The reddish light which penetrates into the flower is in the part of the spectrum which is invisible to the bees. Van der Pijl (pers. comm.) observed in Portugal a translucent part in the base of the galea of *S. lingua*. Such a 'light window' is absent in other *Serapias* species.

Night sleeping of male bees in other flowers is well known, e.g., in *Anemone*, *Papaver*, *Tulipa* and *Phlomis* in the area of the present *Serapias* observations.

Bees which sleep in *Serapias* flowers enjoy a shelter from wind and rain (GUMPRECHT 1977). In the morning, a bee which has stayed overnight in the *Serapias* flower is warmed-up. Therefore, staying in the heated flowers causes the bees to become active earlier in the morning and enables them to reduce the energy expenditure in preflight warming-up. This microclimatic condition forms a floral attractant (cf. HEINRICH & RAVEN 1972) comparable with that of some arctic flowers (KEVAN 1975) and alpine flowers (LACK 1976). VAN DER PIJL & DODSON (1966, p. 39) remark: 'as some of these bees carried many pollinia (of *Serapias*) they must be regular visitors in the daytime too.' However, during daytime, the bees were not observed to visit the flowers, except in cold or rainy weather. In the afternoon, before sleeping, during the movements from flower to flower, the bees can collect many pollinia within a few minutes. In this way the bees act as effective pollinators, which explains the high yield in the field in comparison to the fruit set in screened flowers, which, nevertheless, show some autogamy.

The idea that the *Serapias* flower is an imitation of a hole to sleep in also explains why a bee visits several flowers. After entering, the bee will find the way

blocked by the column, and after some pushing (which might help in the deposition of the pollinia) the bee will move out and enter another flower. This behaviour will be repeated until the bee finally will find the suitable place for sleeping.

The evidence indicates that the *Serapias* flowers function as holes for the bees, and therefore, could be regarded as mimics. The mimic is deceptive because the bee is attracted to the 'hole' forms, although the shortness of the tube keeps the bee moving between the flowers. In this way *Serapias* presents another example of the mimicry capacities of the terrestrial orchids (DAFNI & IVRI 1980).

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