

Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire

Simon G. Potts, Amots Dafni and Gidi Ne'eman

Potts, S. G., Dafni, A. and Ne'eman, G. 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. – *Oikos* 92: 71–80.

Fire in Mediterranean-type ecosystems produces catastrophic changes in plant-pollinator systems; the recovery of which has been studied by comparing an unburnt mature forest habitat with that of an adjacent recently burnt area (eight years post-fire). The composition, visitation profiles, and effectiveness of the taxonomically diverse pollinator assemblages found on a core nectar providing species (*Satureja thymbra*: Lamiaceae) were examined in these two contrasting habitats. *S. thymbra* in the freshly burnt area had low nectar standing crop and relatively less diverse bee community than an unburnt area which had twice the nectar standing crop and a higher bee diversity and abundance. Both sites supported bee assemblages dominated by the non-native bumblebee *Bombus terrestris*. Spatio-temporal heterogeneity of nectar standing crops and microclimatic conditions were sufficient to explain the form and magnitude of the diurnal foraging profiles at each site in relation to species specific foraging and flight abilities. *B. terrestris*, *Apis mellifera* and native solitary bees were the three primary guilds visiting *S. thymbra* and varied in the efficiency with which they delivered conspecific pollen grains to receptive stigmas. A pollinator effectiveness index for these three guilds was calculated based on floral visitation rates and pollen delivery efficiency and reflected the actual levels of effectiveness of each guild within and across the two habitat types. There was no overall inter-community difference in pollination effectiveness as the bee assemblages in both habitats were sufficient to produce maximum fruit set in *S. thymbra*, though the relative contribution of each guild varied intra-communally. Pollen limitation was not found to occur in either habitat.

S. G. Potts, School of Biology, Univ. of St. Andrews, St. Andrews, UK KY16 9TS (sgp@st-and.ac.uk). – A. Dafni, Inst. of Evolution, Univ. of Haifa, Haifa 31905, Israel. – G. Ne'eman, Dept of Biology, Univ. of Haifa at Oranim, Tivon 36006, Israel.

Mediterranean shrub communities are composed of patches of vegetation locked in continual regeneration towards climax maquis through a plethora of habitat perturbations including fire, grazing and other anthropogenic activities (Mooney 1986, Naveh 1990). The prominent role of fire in structuring mediterranean-type communities (Goldammer and Jenkins 1989, Blondel and Aronson 1995) has resulted in an array of adaptive traits in post-fire successional vegetation allowing rapid re-establishment (Trabaud 1987). Forms of vegetative

reproduction and seedling recruitment in response to fire have been intensively studied (e.g. Naveh 1990, Keeley 1991, 1994, and references therein) yet the role of the changing pollinator environment has received comparatively little attention (but see Moldenke 1979, Petanidou and Ellis 1996) and consequent pollination effectiveness remains untested. Post-fire phrygana vegetation contains a high proportion of obligate seeders which are entomophilous and so depend upon adequate insect pollination for successful seed production (Her-

Accepted 11 August 2000

Copyright © OIKOS 2001

ISSN 0030-1299

Printed in Ireland – all rights reserved

lera 1987a, Petanidou and Vokou 1990, Shmida and Dukas 1990). The Mediterranean basin, and Israel in particular, supports one of the most diverse bee communities worldwide (Michener 1979, O'Toole 1991) and its post-fire recovery has crucial ecological and evolutionary consequences for the flowering plants dependent upon them for pollination. The success with which flowering plants are able to re-establish themselves will be affected by the availability of both effective pollinators and resources (Vaughton and Ramsey 1994); the increased frequency of man-made fires (Kliot and Keidar 1992) and the introduction of non-native bees (Dafni and Shmida 1996) will inevitably influence the dynamic responses of the pollinator environment.

In Israel, solitary bees dominate the pollinator assemblages and are estimated to be comprised of more than 1000 species (O'Toole pers. comm.); in addition commercial honeybees are common and recently the non-native bee *Bombus terrestris* (Linnaeus 1758) (Apidae) has dramatically increased in abundance as its range has expanded throughout Israel in the last few decades (Dafni and Shmida 1996). To investigate the effects of fire on pollinator-plant interactions we have examined the shrub *Satureja thymbra* (L.) (Lamiaceae) in recently burnt phrygana and in mature unburnt phrygana. *S. thymbra* is a perennial, multi-branched, aromatic dwarf shrub with bright pink flowers borne in dense rounded distant whorls. It is a characteristic phrygana plant generally associated with disturbed habitats such as recently burnt, cleared and grazed areas and distributed throughout the eastern Mediterranean (Blamey and Grey-Wilson 1993). In Israel, blooming is from mid-April to early June; it is the only plant to provide any significant quantity of nectar during this period, thus it can be considered a core plant species (Ne'eman et al. 2000) as it supports a large number of flower visitors of which bees are the most abundant group.

The fitness and reproductive success of flowering plants will depend in part upon the abiotic resources available in the habitat and also the "quality" of the pollinator assemblage present. For a given pollinator species, pollination effectiveness varies with individual traits of mouthpart morphology (Richards 1987, Nilsson 1988), flower handling efficiency (Cane et al. 1985, Richards 1987, Wilson and Thomson 1991), floral constancy (Waser 1978, 1986, Thomson et al. 1981), intraplant floral gender preferences (Herrera 1987b, Eckhart 1992), interplant flight distances (Herrera 1987b, Pellmyr and Thompson 1996), thermal biology (Corbet et al. 1993, Herrera 1995); and also community level traits of pollinator assemblage composition (Herrera 1988, Conner and Neumeier 1995), differential species visitation rates (Herrera 1989, Cane and Payne 1993, Olsen 1997) and temporal foraging profiles (Schaffer et al. 1979, Stone et al. 1996).

This study addresses the overall pollination effectiveness of bee communities in two contrasting habitats

(burnt and unburnt Mediterranean phrygana) and partitions this into the relative contributions made by various bee guilds in relation to seed-set for the core plant species *S. thymbra*.

Materials and methods

Study sites

The study was undertaken within an area of maquis on Mount Carmel, 3–7 km east of Haifa, Israel, between 7 May 1997 and 25 May 1997. Two sites were used: the first in a clearing within unburnt maquis at Ya'ar Haya'aranim (35°1'52"E, 32°45'8"N) and the second in recently burnt phrygana (September 1989) near the Khreibeh junction (35°2'57"E, 32°44'52"N). These were chosen as being characteristic of each habitat type and had the same elevation (475 m a.s.l.), soil type (soft calcareous Rendzina), aspect (N.W. facing) and were at least 0.5 km away from closest border of the fire.

The maquis was a mixed *Pinus halepensis* woodland dominated by shrubs and multistem dwarf trees. Heavy grazing, cutting and trail making activities have resulted in exposed areas of phrygana comprising *Satureja thymbra* in transition to *Genista fasselata*–*Thymelea hirsuta* association and the habitat is a mosaic of patches and corridors of early succession vegetation within large stands of mixed woodland. In contrast, the burnt area consisted of relatively uniform coverage of phrygana vegetation in the early successional stage of maquis regeneration (eight years post-fire) and was dominated by dwarf shrubs of *Cistus* spp., *Satureja thymbra*, *Sarcopoterium spinosum* and *Genista fasselata*, and *Pinus halepensis* seedlings.

Flower phenology and nectar profiles

Before the main study five individual flowers from each of four different *S. thymbra* plants were marked at the burnt site and flowering progress and time of pollen availability recorded throughout the day from bud opening to flower wilting. Concurrently, stigmas were removed from 20 other flowers at various developmental stages and the period of receptivity and receptive area of the stigma located using the Baker, peroxidase and H₂O₂ tests (Dafni 1992).

Five representative *S. thymbra* plants (with ca 1000 flowers each) were selected at each site and used as the focal study plants with investigations being carried out on one plant each day with alternation between sites (weather conditions varied little throughout the 10 d). Daily nectar profiles were obtained by sampling 10 flowers each hour from 05:00 to 17:30: volume was determined by extracting nectar with 1 µl microcapillaries (Camlab, UK) and concentration, as sucrose

equivalent concentration (%), using a field refractometer modified for small volumes (Bellingham & Stanley, UK). In addition to each focal plant with unrestricted visitation (designated 'open'), a second neighbouring plant of similar size was covered with 1-mm-diameter netting at 05:00 before the arrival of the first flower visitors (designated 'bagged') and nectar profiles for these plants obtained by the same method. Microclimatic measurements of ambient air temperature and relative humidity were made hourly throughout the nectar sampling period.

Flower visitors

On each focal plant all flower visitors were caught during a 30-min period of each hour between 05:00 and 17:30. Those which could be unequivocally identified in the field were released away from the focal plant, while the remainder were retained for subsequent identification in the laboratory. The abundance of visiting insects was great at both sites and the sampling procedure was not considered to have a noticeable effect on the local insect assemblages. Bees were by far the most common visitors and were assigned to one of the following categories: *Bombus terrestris*, *Apis mellifera*, solitary bees (subdivided into: *Eucera helvola*, *Chalicodoma* sp., *Osmia* sp. and other solitary bees). Visits were recorded irrespective of whether a particular insect had been to the plant previously; and mean visit frequency (VF) was standardised by calculating the number of flower visits/1000 flowers/hour to control for any variation resulting from differences in the number of flowers per plant. The number of flowers visited in a bout (NF) for each bee type was recorded so that the absolute visitation rate (AVR) could be calculated as: $VF \times NF$.

The mouthparts of fresh bee specimens were removed by dissection and functional tongue lengths then measured using a binocular microscope with a calibrated ocular according to the methods of Harder (1982); pinned specimens were relaxed before measuring. The functional proboscis for long-tongued bees was measured as the distance from the base of the prementum to the tip of the glossa, and for short-tongued bees from the base of the mentum to the tip of the glossa.

Voucher specimens have been deposited at Oxford University Museum and the Institute of Evolution, Haifa.

Pollen deposition on stigmas

At each site several inflorescences on several plants were covered with 1-mm netting, having previously marked all unopened buds. During the next three days the netting was removed and an individual of a given bee category allowed to visit a single flower before

replacing the netting. Each flower was then carefully removed and placed in a separate vial for transportation to the laboratory. Within 6 h of collection stigmas were removed, stained with a mix of phloxine and methyl green and the number of conspecific pollen grains on the receptive area of the stigma counted (Dafni 1992: 83–84) and the mean number of pollen grains deposited (PG) for each bee type per visit was calculated.

An index of pollinator effectiveness (PE) was estimated as the absolute number of pollen grains that a given bee type could potentially deposit on a stigma during its receptive period: $PE = \text{time receptive stigma was exposed to bees} \times \text{hourly AVR} \times \text{PG}/1000$. As stigmas were receptive for 43 h from 08:00 on the third day after flower opening (see results), then it is possible to calculate the absolute number of bee visits a single stigma could receive by summing the AVRs for day 3 (08:00 to 17:00) and day 4 (05:00 to 17:00) and dividing this total by 1000 (AVRs are a rate per 1000 flowers); multiplying this value by the PG of a particular bee group produces estimates of the PE of *Bombus*, *Apis* and solitary bees at each site. The PE for solitary bees is a composite of the values of the three solitary genera for which PG values were available, and were weighted in the calculation in accordance with their relative abundance given in Table 2.

Fruit set and nutlet mass

Fruit set was determined by removing the dried calyces from the fifth terminal whorl of 10 randomly selected inflorescences of each focal plant at the end of the flowering season and before dispersal (15 June 1997). The inflorescences flower simultaneously in *S. thymbra* and the fifth whorl was selected as it was known to have been in full flower during the period that the visitors were censused. A sample of 100 calyces was randomly selected and the nutlets collected by first crushing and sieving the material and then by separating the nutlets under a binocular microscope. In 1994 and 1995 fruit set was also determined for 10 individual plants at the burnt site.

For *S. thymbra*, each flower can potentially produce four nutlets and so the percentage fruit set for each plant was calculated as: $(\text{total number of nutlets}/100 \text{ flowers}/4) \times 100$. Mean nutlet mass for each plant was determined by weighing the same nutlets and dividing by the number in the sample.

Statistical analysis

The effects of site and bee type were partitioned using one- or two-way ANOVA with planned comparisons of means tested using the least significant difference

Table 1. Mean daily volumes and concentrations of nectar in flowers of open and bagged plants of *Satureja thymbra* at the burnt and unburnt sites. The nectar from 10 flowers on five plants from each site was measured every hour for 12 h through the day and the hourly mean of the five plants for each site calculated. Each value in the table is the mean \pm SE of the individual hourly means ($n = 12$ for all cases).

Site	Open		Bagged	
	Volume (μ l)	Concentration (%)	Volume (μ l)	Concentration (%)
Burnt	0.03 \pm 0.01	40.0 \pm 3.6	0.20 \pm 0.02	45.5 \pm 2.3
Unburnt	0.02 \pm 0.01	35.4 \pm 2.6	0.56 \pm 0.06	44.1 \pm 4.5

method (LSD test) and unplanned comparisons using Tukey's honest significant difference method (HSD test) in accordance with Sokal and Rohlf (1995). Differences in the activity (AVR) profiles across sites for each bee were tested using the Kolmogorov-Smirnov test. All means are given together with standard errors and sample sizes in parentheses afterwards. Calculations were made using Microsoft Excel 97 and Statistica 4.5.

Results

Flower phenology and stigma receptivity

Flowers were hermaphroditic, protandrous and had a lifespan of 3 to 4 d with a mean of 89.4 ± 11.1 h (20) (measured from the onset of anthesis until the stigma wilted). Anther dehiscence was concurrent with flower opening (05:00 to 08:00 on day 1) and from an initial peak of pollen availability there was a steady decline until the end of the second day, at which point pollen was almost entirely depleted by flower visitors. At the start of anthesis the style was hidden within the corolla tube, the stigma had not yet bifurcated, was non-receptive and nectar was absent. Rapid stylar growth followed, resulting in exposure beyond the anthers and was accompanied by splitting of the stigma at a mean flower age of 46.4 ± 3.1 h (20). Bifurcation generally occurred between 08:00 and 10:00 on the third day after bud opening and the bifid stigma was receptive on the inside surface of the stigmatic lobe until wilting ensued. Following bifurcation, nectar secretion commenced and pollen availability remained negligible. The time the flower remained receptive was therefore approximately 43 h ($89.4 - 46.4$). No difference in flowering phenology was observed as plants flowered simultaneously at both sites.

Nectar volume and concentration

The daily means for nectar volumes and concentrations are given in Table 1. In the open condition nectar volume was negligible ($< 0.03 \mu$ l) and there was no significant difference across sites ($F_{1,22} = 0.51$, $P = 0.485$); however, the much greater nectar volumes found in the unvisited bagged plants indicates the high

efficiency of harvesting of the nectar crop through the day. The overall volume of nectar present in flowers at the unburnt site was significantly greater than for the burnt site ($F_{1,22} = 31.73$, $P < 0.001$) with large intersite differences in volume recorded from 06:00 to 12:00 and similar volumes thereafter (Fig. 1A).

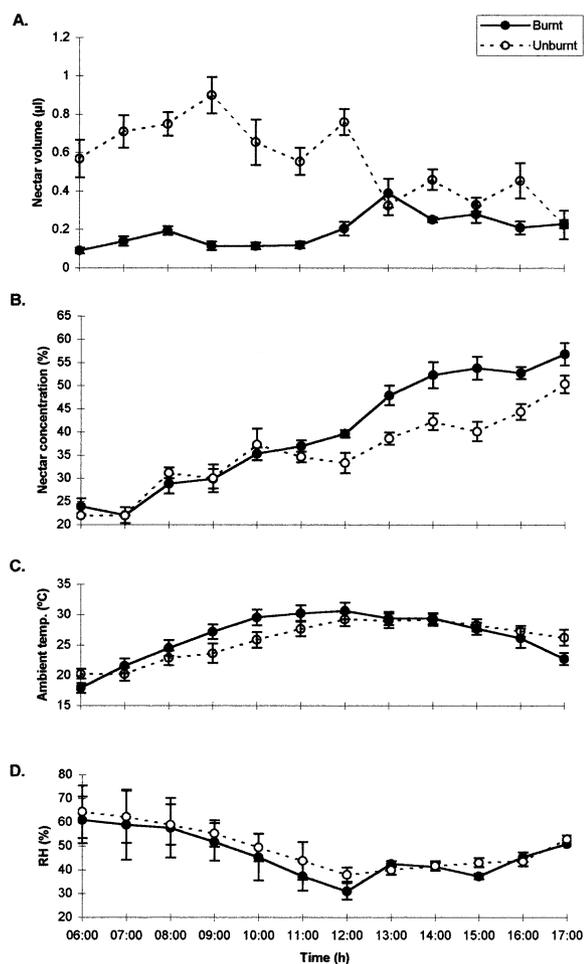


Fig. 1. Mean daily nectar profiles for *Satureja thymbra* for five days of measurement at the burnt and unburnt sites. Hourly mean \pm SE of five focal study plants (with 10 flowers sampled from each plant) for: A) nectar volume and B) nectar concentration. Mean daily microclimate profiles for the corresponding days for: C) ambient temperature and D) relative humidity.

Table 2. Percentage of individuals comprising the bee fauna visiting *Satureja thymbra* over a 10-d period between 7.5.97 and 25.5.97, at the burnt (822 individuals) and unburnt (1075 individuals) sites. Only species contributing more than 1% of the total for each site are included.

Family Species	% bee fauna individuals	
	Burnt site	Unburnt site
Apidae		
<i>Bombus terrestris</i>	29.0	37.7
<i>Apis mellifera</i>	17.9	9.6
Anthophoridae		
<i>Anthophora orientalis</i>		1.4
<i>Eucera helvola</i>	5.0	2.1
<i>Eucera</i> sp. 1		2.8
Megachilidae		
<i>Chalicodoma montenegrina</i>	15.3	7.2
<i>Chalicodoma parietinum</i>		5.1
<i>Hoplitis</i> sp.1	2.1	1.2
<i>Megachile giraudi</i>		2.6
<i>Megachile lagopoda</i>		3.1
<i>Osmia sybaritafossoria</i>	13.9	9.5
<i>Osmia versicolor</i>	7.3	7.5
<i>Protosmia longiceps</i>	4.3	3.6
<i>Rhodanthidium septempunctatum</i>	4.1	6.6
Andrenidae		
<i>Andrena flavipes</i>	1.2	

The mean daily nectar concentrations were not significantly different across sites for open ($F_{1,22} = 1.14$, $P = 0.298$) or bagged plants ($F_{1,22} = 0.08$, $P = 0.786$). The temporal profiles of nectar concentration showed a steady increase in concentration through the day with very little difference between sites (Fig. 1B). Differences in microclimatic conditions were negligible between days and across sites throughout the study period, but varied markedly within days (Fig. 1C, D).

Flower visitor diversity and abundance

During the study period, the total number of flower visitors recorded at the burnt site was 913, comprising 27 species, and at the unburnt site 1191, comprising 34 species. At both sites, bees made up ca 94% of all individuals and species richness was greater in the

unburnt site (30) than in the burnt site (22); detailed analysis of the diversity of these two bee assemblages will be presented elsewhere (S. G. Potts unpubl.). Non-apid visitors included: *Eristalis tenax* (Syrphidae), an unidentified syrphid, a bee fly (Bombyliidae), a nymphalid butterfly (Nymphalidae), *Macroglossum stellatarum* (Sphingidae) and a *Philanthus* sp. (Sphecidae); all these were very rare (< 5 visits) except for *E. tenax* and the nymphalid that visited very few flowers in a sequence (generally only one with modes of four and six, respectively). To facilitate analysis all visitors making up less than 1% of the fauna and also the non-apid visitors were excluded; the remaining species are given in Table 2. The excluded rare bee species were: two *Synhalonia* spp., three *Eucera* spp., *Amegilla albigena* and one *Nomada* sp. (Anthophoridae); *Chalicodoma siculum*, two other *Ch.* spp., one *Osmia* sp. and three *Megachile* spp. (Megachilidae); three *Andrena* spp. (Andrenidae); three *Halictus* spp. and three *Lasioglossum* spp. (Halictidae).

The mean number of flowers visited during an intraplant forage sequence (NF) differed significantly between bee groups ($F_{2,159} = 12.15$, $P < 0.001$) but not across sites ($F_{1,159} = 0.07$, $P = 0.789$) and there was no interaction between bee type and site ($F_{2,159} = 1.79$, $P = 0.170$). The NF for *Bombus terrestris* (Table 3) was significantly greater than for *Apis mellifera* and solitary bees (LSD test: $P = 0.005$ and $P < 0.001$ respectively), and the NF for *Apis* was higher than for solitary bees though the difference was not significant ($P = 0.068$).

The absolute visitation rate (AVR) profile across bee groups and across sites is given in Fig. 2. and the daily means in Table 3. There was a rapid increase in *Bombus* foraging activity during the first hour of observation (05:00–06:00) followed by a steady decrease through the day until foraging stopped after 17:00 (Fig. 2A). In contrast, both *Apis* and solitary bees showed distinctive unimodal activity patterns with highest AVRs between 09:00 and noon (Fig. 2B, C); the onset of foraging was approximately 2 h later than for *Bombus*. The form of the AVR profiles was very similar between sites for each bee group, however, there were striking quantitative differences between sites: hourly AVRs were greatest in the unburnt site for *Bombus* whereas for *Apis* and

Table 3. Mean number of flowers visited (NF) by various bee types during a foraging bout on a single *Satureja thymbra* plant, mean daily absolute visitation rates (AVR; calculated as the mean of 13 sampling hours for the mean of five plants at each site) and pollinator effectiveness index (see text for details). Values with similar letters are not significantly different (HSD test, $P < 0.05$).

Measure	Site	<i>Bombus terrestris</i>	<i>Apis mellifera</i>	Solitary bees
NF	Burnt	6.25 ± 10.7 (23)	47.8 ± 6.1 (41)	29.9 ± 4.5 (68)
	Unburnt	88.2 ± 13.0 (15)	31.2 ± 6.7 (5)	29.9 ± 12.7 (18)
AVR ($n = 13$)	Burnt	278 ± 46 ^{ab}	122 ± 31 ^a	338 ± 88 ^{ab}
	Unburnt	508 ± 58 ^b	42 ± 6 ^a	242 ± 43 ^a
PE Index	Burnt	13.0	9.7	18.5
	Unburnt	24.5	3.4	13.0

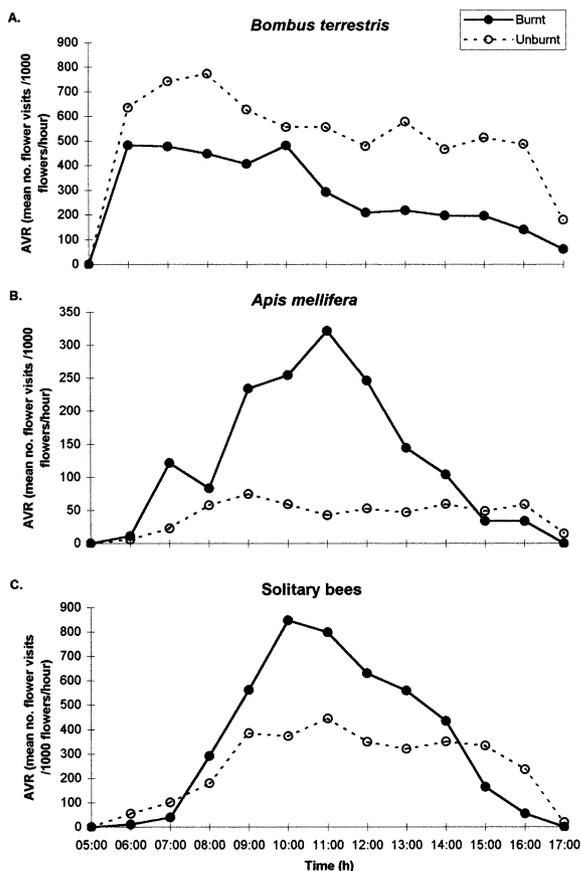


Fig. 2. Absolute visitation rate (AVR; see text for details) profiles for bees on *Satureja thymbra* in the burnt and unburnt study sites (mean AVR for five plants at each site): A) *Bombus terrestris*, B) *Apis mellifera* and C) solitary bees.

solitary bees the burnt site showed the highest levels of foraging activity (Kolmogorov–Smirnov test: *Bombus*, $P < 0.01$; *Apis*, $P < 0.05$; solitary, $P > 0.05$). The maximum AVRs recorded for *Bombus* and solitary bees were quite similar, viz. 500–800, and much greater than those for *Apis*, viz. 50–300 (Fig. 2). There were significant differences in the mean daily AVRs (Table 3); only *Bombus* exhibited differential rates across habitats (HSD test: $P = 0.023$). Within the burnt site solitary bees had significantly higher AVRs than *Apis* ($P = 0.047$) and within the unburnt site both *Bombus* ($P < 0.001$) and solitary bees ($P = 0.007$) had significantly higher AVRs than *Apis*.

The mean functional tongue lengths of bees visiting *S. thymbra* varied considerably: *B. terrestris* (7–9 mm), *A. mellifera* (4–6 mm), large solitary bees of *Eucera* and *Chalicodoma* spp. (5–10 mm) and the small solitary bees of *Osmia* spp. (2–4 mm).

Pollen deposition by flower visitors

There were significant differences ($F_{6,341} = 14.15$, $P < 0.001$) in the mean number of pollen grains found on the stigma (PG) after different pollination treatments (Table 4), but no overall difference between sites ($F_{1,341} = 1.09$, $P = 0.297$). PG, under open visitation, for the burnt site was significantly higher (HSD test: $P < 0.001$) than for the unburnt site, but there were no differences between sites for the various bee species (all $P > 0.648$) (Table 3). The highest PG was recorded in the open condition and the lowest in the unvisited flowers and this difference was significant (burnt, $P < 0.001$; unburnt $P = 0.006$). *Apis* delivered the most pollen grains (3.2 ± 0.6 (48)), followed by the large solitary bees of *Chalicodoma* spp. (2.8 ± 0.8 (13)) and *Eucera* spp. (2.7 ± 0.9 (15)), then *Bombus* (2.1 ± 0.6 (96)), with the small solitary bee *Osmia* spp. delivering the least (1.5 ± 0.4 (73)).

At the burnt site solitary bees had the highest pollinator effectiveness, which was twice that of *Apis* while *Bombus* had an intermediate value; in contrast, at the unburnt site *Bombus* had a PE almost twice that of solitary bees which in turn was four times that of *Apis* (Table 3). The total PE for each site (sum of individual PEs) was very similar (burnt, 41.2; unburnt, 40.9) indicating that approximately 41 pollen grains could be delivered to a receptive stigma during a flower's lifespan.

Fruit set and nutlet mass

Across sites, the number of nutlets per flower (burnt, 3.47 ± 0.09 ; unburnt, 3.33 ± 0.27) and so the estimated percentage fruit sets (burnt, $86.7 \pm 2.3\%$; unburnt, $83.3 \pm 6.8\%$) were very similar ($F_{1,8} = 0.22$, $P = 0.648$). In the burnt area, in 1994 the fruit set was found to be $44.6 \pm 11.0\%$ and in 1995, $29.4 \pm 14.0\%$. In 1997, the mean nutlet mass was significantly greater ($F_{1,8} = 11.66$, $P = 0.009$) in the burnt site (0.63 ± 0.03 mg) than in the unburnt site (0.51 ± 0.02 mg).

Table 4. Mean number of conspecific pollen grains deposited on the receptive area of stigmas of *Satureja thymbra* under seven pollination treatments.

Treatment	Burnt	Unburnt
Open pollinated	12.1 ± 3.9 (18)	6.4 ± 0.9 (46)
Unvisited	1.5 ± 0.9 (24)	1.7 ± 0.8 (24)
<i>Bombus terrestris</i>	2.2 ± 1.0 (48)	1.9 ± 0.6 (48)
<i>Apis mellifera</i>	4.1 ± 0.7 (16)	2.7 ± 0.9 (32)
<i>Eucera</i> spp.	2.6 ± 1.2 (7)	2.9 ± 1.0 (8)
<i>Chalicodoma</i> spp.	2.0 ± 1.0 (3)	3.1 ± 1.0 (10)
<i>Osmia</i> spp.	1.3 ± 0.4 (39)	1.8 ± 0.6 (34)

Discussion

Nectar standing crop and bee visitation

The differences in nectar volumes between sites in the bagged plants (Table 1) can not be attributed to differences in microclimate or floral visitation and so must be linked to the resources available to the individual plants and, in particular, access to water (Pleasants 1983), as photosynthetic sugar production is generally assumed to be relatively inexpensive (Southwick 1984, Harder and Barrett 1992; but see Pyke 1991) and there was no restriction on access to sufficient sunlight as the two sites were unshaded. Post-fire soils have reduced water retention capacities (Rambal 1989, Molina and Llinares 1998) though on Mount Carmel this effect may be diminished by 6–8 years post-fire (Inbar et al. 1999). In addition, less water may be available in burnt sites as local competition for water will be more intense as the shrub cover is much higher there than in unburnt sites (Schiller et al. 1997, Dafni and Potts unpubl.); *S. thymbra* will compete more directly for water with its functional analogues than with *Pinus halepensis*.

Bombus terrestris was the most dominant visitor to *Satureja thymbra* at both the burnt (29.0% of bee visits) and unburnt (37.7%) sites (Table 2); its peak visitation period (06:00–09:00) coincided with the maximum availability of nectar at the unburnt site (Fig. 2). As a habitat with a higher floral resource abundance will promote increased bee abundance (Moldenke 1975), it follows that the unburnt site will support more large bees, with high energetic demands during foraging, than the burnt site. The peak AVR for honeybees and solitary bees were later than for the bumblebees and this can be attributed to differences in abilities of resource harvesting, thermoregulation or other life history trait across bee groups. Bumblebees are much more efficient thermoregulators than either honeybees or solitary bees (Stone and Willmer 1989) and so are generally less constrained in foraging and flight activities by lower ambient temperatures (Willmer 1983), although some solitary bee species are known to forage at low ambient temperatures and before dawn (e.g. Willmer and Stone 1997). Mean ambient temperatures at both sites were less than 22°C before 07:00 (Fig. 1A) and only *B. terrestris* was observed foraging in any numbers until this time. This type of temporal partitioning of pollinator abundance through thermal constraints is a well-documented phenomenon (e.g. Willmer and Corbet 1981, Stone et al. 1988, Herrera 1990) and it has specifically been shown that *B. terrestris* is able to forage at lower ambient temperatures and therefore earlier in the day than honeybees (Corbet et al. 1993).

Nectar harvesting ability is dependent on, amongst other factors, nectar ingestion rates and functional tongue lengths (Harder 1983). *Bombus* spp. have longer

glossae (Knuth 1906, this study) than many solitary bees and *Apis*, and larger bees tend to have higher nectar imbibing rates than smaller ones (Plowright and Lavery 1984, Roubik 1989). The functional corolla tube length of *S. thymbra* is 8.0 mm (Dafni 1991) which indicates that nectar was easily accessible for *B. terrestris*, *Apis*, and the large solitary bees, but not for smaller solitary bees. In another study of flowering plants in the Mediterranean phrygana, it was found that there was effective exclusion of both solitary and honeybees by *B. terrestris* early in the day (Dafni and Shmida 1996). It was shown that, by excluding *B. terrestris* by bagging plants at 05:00 and then opening them at 09:00, significantly higher abundances of non-*Bombus* flower visitors were observed foraging on these plants than in equivalent unbagged plants and this was suggestive of competitive exclusion through superior exploitation of available floral nectar resources. In the present study, the efficient nectar removal by *B. terrestris* prior to other bee visitations, dramatically reduced the nectar standing crop at both sites (Table 1) and it would seem likely that this would markedly reduce the size of other bee populations in the long term by limiting floral resources available for their reproductive output.

The other major floral resource in this system was pollen; though available in *S. thymbra*, this species remained primarily a nectar providing plant. Examination of pollen loads of *B. terrestris* has revealed negligible pollen from *S. thymbra* relative to five other co-flowering species (Ne'eman et al. 1998) and during this period in the season *Hypericum triquetrifolium*, *Myrtus communis* and *Cistus* spp. were known to be the main pollen providers for the majority of bees (pers. obs.). These primary pollen species were common in both the burnt and unburnt sites and were easily within the foraging range of all the visitors to our experimental plants. Additionally, following > 100 h of intensive observation of bee visitation to *S. thymbra* (this study) only a few small solitary bees were ever recorded to actively collect pollen while all the large solitary bees and social bees restricted their visits to nectar foraging.

The total sum of daily AVR for each site (from Table 3) were 738 in the burnt area and 792 in the unburnt area; the similar values were, however, partitioned quite differently in terms of bee type and their associated nectar harvesting efficiency. The unburnt site had a much greater overall energy availability and this was utilised primarily by a large abundance of *B. terrestris* individuals with high energy demands throughout the day, so that the abundance of solitary and honeybees may have been limited through restricted energy availability. In contrast, at the burnt site, there was less overall nectar present in *S. thymbra* and consequently fewer *B. terrestris* through the day, and the higher abundances of other bee species may have been the result of the nectar standing crop being

energetically sufficient to support only bee species with lower overall energetic requirements. This type of partitioning of a single resource between social and solitary bees, in relation to energetic costs of foraging and thermal limitations, has been documented and modeled by Schaffer et al. (1979). Similarly, in the present study, the characteristics of the flower foraging profiles through time and across sites are likely to be explained by differences in absolute nectar standing crop through time in conjunction with species specific energetic demands, functional tongue lengths and also thermoregulatory abilities. It should, however, be noted that as *B. terrestris* is a recent introduction to the area and bee communities in the two habitats may not have reached their equilibria; consequently these results should be applied to other situations with caution.

Intra- and inter-community differences in pollination effectiveness

Large native bees were generally more efficient at delivering pollen grains to a receptive stigma than were bumblebees or small solitary bees (Table 4), and this might be expected as native bee populations should be better adapted to pollinating a core species than recently introduced generalist bees (Westerkamp 1991, Paton 1993, Kearns and Inouye 1997), as there will be selection for close spatial matching of floral morphology with the most effective pollinators (Galen et al. 1987). Bumblebees are also known to have significantly shorter visit duration per flower than some other bees (Richards 1987, Olsen 1997) and, assuming effective pollen delivery is a function of time spent in contact with floral structures, then it is expected that *B. terrestris* may not be as efficient at delivering pollen grains from its body to a receptive stigma as contact time is relatively short when compared to other similar sized bees which spend more time on individual flower visits.

B. terrestris has only been present as a flower visitor in Mt. Carmel for ca 25 years (Dafni and Shmida 1996); however, when the large number of visits to *S. thymbra* flowers are taken into account there are sufficient numbers of pollen grains being deposited by this species for it to contribute to the high level of seed production. From our data it appears that very few bee visits are required to leave the equivalent number of pollen grains found in the open treatment (Table 4); the reasons for this phenomenon may relate to the highly disturbed habitat that *S. thymbra* is characteristic of, and are discussed later.

Both sites were closely matched in the percentage fruit set (ca 85%) and this is the maximum level generally found for this species on Mt. Carmel (A. Dafni unpubl.); such a high level of nutlet production indicates that pollination is not a limiting factor in itself. Nutlet mass varied across sites and can be attributed to

differences in mineral-based resource availability, as the burnt site will have elevated levels of many soil micronutrients (e.g. P, K and N) following the fire which are important in seed development (Rundel 1981, Kutiel and Naveh 1987, le Maitre and Midgley 1992). Zimmerman (1988) also suggests that when seed-set is resource limited, the amount of pollen delivered may be an important component of seed quality (mass) through pollen grain competition for ovules (Mulcahy et al. 1988) and selective abortion of seeds (Haig and Westoby 1988). It may also be that pollen production per flower at the burnt site was higher due to resource availability and this may have contributed to the greater number of grains being deposited; however, this was beyond the scope of the present study and not necessary in order to explain the observed differences.

Bertin (1988) supports Cruden's (1977) suggestion that 2–7 pollen grains per ovule deposited on a stigma are typically required to maximise seed set; and therefore for Lamiaceae, in which each flower has four ovules, an estimate of 8–28 pollen grains are sufficient to attain this. In the burnt site this number of pollen grains was achieved by combining the pollination effectiveness of solitary and honeybees alone (PE = 18.5 and 9.7 respectively; Table 3); in contrast, in the unburnt site the smaller contribution made by these two groups (PE = 13.0 and 3.4) might not be adequate in the absence of the non-native *B. terrestris*. Referring to the number of pollen grains in flowers under open pollination (Table 4) it is apparent that these values (burnt, 12; unburnt, 6) are considerably less than are found by summing the PEs for each bee group. This discrepancy may be due to reasons connected with pollen packing on a receptive stigma. Our calculations of PE were based on summed single visits to virgin flowers where there was virtually no pollen already present so that there would be the maximum sticky area of exposed stigmatic surface present to contact with vector borne pollen. However, in the open condition, subsequent visits may not deposit as much pollen as a single visit (Spears 1983) and there may be physical interference from grains previously deposited due to the stigmatic surface becoming increasingly clogged as visit number increases (Ashman et al. 1993); in our study, the highest number of grains recorded on the stigmatic surface was 42 and visual inspection indicated that this might approach to the maximum number which could be situated close enough to the stigmatic surface for germination to proceed.

Bombus terrestris contributes a significant amount to the overall PE at both sites (Table 3); however, this may be an overestimate of its actual contribution as a large proportion of *B. terrestris* AVR's occurred before the stigma became receptive on the first morning of exposure (day 3, 08:00). Following stigmatic surface exposure the ratio of *Bombus*: other bee visitations decreased through time as solitary bees and honeybees

foraged in increasing numbers; during this period (08:00 onwards) the first such visitors may therefore be the most important in terms of pollen involved in the fertilisation process (Spears 1983). Late arriving pollen may be precluded from ovule fertilisation (Spira et al. 1996) and, even though this was not directly tested in our study, we hypothesize that pollen grains delivered by *B. terrestris* may not contribute to the overall reproductive output of *S. thymbra* as much as those delivered by solitary bees and *Apis*.

Acknowledgements – We would like to thank Pat Willmer and L. Anders Nilsson for constructive comments on the manuscript and Chris O'Toole for help in identifying the bees. SGP was funded by the Balfour Diamond Jubilee Trust and Natural Environment Research Council (GR3/11743) and AD by the Henk and Dorothy Schussheim Fund for Ecological Research on Mount Carmel.

References

- Ashman, T. L., Galloway, L. F. and Stanton, M. L. 1993. Apparent vs. effective mating in an experimental population of *Raphanus sativus*. – *Oecologia* 96: 102–107.
- Bertin, R. I. 1988. Paternity in plants. – In: Doust, L. J. and Doust, L. L. (eds), *Plant reproductive ecology: patterns and strategies*. Oxford Univ. Press, pp. 30–59.
- Blamey, M. and Grey-Wilson, C. 1993. *Mediterranean wild flowers*. – Domino Books.
- Blondel, J. and Aronson, J. 1995. Biodiversity and ecosystem function in the Mediterranean basin: human and non-human determinants. – In: Davis, G. W. and Richardson, D. M. (eds), *Mediterranean-type ecosystems: the function of diversity*. Springer-Verlag, pp. 43–119.
- Cane, J. H. and Payne, J. A. 1993. Regional, annual and seasonal variation in pollinator guilds: intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). – *Ann. Entomol. Soc. Am.* 86: 577–588.
- Cane, J. H., Eickwort, G. C., Wesley, F. R. and Spielholz, J. 1985. Pollination ecology of *Vaccinium stamineum* (Ericaceae: Vaccinioideae). – *Am. J. Bot.* 72: 135–142.
- Conner, J. K. and Neumeier, R. 1995. Effects of black mustard population size on the taxonomic composition of pollinators. – *Oecologia* 104: 218–224.
- Corbet, S. A., Fussell, M., Ake, R. et al. 1993. Temperature and the pollinating activity of social bees. – *Ecol. Entomol.* 18: 17–30.
- Cruden, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. – *Evolution* 31: 32–46.
- Dafni, A. 1991. Advertisement, flower longevity, reward and nectar protection in Labiatae. – *Acta. Hortic.* 288: 340–346.
- Dafni, A. 1992. *Pollination biology: a practical approach*. – Oxford University Press.
- Dafni, A. and Shmida, A. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt. Carmel, Israel. – In: Matheson, A., Buchmann, S. L., O'Toole, C. et al. (eds), *The conservation of bees*. Academic Press, pp. 184–200.
- Eckhart, V. M. 1992. Spatio-temporal variation in abundance and variation in foraging behavior of the pollinators of gynodioecious *Phacelia linearis* (Hydrophyllaceae). – *Oikos* 64: 573–586.
- Galen, C., Zimmer, K. A. and Newport, M. E. 1987. Pollination in floral scent morphs of *Polemonium viscosum*: a mechanism for disruptive selection on flower size. – *Evolution* 41: 599–606.
- Goldammer, J. G. and Jenkins, M. J. 1989. *Fire in ecosystem dynamics*. – SPB Academic Publ.
- Haig, D. and Westoby, M. 1988. Inclusive fitness, seed resources and maternal care. – In: Doust, L. J. and Doust, L. L. (eds), *Plant reproductive ecology: patterns and strategies*. Oxford Univ. Press, pp. 60–79.
- Harder, L. D. 1982. Measurement and estimation of functional proboscis length in bumblebees (Hymenoptera: Apidae). – *Can. J. Zool.* 60: 1073–1079.
- Harder, L. D. 1983. Flower handling efficiency of bumble bees: morphological aspects of probing time. – *Oecologia* 57: 274–280.
- Harder, L. D. and Barrett, S. C. H. 1992. The energy cost of bee pollination for *Pontederia cordata* (Pontederiaceae). – *Funct. Ecol.* 6: 226–233.
- Herrera, C. M. 1987b. Components of pollinator “quality”: comparative analysis of a diverse insect assemblage. – *Oikos* 50: 79–90.
- Herrera, C. M. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. – *Biol. J. Linn. Soc.* 35: 95–125.
- Herrera, C. M. 1989. Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity” component in a plant-pollinator system. – *Oecologia* 80: 241–248.
- Herrera, C. M. 1990. Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. – *Oikos* 58: 277–288.
- Herrera, C. M. 1995. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. – *Ecology* 76: 1516–1524.
- Herrera, J. 1987. Flower and fruit biology in southern Spanish Mediterranean shrublands. – *Ann. Mo. Bot. Gard.* 74: 69–87.
- Inbar, M., Wittenberg, L. and Tamir, M. 1999. The effect of wildfire on the hydrological and sedimentological regime of a burnt natural pine forest. – In: Neeman, G. and Izhaki, I. (eds), *MEDPINE-International Workshop on Mediterranean pine*. Univ. of Haifa, 27 p.
- Kearns, C. A. and Inouye, D. W. 1997. Pollinators, flowering plants, and conservation biology. – *BioScience* 47: 297–307.
- Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. – *Bot. Rev.* 57: 81–116.
- Keeley, J. E. 1994. Seed-germination patterns in fire-prone Mediterranean-climate regions. – In: Arroyo, M. T. K., Zedler, P. H. and Fox, M. D. (eds), *Ecology and biogeography in Mediterranean ecosystems in Chile, California and Australia*. Springer-Verlag, pp. 239–273.
- Kliot, N. and Keidar, G. 1992. Man-made forest fires in Israel. – *Ofahim Be'geografia* 8: 23–34 [in Hebrew with English summary].
- Knuth, P. 1906. *Handbook of flower pollination*. – Clarendon Press.
- Kutiel, P. and Naveh, Z. 1987. Soil properties beneath *P. halepensis* and *Quercus calliprinos* trees on burned and unburned mixed forest on Mt Carmel, Israel. – *For. Ecol. Manage.* 20: 11–24.
- le Maitre, D. C. and Midgley, J. J. 1992. Plant reproductive ecology. – In: Cowling, R. (ed.), *The ecology of Fynbos, nutrients, fire and diversity*. Oxford Univ. Press, pp. 135–174.
- Michener, C. D. 1979. Biogeography of the bees. – *Ann. Mo. Bot. Gard.* 66: 277–347.
- Moldenke, A. R. 1975. Niche specialization and species diversity along an altitudinal transect in California. – *Oecologia* 21: 219–242.
- Moldenke, A. R. 1979. Pollination ecology as an assay for ecosystemic organization: convergent evolution in Chile and California. – *Phytologia* 42: 415–454.

- Molina, M. J. and Llinares, J. P. 1998. Effects of fire intensity on the soil properties related to structure: organic matter, aggregate stability and water retention capacity. – In: Trabaud, L. (ed.), Fire management and landscape ecology. International Association of Wildland Fire, Washington, pp. 35–50.
- Mooney, H. A. 1986. Lessons from Mediterranean-climate regions. – In: Wilson, E. O. and Peter, F. M. (eds), Biodiversity. National Academy Press, pp. 157–165.
- Mulcahy, D. L., Curtis, P. S. and Snow, A. A. 1988. Pollen competition in natural populations. – In: Jones, C. E. and Little, R. J. (eds), Handbook of experimental pollination ecology. Van Nostrand Reinhold, chapter 16.
- Naveh, Z. 1990. Fire in the Mediterranean: a landscape ecological perspective. – In: Goldammer, J. E. and Jenkins, M. J. (eds), Fire in ecosystem dynamics. SPB Acad. Publ., pp. 1–22.
- Ne'eman, G., Dafni, A. and Potts, S. G. 1998. A new pollination probability (PP) index for pollen load analysis as a measure for pollination effectiveness of bee populations. – J. Apic. Res. 38: 19–23.
- Ne'eman, G., Dafni, A. and Potts, S. G. 2000. The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. – Plant Ecol. 146: 97–104.
- Nilsson, L. A. 1988. The evolution of flowers with long corolla tubes. – Nature 334: 147–149.
- Olsen, K. M. 1997. Pollination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris* (Asteraceae). – Oecologia 109: 114–121.
- O'Toole, C. 1991. Wild bees, systematics and the pollination market in Israel. – Antenna 15: 66–72.
- Paton, D. C. 1993. Honeybees in the Australian environment. – BioScience 43: 95–103.
- Pellmyr, O. and Thompson, J. N. 1996. Source of variation in pollinator contribution within a guild: the effects of plant and pollinator factors. – Oecologia 107: 595–604.
- Petanidou, T. and Vokou, D. 1990. Pollination and pollen energetics in mediterranean ecosystems. – Am. J. Bot. 77: 986–992.
- Petanidou, T. and Ellis, W. N. 1996. Interdependence of native bee faunas and floras in changing Mediterranean communities. – In: Matheson, A., Buchmann, S. L., O'Toole, C. et al. (eds), The conservation of bees. Academic Press, pp. 201–226.
- Pleasants, J. M. 1983. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). – Am. J. Bot. 70: 1468–1475.
- Plowright, R. C. and Laverty, T. M. 1984. The ecology and sociobiology of bumble bees. – Annu. Rev. Entomol. 29: 175–199.
- Pyke, G. H. 1991. What does it cost a plant to produce floral nectar? – Nature 350: 58–59.
- Rambal, S. 1989. Fire and water yield: a survey and predictions for global change. – In: Moreno, J. M. and Oechel, W. C. (eds), Role of fire in Mediterranean-type ecosystems. Springer-Verlag, pp. 96–116.
- Richards, K. W. 1987. Diversity, density, efficiency, and effectiveness of pollinators on cicer milkvetch, *Astragalus cicer* L. – Can. J. Zool. 65: 2168–2176.
- Roubik, D. W. 1989. Ecology and natural history of tropical bees. – Cambridge Univ. Press.
- Rundel, P. W. 1981. Fire as an ecological factor. – In: Lange, O. L., Noble, P. S., Osmond, C. B. and Zeigler, H. (eds), Physiological plant ecology I: Responses to the physical environment. Springer-Verlag, pp. 501–538.
- Schaffer, W. M., Jensen, D. B., Hobbs, D. E. et al. 1979. Competition, foraging energetics, and the cost of sociality in three species of bees. – Ecology 60: 976–987.
- Schiller, G., Ne'eman, G. and Korol, L. 1997. Post-fire vegetation dynamics in a native *Pinus halepensis* Mill. forest on Mt. Carmel, Israel. – Isr. J. Plant Sci. 45: 297–308.
- Shmida, A. and Dukas, R. 1990. Progressive reduction in the mean body sizes of solitary bees active during the flowering season and its correlation with the sizes of bee flowers of the mint family (Lamiaceae). – Isr. J. Bot. 39: 133–141.
- Sokal, R. R. and Rohlf, F. J. 1995. Biometry: the principles and practice of statistics in biological research. – W. H. Freeman.
- Southwick, E. E. 1984. Photosynthate allocation to floral nectar: a neglected energy investment. – Ecology 65: 1775–1779.
- Spears, E. E., Jr. 1983. A direct measure of pollinator effectiveness. – Oecologia 57: 196–199.
- Spira, T. P., Snow, A. A. and Puterbaugh, M. N. 1996. The timing and effectiveness of sequential pollination in *Hibiscus moscheutos*. – Oecologia 105: 230–235.
- Stone, G. N. and Willmer, P. G. 1989. Warm-up rates and body temperature in bees: the importance of body size, thermal regime and phylogeny. – J. Exp. Biol. 147: 303–328.
- Stone, G. N., Amos, J. N., Stone, T. F. et al. 1988. Thermal effects on activity patterns and behavioural switching in a concourse of foragers on *Stachytarpheta mutabilis* (Verbenaceae) in Papua New Guinea. – Oecologia 77: 56–63.
- Stone, G. N., Willmer, P. and Nee, S. 1996. Daily partitioning of pollinators in an African *Acacia* community. – Proc. R. Soc. Lond. B 263: 1389–1393.
- Thomson, J. D., Andrews, B. J. and Plowright, R. C. 1981. The effect of foreign pollen on ovule development *Diervilla lonicera* (Caprifoliaceae). – New Phytol. 90: 777–783.
- Trabaud, L. 1987. Fire and survival traits of plants. – In: Trabaud, L. (ed.), The role of fire in ecological systems. SPB Acad. Publ., pp. 65–99.
- Vaughton, G. and Ramsey, M. 1994. Pollinators and seed production. – In: Kigel, J. and Galili, G. (eds), Seed development and germination. Dekker, pp. 475–490.
- Waser, N. M. 1978. Interspecific pollen transfer and competition between co-occurring plant species. – Oecologia 36: 223–236.
- Waser, N. M. 1986. Flower constancy: definition, cause, and measurement. – Am. Nat. 127: 593–603.
- Westerkamp, C. 1991. Honeybees are poor pollinators – why? – Plant Syst. Evol. 177: 71–75.
- Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. – Ecol. Entomol. 8: 455–469.
- Willmer, P. G. and Corbet, S. A. 1981. Temporal and microclimatic partitioning of the floral resources of *Justicia aurea* amongst a concourse of pollen vectors and nectar robbers. – Oecologia 51: 67–78.
- Willmer, P. G. and Stone, G. N. 1997. Temperature and water relations in desert bees. – J. Therm. Biol. 22: 453–465.
- Wilson, P. and Thomson, J. D. 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. – Ecology 72: 1503–1507.
- Zimmerman, M. 1988. Nectar production, flowering phenology, and strategies for pollination. – In: Doust, L. J. and Doust, L. L. (eds), Plant reproductive ecology: patterns and strategies. Oxford Univ. Press, pp. 157–178.