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POLLINATION OF *ORCHIS CASPIA*—A NECTARLESS PLANT WHICH DECEIVES THE POLLINATORS OF NECTARIFEROUS SPECIES FROM OTHER PLANT FAMILIES

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SUMMARY

(1) *Orchis caspia*, which produces no nectar and therefore provides no reward for pollination, exploits inconsistency in the behaviour of several species of bees (*Anthophora* sp., *Eucera clypeata*, *E. nigrifacies* and *Melecta mediterranea*), which are the legitimate pollinators of some nectariferous species (*Asphodelus microcarpus*, *Bellevalia flexuosa* and *Salvia fruticosa*).

(2) The bees are deceived through their low ability to discriminate *Orchis caspia* from the nectariferous species. No specialist modifications of the insect are required for pollination of *O. caspia*.

(3) *Orchis caspia* shares pollinators with *O. israelitica* and this may lead to formation of hybrids between the two species.

INTRODUCTION

How nectarless *Orchis* species are pollinated is enigmatic (Faegri & van der Pijl 1979, p. 58). The most controversial point concerns the possible reward for the pollinator. Darwin (1862) and Knuth (1909) postulated that the pollinators extract sap from cells of the spur. Daumann (1941) queried this idea and considered the empty spurs to be false nectaries.

Delpino (1873–4) accepted the idea of Sprengel (1793) about 'Scheinsaftblumen' (false nectary flowers) and argued that these orchids are visited only during the first two or three days of flowering, when visiting bumble bees have newly emerged. At that stage, the bees have not become acquainted with appropriate nectariferous flowers but soon recognize the deception and learn to avoid the nectarless ones. This explanation was repeated by van der Pijl & Dodson (1966) and van der Pijl (1966). Nilsson (1980, 1981) gave evidence for such a deception in the related genus *Dactylorhiza*; *D. sambucina* (L.) Soo. is exclusively pollinated by bumble bee queens who visit when they are newly emerged after hibernation and are inexperienced and unconditioned to the nature of pollen sources.

Dafni & Ivri (1979) suggested that the pollination of nectarless species of *Orchis* might be based on visual and even olfactory deception. A close visual resemblance was found between *O. israelitica* Baumann & Dafni and *Bellevalia flexuosa* Boiss. (Liliaceae), which share the same pollinators. This was described as 'floral mimicry' (Dafni & Ivri 1981). Olfactory deception exists in *Orchis galilaea* (Bornm. & Schultze) Schltr., to which only males of *Halictus marginatus* Bralle are attracted. These alone pollinate the plant although female bees are present in the neighbourhood (Bino, Dafni & Meeuse 1982). *Orchis papilionacea* L. is pollinated, in Elba, by territorial patrolling males of *Eucera tuberculata* Fabr. (Vogel 1972).

All these hypotheses, however, cannot explain the pollination of several other *Orchis* species. In these species the flowers are not visually similar to any other sympatric species

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and do not seem to attract bees by sexual deception, nor are they favoured by regular patrolling routes. *Orchis caspia* Trautv., one of the commonest orchids of Israel (Dafni 1981), is such a species.

The present study examines the hypothesis that *O. caspia* deceives the pollinators of other, not visually similar, rewarding species and harnesses them as its pollination agents.

MATERIALS AND METHODS

Field observations

The field observations were made during 1975 to 1981 at several localities in Lower Galilee: Mt Ahim (35°16′N, 32°49′E) and at Beit-Oren Junction, Ya'ar Ha'yaaranim, Isfia, Nahal Alon, Haifa University, Giv'at Ha'hagana, Horshat Ha'arbaeem and Nesher quarry on Mt Carmel (35°02′N, 32°44′E). Phenological records were made, twice a week during the 1981 season, for twenty marked plants of *Asphodelus microcarpus* Viv., *Bellevalia flexuosa*, *Orchis caspia*, and *Salvia fruticosa* Mill. (= *S. triloba* L. fil.) at Beit-Oren Junction. The proportion of flowers setting fruits was recorded for several populations of *Orchis caspia* at Mt Carmel during April 1981.

The possibility of spontaneous self-pollination in *O. caspia* and *O. israelitica* was examined in thirty plants of each species by covering them with fine netting to prevent insect visits. No capsules were produced on such plants which indicates that insects are needed for effective pollination.

Orchis caspia is very common on Mt Carmel and flowers simultaneously with several other plant species which have purple, violet, pink or blue flowers such as: *Anchusa italica Retz.*, *A. undulata* L. (= *A. hybrida* Ten.), *Asphodelus microcarpus*, *Bellevalia flexuosa*, *Salvia fruticosa.* and *S. palaestina Benth.* All these species were observed carefully to establish whether or not they shared the same pollinators as *Orchis caspia.* Preliminary observations revealed that *Eucera clypeata* Erichs. pollinates both *Orchis caspia* and *O. israelitica.* This bee also visits *Asphodelus microcarpus* and *Bellevalia flexuosa.* These findings led me to choose a site where all these species flowered simultaneously.

Observation plots 100 × 20 m were established at each site and insects were captured along a transect 100 × 2 m every hour during the observation periods. All the insects that visited *Asphodelus microcarpus*, *Bellevalia flexuosa*, *Orchis caspia* and *Salvia fruticosa* were caught with butterfly nets and identified (except for some incidental visitors to *Asphodelus microcarpus* which never visited *Orchis*). Each insect was numbered and carefully examined with a hand lens to see if it carried any *Orchis* pollinaria.The pollinaria of *O. israelitica* are smaller (5 mm) and more deeply yellow than those of *O. caspia* (6–7 mm). Hybrids were rare at the site and their pollinaria approached the form of those of *O. caspia.*

RESULTS

Phenology and pollination

Table 1 shows that the flowering period of *Orchis caspia* initially overlaps those of *Asphodelus microcarpus* and *Bellevalia flexuosa*, and with that of *Salvia fruticosa* towards its end. Table 2 shows the extent to which pollinators of the nectar-bearing species (*Asphodelus microcarpus*, *Bellevalia flexuosa* and *Salvia fruticosa*) had also visited and

TABLE 1. Flowering periods in 1981 of species growing together on Mt Carmel, Israel. The date on which the maximum number of flowers was observed per plant is considered that of peak flowering.

	Beginning of flowering	Peak flowering	End of flowering
Asphodelus microcarpus	2 February	5–10 March	30 March
Bellevalia flexuosa	20 February	10 March	19 March
Orchis caspia	13 February	10 March	25 March
Salvia fruticosa	18 March	8–15 March	10 May

pollinated *Orchis caspia*. The species *Asphodelus microcarpus* is very common and has a large flowering stem containing up to 100 flowers; it served as a main source of nectar for *Anthophora* sp. and *Eucera clypeata*, but less so for *Melecta mediterranea* Gnib. The geophyte *Bellevallia flexuosa* is 10–20 cm high and bears loose spikes each with up to twenty flowers; it appears in patches of five to twenty plants scattered over the observation plot, and attracts the same visitors as *Asphodelus microcarpus* but also many species of *Bombylius*, which were never found with pollinaria of *Orchis caspia*. At Nahal Alon, *Salvia fruticosa* was the main source of nectar for many insects; it is a bushy chamaephyte bearing hundreds of flowers. Of the numerous different visitors only *Eucera clypeata* and *E. nigrifacies* also pollinated *Orchis caspia*. Visitors to *O. caspia* were infrequent but were of the same species as found on the other species (except *Bombylius*).

Orchis israelitica (Table 3) was pollinated by *Bombylius* sp. which also pollinated *Bellevalia flexuosa* and by *Eucera clypeata* which also pollinated *Asphodelus microcarpus*, *O. caspia* and, rarely, *Bellevalia flexuosa*. Figure 1 illustrates these relationships. Table 4 shows the proportion of *Orchis caspia* flowers which produced capsules at the various sites in relation to the presence or absence of other plant species which were also pollinated by the pollinators of *O. caspia*. In general this proportion increased with incidence of such other species.

Pollinators and their behaviour

Eucera clypeata pollinates *Asphodelus microcarpus*, *Bellevalia flexuosa* and *Salvia fruticosa* (Table 2) and in doing so receives nectar. It may also be responsible for production of hybrid swarms between *Orchis caspia* and *O. israelitica* (= *O.* × *feinbruniae* (Dafni & Baumann 1982)) for it was the only insect bearing pollinaria of both potential parents (Table 3). This bee is polylectic (Table 2) and visits several species in the same foray. Many shifts of *Eucera clypeata* from *Asphodelus* to *Bellevalia*, *Orchis* or *Salvia* were observed at Mt Carmel on the same foray. *Anthophora* sp. showed a similar pattern to *Eucera clypeata* except for visits to *Orchis israelitica*.

Bombylius sp. (a dipteran) is the most common pollinator of *Bellevalia flexuosa*. It is also a secondary pollinator of *Orchis israelitica*, but ignores *O. caspia* and *Salvia fruticosa*. It is also polylectic. The bee *Eucera nigrifacies* Lep. pollinates both *Orchis caspia* and *Salvia fruticosa*, but has not been observed on any other of the plant species discussed here.

Melecta mediterranea is a rare bee which pollinates *Asphodelus microcarpus* and *Orchis caspia*. It was seen on *Anchusa undulata* L. and on *Salvia palaestina* Benth., which were rare in the observation area, but it is likely that these two species may be nectar donors for *Orchis caspia* pollinators.

TABLE 2. Number of insects visiting four plant species growing together at various sites in Israel in 1981 and the incidence with which pollinaria of *Orchis caspia* were found attached to them at the times of their visits.

Locality	Date and local time	Insect species: *Anthophora* sp. Number recorded	% with *Orchis caspia* pollinaria	Pollinaria per bee ($\bar{x} \pm$ S.D.)	*Eucera clypeata* Number recorded	% with *Orchis caspia* pollinaria	Pollinaria per bee ($\bar{x} \pm$ S.D.)	*Melecta mediterranea* Number recorded	% with *Orchis caspia* pollinaria	Pollinaria per bee ($\bar{x} \pm$ S.D.)
On *Asphodelus microcarpus*										
Ya'ar Haya'aranim	9 March 09.30–14.00	25	8	2·5 ± 1·5	39	55	3·8 ± 2·8	20	10·0	1·0 ± 1·0
	10 March 10.00–15.00	31	3	3·0 ± 1·7	54	48	2·6 ± 2·1	8	12·5	1·0 ± 0
Ramot Remez	14 March 09.00–14.30	19	0	0	47	37	2·8 ± 1·4	0	0	0
Ya'ar Haya'aranim	15 March 09.30–13.00	17	11	2·5 ± 2·0	38	25	4·7 ± 2·5	13	8·0	2·0 ± 0
	17 March 10.00–15.30	71	23	3·2 ± 1·6	29	24	3·4 ± 1·7	5	0	0
On *Bellevalia flexuosa*									*Bombylius* sp.	
Ya'ar Haya'aranim	9 March 09.30–14.00	42	5	1·0 ± 0	49	29	3·1 ± 1·9	62	0	0
	10 March 10.00–15.00	32	7	1·0 ± 1·2	36	24	1·6 ± 1·4	49	0	0
	15 March 09.30–13.00	24	2	1·0 ± 0	26	31	2·1 ± 1·3	53	0	0
On *Orchis caspia*										
Beit-Oren Junction	8 March 08.30–17.30	2	0	0	10	66	2·1 ± 1·3			
Ya'ar Haya'aranim	10 March 10.00–15.00	4	50	2·0 ± 0	9	47	2·0 ± 2·1			
	15 March 09.30–16.00	6	60	2·3 ± 1·8	15	74	2·6 ± 1·5			
On *Salvia fruticosa*		*Eucera nigrifacies*								
Nahal Alon	19 March 10.00–14.30	19	48	2·1 ± 1·5	29	34	1·8 ± 1·1			
	20 March 10.00–14.00	42	24	1·5 ± 1·3	35	33	1·6 ± 1·2			

TABLE 3. The number of insect visitors to *Asphodelus microcarpus* and *Bellevalia flexuosa* growing in 1981 in Mt Ahim, Israel, which bore pollinaria of *Orchis caspia* (*O.c.*), *O. israelitica* (*O.i.*), both or neither.

Date	Local time	*Anthophora* sp. with pollinaria of			*Eucera clypeata* with pollinaria of				*Megachile* sp. without pollinaria	*Melecta mediterranea* without pollinaria
		O.c.	*O.i.*	None	*O.c.*	*O.i.*	Both	None		
On *Asphodelus microcarpus*										
8 March	09.00–15.30	2	0	37	22	3	1	75	41	8
11 March	09.30–14.30	1	0	28	9	1	0	47	32	6
15 March	09.00–14.30	4	0	41	14	2	0	62	61	4

		Anthophora sp. without pollinaria	*Bombylius* sp. with pollinaria of			*Eucera clypeata* with pollinaria of				*Halictus* sp. without pollinaria
			O.c.	*O.i.*	None	*O.c.*	*O.i.*	Both	None	
On *Bellevalia flexuosa*										
25 February	09.30–14.30	11	0	19	81	7	2	1	38	19
5 March	09.00–15.00	9	0	14	97	8	3	0	41	24
8 March	09.00–15.30	13	0	11	103	11	2	1	29	11

TABLE 4. Capsule production of *Orchis caspia* at sites on Mt Carmel, Israel, in the presence or absence of nectar-bearing plant species. Plants were examined at the end of the flowering period (12–15 April 1981). $n = 60$.

	Presence of nectar-bearing species			Flowers bearing capsules on each plant (% ± 2 S.D.)
	Asphodelus	*Bellevalia*	*Salvia*	
Beit-Oren Junction	+	+	+	86·0 ± 2·3
Ya'ar Ha'yaaranim	+	+	−	67·1 ± 4·5
Isfia	+	+	−	71·2 ± 4·3
Nahal Alon	−	−	+	51·3 ± 2·9
Haifa University	−	+	−	36·0 ± 2·8
Giv'at Ha'hagana	+	−	−	45·1 ± 2·9
Horshat Ha'arbaeem	−	−	−	16·0 ± 2·1
Nesher quarry	−	−	−	11·3 ± 2·4

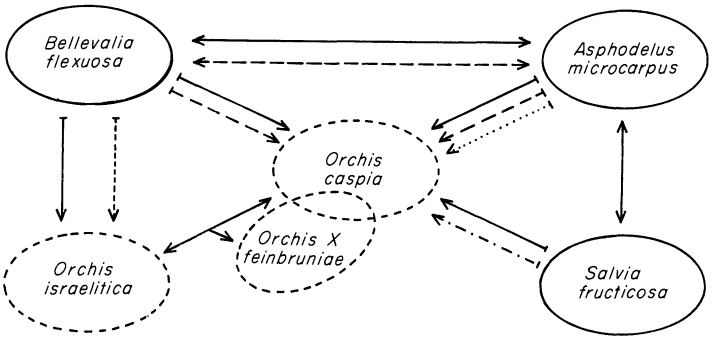

FIG. 1. Interrelationships between (:) nectarless *Orchis* species, (O) nectariferous plant species and their pollinators at sites on Mt Ahim and Mt Carmel, Israel. The lines indicate which plant species share particular pollinator species and the direction arrows the presumed sequence of visits. Symbols for insect pollinators: ——, *Eucera clypeata*; –·–·–, *E. nigrifacies*; ------, *Bombylius* sp.; – – –, *Anthophora* sp.; ·····, *Melecta* sp.

DISCUSSION

The repeated visits of the bees (especially *Anthophora* sp. and *Eucera clypeata*) to several plant species suggests a low ability to discriminate between the different types of flowers. The large mean number of pollinaria attached per bee (Table 2), as recorded throughout the flowering season, indicates that the visits were not casual mistakes of unconditioned bees as was found in the case of *Bombus* queens pollinating *Dactylorhiza sambucina* (Nillson 1981) and, by Ackerman (1981), for *Calypso bulbosa* L. Oakes which is pollinated also by *Psithyrus* females.

In terms of community function (Baker, Cruden & Baker 1971), it is clear that if the same plants are pollinated without making nectar available (deceptive pollination syndromes), other (rewarding) species, which do so, must compensate the deceived pollinators. The same vector will then pollinate the one species as a result of deception and will receive a reward as the legitimate pollinator of the other one. This was found in the present study, but more than one pollinator was involved.

The rewarding species *Asphodelus microcarpus*, *Bellevalia flexuosa* and *Salvia fruticosa* share their pollinators with *Orchis caspia* and to some extent also with *Orchis israelitica*. Since *O. caspia* is nectarless the rewarding species, therefore, subsidize the energetic expenditure of the non-rewarding species.

Faegri & van der Pijl (1979, p. 51) noted that the absence of any primary attractant in the genus *Orchis* must be connected with 'parasitic mimesis' (Vogel 1975), i.e. the resemblance of the deceptive blossoms to truly rewarding ones; the present study sustains this view. The implication is that the deceiving flower should resemble the rewarding flowers. Such a mechanism was suggested by Ackerman (1981) for *Calypso bulbosa* and by Brown & Kodric-Brown (1979) for a community of humming bird-pollinated flowers. In its floral morphology and colouring, however, *Orchis caspia* differs strikingly from its pollination subsidizers. Thus, it is hard to believe that *O. caspia* contributes to the 'attractive appeal of the community', as described for other nectarless species which mimic rewarding species (Macior 1971; Heinrich 1975) or one another (Thien & Marcks 1972; Schemske 1980).

A large proportion of *O. caspia* in the stand of vegetation might raise the chances of a pollinator learning its characteristics and subsequently avoiding it. At most of the sites (Tables 2, 3 and 4) *Asphodelus microcarpus* or *Salvia fruticosa* or both, outnumbered *Orchis caspia* at least by 50:1, whereas *Bellevalia flexuosa* did not outnumber *Orchis caspia*. A minority of the mimic is essential to establish a mimetic complex (Ford 1975, p. 254), and the rate of capsule production of *O. caspia* was significantly lower (Table 4) when it grew alone than when it grew sympatrically with one or more of the rewarding species.

In deceptive pollination syndromes, the benefit is unilateral, and is probably not the result of co-evolution but of a harnessing of the behavioural patterns of the pollinators. This assumption could explain why *O. caspia* attracts pollinators from different rewarding species in different localities according to the prevailing nectariferous species. The deceptive species exploits existing established relations between rewarding flowers and their legitimate pollinators. This view is supported by van der Pijl & Dodson (1966, p. 196) who noted that most of the known pollinators of orchids have probably developed their specialized characteristics as adaptations to other and much older plant groups. In the case of *Orchis* pollination, there is no need for special adaptations of the bees, and this situation enables a relatively rapid shift towards deception. The deception is based on the provision of an open pollination niche by the poor discriminative ability of the pollinators.

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