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Reward partitioning in *Capparis* spp. along ecological gradient

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Summary. The genus *Capparis* is represented in Israel by three taxons of the section *spinosa.* The pollinators of the three taxa are hawkmoths, crepuscular bees of the genus *Proxylocopa* and various daily bees. However, the efficiency of the different pollinators is very varied with respect to the individual taxons. Hawkmoths were frequently observed as pollinators of *C. spinosa* var. *aravensis* and *C. ovata*, but rarely on *C. spinosa* var. *aegyptia.* All the other bees, on the other hand, were found abundantly on all three taxons, all over the country.The three taxa all provide different rewards for their particular pollinators. Bees visiting *C. spinosa* var. *aegyptia* are provided with a lot of pollen but a relatively small amount of nectar, with a low sugar content. *C. spinosa* var. *aravensis* and *C. ovata* (the flowers visited more by hawkmoths), have less pollen but a higher amount of nectar which has a higher concentration of sugar. In drier habitats the emphasis of the reward provided by the flowers is nectar, whilst in the Mediterranean habitats it is the pollen which is the reward, without any connection to the systematic origin of the plant.

Key words: *Capparis* – Reward – Hawkmoths – Bees – *Proxylocopa*

Floral adaptations to different habitats as reflected by the mode of pollination are well documented in literature (Grant and Grant 1965; Faegri and Van der Pijl 1979; Proctor and Yeo 1973). Well known examples are beetle pollination as being characteristic to tropical zones (Faegri and Van der Pijl 1979), bee pollination to semi-arid and arid regions (Michener 1979) and hawkmoths as being very common pollinators in tropical habitats (Opler 1983).

In spite of the voluminous information that has been gathered on morphological flower characters, there is scant information that can relate certain habitats to certain flower reward characters. In other words, we still do not know the role of the habitat as inducing selective pressures for certain rewards in flowers towards a specific pollinator.

In order to look at this problem we chose the genus *Capparis* (section *Capparis*) in Israel which occupies diverse habitats. We attempted to examine each taxon's reward in correlation with its pollinators in its distinctive habitat. In this paper we examined the following species:

1. *Capparis spinosa* var. *aegyptia* (Lam.) Boiss.
2. *Capparis spinosa* var. *aravensis* Zoh.
3. *Capparis ovata* var. *plaestina* Zoh.

The two latter taxa are considered as derivatives of *Capparis spinosa* var. *aegyptia* (Zohary 1960) and their identification, breeding systems and interrelationships are discussed elsewhere (Ivri 1985)

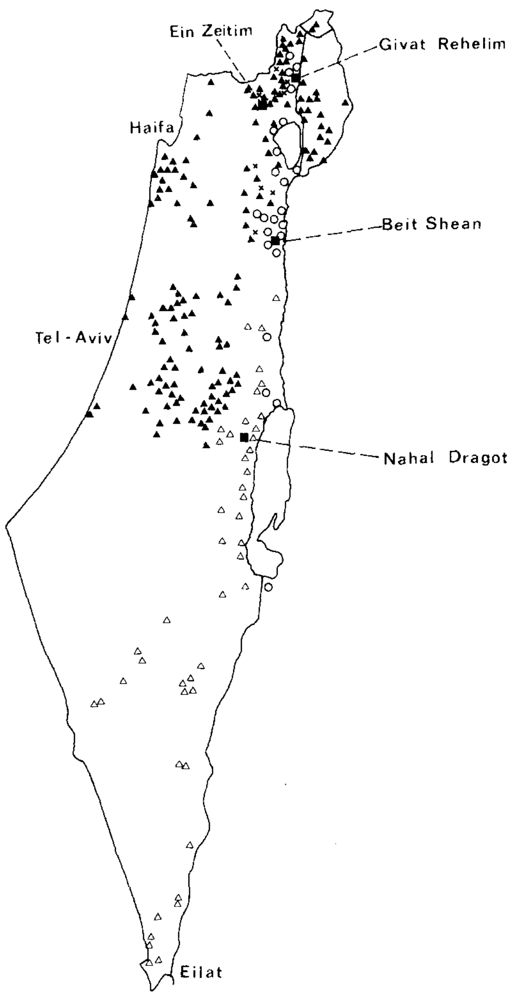

Fig. 1. Distribution map of *Capparis* sect. *Spinosa* in Israel. ○ *C. ovata*; ▲ *C. spinosa* var. aegyptia; △ *C. spinosa* var. aravensis; x Hybrid; Scale 1:1, 746, 126

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Table 1. The habitats and characteristics of *Capparis* taxa

Taxon	Observation site[a]	Chorotype	Altitude in metres (a.s.l.)	Yearly mean temperature (C°)	Annual precipitation (mm)	Common plants associated
Capparis spinosa var. *aegyptia*	Ein Zeitim	Mediterranean	700 m	16	700–800	*Ballota undulata, Sideritis pullulans, Majorana syriaca, Foeniculum vulgare, Ononis natrix, Echinops adenocaulis*
C. spinosa var. *aegyptia*	Givat Rehelim	Borderline between Mediterranean and Irano-Turanian	180 m	20	400–500	*Ballota undulata, Majorana syriaca, Varthemia iphionoides, Echinops adenocaulus, Rubus sanctus, Verbascum sinuatum*
C. Ovata var. *palaestina*	Givat Rehelim					
C. ovata var. *palaestina*	Beit Shean	Irano-Turanian	–150 m	22	300–400	*Ziziphus spina-christi, Atriplex halimus, Commicarpus africanus, Whithania somnifera*
C. spinosa var. *aravensis*	Nahal Dragot	Saharo-Arabian	–370 m	24	50–150	*Atriplex halimus, Ochradenus baccatus Tamarix* sp., *Echinops polyceras*

[a] For location see Fig. 1

Materials and methods

Plants were observed frequently during the years 1981–1984 in four locations within the natural habitats of each taxon.

A distribution map (Fig. 1) was prepared by "Rotem" (The Israel Plant Information Centre) with additional records from the Herbarium of the Hebrew University in Jerusalem, Israel.

Metereological data were recorded at adjacent metereological stations (not further away than 2 km). Local measurements were taken for temperature and relative humidity by hand psychrometer.

Insects visiting flowers were detected during day-time by direct observation (7 × 50 binocular) and by night with the aid of "Flir" Forward looking infrared (Inframetrix IRTV 445). Bee tagging was done by "Humbrol" dyes. Flower bagging was carried out before anthesis with organdy fine mesh cloth. Pollen evaluation was done by squeezing and soaking full anthers in acetone on P.V.C. slides and weighing pollen grains which remained out after acetone evaporation. Nectar was withdrawn by calibrated microcapillaries. Nectar concentration assessed as an equivalent to sucrose concentration was measured by pocket refractometer (Bellingham and Stanley, Tunbridge Wells, UK). Amounts of sugars were calculated by multiplying nectar volume by its concentration with the proper correction (Bolten et al. 1979; Inouye et al. 1980). Amino acid concentration in fresh nectar was assessed according to the "histidin method" (Baker and Baker 1973). Statistics calculation were made by using *t* test and Duncan Muliple Range test for paired and grouped populations accordingly.

Results

The genus *Capparis* has a world-wide distribution and comprises about 250 species, most of them in the Tropics, only few growing under temperate conditions (Jacobs 1965; Zohary 1966).

Common characters of these taxa are: large white zygomorphic flowers (5–8 cm), many stamens and an elevated ovary (gynophore). The anthesis of each taxon begins at one afternoon and ceases on the next midday (Ivri 1985). The flowers are white with a sweet scent, which is typical to night bloomers adapted to hawkmoth pollination (Faegri and Van der Pijl 1979; Brantjes 1973).

The habitats and characteristics of *Capparis'* taxa are presented in Table 1.

Flower reward

Nectar volume and concentartion, total sugar amount, pollen grain weight and number and an evaluation of the amino acids content were recorded (Table 2).

Capparis spinosa var. *aegyptia* has a significantly higher number of stamens and pollen grain weight as compared to *C. ovata* var. *palaestina* and to *C. spinosa* var. *aravensis* using *t* test Analysis ($P < 0.001$).

The Duncan analysis for total amino acids in nectar shows that *C. spinosa* var. *aegyptia* are richer than the other taxa and thus are grouped together ($P < 0.001$). *C. ovata* are grouped separately. However, *C. spinosa* var. *aravensis* is separated as a solitary median group.

Flower pollinators

Flowers of *Capparis* are visited by serveral insects, most of which have low pollination efficiency. The main pollinators are the hawkmoths (Sphingidae) and large bees (Hymenoptera).

The main pollinators and their activity are presented in Table 3. Additional literary information about nectar volume, concentration, total sugars and amino acids is summarized in Table 4.

Discussion and conclusion

The genus *Capparis* is regarded to have originated from a tropical area (Zohary 1960) and according to its flower architecture, anthesis, colour, odour, it is assumed to be pollinated by hawkmoths (Faegri and Van der Pijl 1979; Brantjes 1973). Our results (Table 3) indicated different proportions of each pollinator at the various habitats which were expressed by a different density of hawkmoths compared to bees, and this created a different equilibrium in

Table 2. Reward in the *Capparis* taxa

Taxon and location	Nectar reward			Pollen		Amino acids in histidine score
	Nectar volume in ul.	Concentration in %	Total sugars in mg	No. of stamens per flower	Total pollen per flower in mg	
C. spinosa var. *aegyptia* Ein Zeitim	26.5±5.9 *n*=28	26.2±2.59 *n*=28	6.94	98.8	23.81	6.48±1.17
C. spinosa var. *aegyptia* Givat Rehelim	23.4±7.14 *n*=26	26.2±1.99 *n*=26	6.13	109.3	27.32	7.48±1.12 *n*=12
C. spinosa var. *aravensis* Nahal Dragot	42.1+14.34 *n*=18	35.8±4.87 *n*=18	15.07	80.4		4.71±1.19 *n*=10
C. ovata var. *palaestina* Beit Shean	48.7±11.9 *n*=27	36.1±3.36 *n*=27	17.58	76.8	14.74	3.13±0.9 *n*=17
C. ovata var. *palaestina* Givat Rehelim	61.02±16.01 *n*=18	35.6±2.91 *n*=28	21.17	71.2	13.67	3.27±1.12 *n*=16

Duncan multiple range test for nectar volume shows that *C. spinosa* var. *aegyptia* are grouped together and are significantly ($P<0.0001$) different from *C. spinosa* var. *aravensis*, which is grouped together with *C. ovata* var. *palaestina*

Table 3. Main pollinators, their feeding preferences and activity periods in *Capparis* taxa

Pollinator	Systematic group	Time of pollinator activity	Taxons and habitats				
			C. spin. var. *aegypt.* Ein Zeitim	*C. spin.* var. *aegypt.* G. Rehelim	*C. spin.* var. *aravensis* Nahal Dragot	*C. ovata* var. *palaest.* Beit Shean	*C. ovata* var. *palaest.* G. Rehelim
Celerio lineata- Livornica	Sphingidae	Dusk	N (18.8)	–	N (33)	N (36.4)	N (38.5)
Herse convolvuli	Sphingidae	Dusk	o	o	o	N	o
Proxylocopa olivieri	Hymenoptera	Dusk-night	P, N (86.7)	P, N (76.6)	o	P, N (81.8)	P, N
Proxylocopa rufa	Hymenoptera	Dusk-night	o	o	P, N (100)	o	o
Xylocopa sulcatipes	Hymenoptera	Day	o	o	P	o	o
Xylocopa pubescens	Hymenoptera	Day	o	P	P	o	P, N
Bombus terestris	Hymenoptera	Day	P	o	o	o	
Apis mellifera	Hymenoptera	Day	P, N (92.3)	P, N (86.8)	P, N (42.85)	P, N (27.3)	P, N

N = nectar consuming, P = pollen gathering, – = pollinators' presence without visits, o = pollinators' absence. The number in brackets represents the percentage of the particular pattern out of the total observation

Table 4. Nectar volume, concentration, total sugars and amino acids as presented in bees' and hawkmoths' flowers – literary data

Source	Nectar volume in ul		Nectar concentration (%)		Total sugars (ug)		Amino acids in histidine sca	
	Bee flowers	Hawkmoth flowers	Bee flowers	Hawkmoth flowers	Bee flowers	Hawkmoth flowers	Bee flowers	Hawkmoth flowers
Opler (1983)	9.75	130.6	–	–				
Cruden et al. (1983)	2.5	42.6	34.9	21.3	0.87	9.07		
Pyke and Waser (1981)	–	–	41.6	22.1				
Baker and Baker (1983)	–	–	46	24.0				
Percival (1965)	–	–	10.74	8.18				
Baker and Baker (1973	–	–	–	–	–	–	5.64	4.86

each location. This relative composition of pollination confers, in turn, various selective pressures in accordance with the local conditions.

Analysis of feeding preference patterns shows that all the hawkmoths are exclusively nectarivorous while all the bees consume nectar as well as pollen. It also showed that all the hawkmoth pollinators were active during the night.

Although *Proxylocopa* is a bee, its activity tends to be more similar to that of hawkmoths (Table 3), while the rest of the bees are typically diurnal. *Apis mellifera* is regarded as an adventive in our region (Crane 1975) and its relative abundance and acitivity cannot be regarded as a result of local selection connected with *Capparis*.

The outcome of such a situation would confer selective pressures according to the relative abundance of each pollinator that could be revealed by redistribution of the floral reward in relation to the main pollinator in each habitat. Analysis of the rewards' components of the various taxa, shows distinctive emphasis in different taxa, which we will try to relate to the pollinators discriminating behaviour and needs.

Capparis ovata var. *palaestina* and *C. spinosa* var. *ara-*

vensis, which grow under warm and semi-arid conditions, are both pollinated by hawkmoths as well as by bees (Table 3). The characteristics of the nectar (Table 2) exemplifies a transitional position between typical hawkmoth flowers and bee flowers (Table 4).

It is noteworthy that under desert conditions *C. spinosa* var. *aravensis* is almost the sole nectar source for the pollinators. Under such conditions nectar supply is important also as a provider of liquids and sugars (Willmer 1983). Under Mediterranean conditions *C. spinosa* var. *aegyptia* blooms at the same time as other nectariferous flowers (Table 1) and the bees have alternative sources for collecting nectar. In this less arid environment this consideration could also be regarded as a possible selective pressure toward less emphasis on nectar reward compensated by more pollen production.

The results concerning amino acid in relation to the sugar concentrations does not correspond to those of Baker and Baker (1975). These authors expect a positive correlation between the two factors, while in *C. spinosa* var. *aegyptia* the sugar concentration is relatively low while the amino acid score is the highest among the examined taxa. The present results sustain the view of Gottsberger et al. (1984), that nectaries could restrict the amino acid flow through the nectar.

The similarity among the taxa, as can be inferred from the nectar and pollen characteristics, masks the taxonomic affinity, *C. spinosa* var. *aravensis* was found to be closer to *C. ovata* than to its co-species var. *aegyptia* (Table 2). These results probably reflect adaptive radiation molded by local selective pressures. Thus, the two *C. spinosa* varieties represent different anthoecotypes which correspond also with morphological characters and were adapted simultaneously to two types of pollinators.

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