



The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland

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Abstract

The recovery of vegetation following fire has been studied intensively in Mediterranean-type ecosystems. Little attention, however, has been given to floral traits, and almost no data have been collected on the effects of fire on pollinator activity and fruit-set. This paper reports the effects of fire on flower visitation rates and the possibly related fruit-set. We compared visitation rates of the main pollinators on four plant core-species in burned and adjacent unburned areas. Measurements were performed at an unburned phrygana (scrub lands), and at a burned area (5–7 years post-fire). Bumble bees and solitary bees were the main taxa of visitors, while few honeybees were recorded. Solitary bees were almost absent from the burned area. Fruit-set was significantly higher in the unburned area for three out of the four plant species. The lower fruit-set in the burned area was possibly the result of low activity of solitary bees which are the main effective pollinators of the examined species. We hypothesize that the populations of the solitary bees were diminished or extirpated either directly by the fire, or indirectly by the scarcity of nectar in the early post-fire years due to dominance of young pine and *Cistus* spp. seedlings. The short foraging range of the solitary bees and their slow invasion rate into the burned area may explain our results.

Introduction

Fire is a major ecological factor in many parts of the globe. The recovery of vegetation after fire has been studied intensively in fire-prone biomes, including Mediterranean-type ecosystems (Naveh 1990). Mediterranean vegetation is resilient to fire and the re-establishment of the pre-fire communities is rapid (Trabaud 1994). Plant species have adaptive traits that allow them to regenerate after fire. Plant species that survive fire and regenerate vegetatively from adventive buds are classified as 'post-fire resprouters' or 'fire persisters'. By contrast, other species in which mature plants are not resistant to fire but seedling recruitment is timed for post-fire conditions, are classified as 'post-fire seeders' or 'fire recruiters' (Keeley 1991). These two post-fire regeneration types represent two different life-history modes common to all

Mediterranean-type ecosystems of the world (Keeley 1994).

Studies of fire-adapted plants have mostly focused on traits that allow fire survival, like adventive buds on the root crown, and the regulation of post-fire germination (Trabaud 1987; Keeley 1991; Thanos et al. 1992; Keeley 1994). However, flowering, pollinators' activity and fruit-set have drawn less attention. Fire is known to increase the flowering in grasses and geophytes in South Africa (Le Maitre & Midgley 1992) and Australia (Gill 1981; Pyke 1987). Some species are known to flower only after fire, and their flowering is stimulated by removal of the canopy (Gill 1981) or by smoke (Keeley 1993). All annual species with refractory seeds that are 'fire followers' germinate almost only during the first post-fire winter. They then grow, flower and produce seeds only during that season (Keeley 1994). Populations of 'post-fire seeders' depend on massive seed production during the early

post-fire period, therefore, they should have bigger, more attractive and more rewarding flowers than those of 'post-fire resprouters' (Carpenter & Recher 1979). However, no supporting evidence was found for this hypothesis when tested (Lamont 1985).

Fire could have an effect on flowering phenology due to the fire-induced changes in the environmental conditions. However, no differences were found in flowering phenology of the same species in sites of various ages since fire and plant communities in southern France (Trabaud & Chanterac 1985). In contrast, in the USA fire season did not affect the number of perennial species flowering in the following year, but differently affected the length and interspecific synchronization of flowering (Platt et al. 1988).

Seed-set is a function of both resource availability (water, macro- and micro-nutrients) and effectiveness of pollen delivery (Kunin; 1993, Vaughton & Ramsey 1994). Following a fire, ash may inhibit germination (Ne'eman et al. 1992; Henig-Sever et al. 1996), but improve growth and seed production (Kutiel & Naveh 1987). We would therefore predict, that in the absence of differences in the pollinating environment, that seed-set would be higher in burned habitats. If an opposing effect on seed production is observed, i.e. seed-set is higher in unburned sites, then this could be accounted by differential pollination effectiveness provided that sufficient evidence from flower visitation records is in accordance with such a phenomenon.

As far as we are aware, almost no studies have been published on the effect of fire on pollinator activity (but see Moldenke 1979) and fruit-set (but see Gill 1981). The aim of this paper is to study the effect of fire on flower visitation rates in four core-species, which were the primary providers of significant quantities of nectar and pollen during the peak season of bee activity, and their fruit-set, by comparing burned and adjacent unburned sites.

Study site and species

The study was carried out on Mount Carmel, 3–7 km east of Haifa, Israel. The elevation is about 300 m, and the distance from the Mediterranean Sea 5–10 km. The climate is typically Mediterranean with annual average precipitation of 600 mm.

Study sites were established in open unburned garigue and phrygana (scrubland) vegetation and in an adjacent burned area (September 1989) where the same core-species were found. Both areas were no

more than two km apart; they were of similar slope, aspect and on the same soil type (Rendzina). The burned area was previously an open mixed *Pinus halepensis* forest, and at the time of this study (5–7 years post-fire) it was dominated by *Cistus salviifolius* and *C. creticus* shrubs (65% cover) and young pine trees (15% cover) (Schiller et al. 1997). The examined species were highly dispersed among the *Cistus* shrubs and pine seedlings. The studied plants in the burned area were located about 1000 m from the fire's border. The unburned area consisted of typical *Sarcopoterium spinosum* phrygana (40% cover) with many other perennial species (e.g., the examined species, which were very common) and about 150 annual species. The unburned phrygana was chosen for the comparison because of the similarity in vegetation structure to the unburned area, and because none of the tested species grows in the understory of an unburned pine forest.

With any unpredictable catastrophic event, such as a major forest fire, it is rare to have available pre-event data matched to the post-event study under consideration as the location and timing of such a catastrophe is unknowable prior to its occurrence. However, we have attempted to reduce the effect of confounding variables in our study by selecting a series of plants representing the two vegetation types. While this does not represent an ideal experimental design it does go some way in minimizing the influence of other environmental factors which might account for the observed differences.

Four plant core-species, which vary in their flowering season, floral structure and pollinator assemblages were chosen. We define core-species as those flowering plants, which are the primary providers of nectar and pollen during the peak season of bee activity. All four species were abundant in both the burned and unburned areas and visited by a taxonomically diverse range of bees encompassing the full size range of bees found during this period. The species were *Asphodelus ramosus* Miller (= *A. aestivus* Brot. = *A. microcarpus* Salzm. et Viv.), *Salvia fruticosa* Miller (= *S. triloba* L. fil.), *Satureja thymbra* L. and *Phlomis viscosa* Poiret. More information on the natural history of these species is presented in Table 1. No differences in flowering phenology were observed between conspecific plants; all flowered simultaneously in the burned and the unburned sites.

Table 1. Natural history traits of the four study plants.

Plant species	Family	Post-fire strategy	Phenology	Breeding system	Visitors
<i>Asphodelus ramosus</i>	Liliaceae	Resprouter	January–March Synchronized across sites	Self incompatible	Solitary bees
<i>Salvia fruticosa</i>	Lamiaceae	Seeder	March–April Synchronized across sites	Self incompatible	Bumblebees, honeybees, solitary bees
<i>Satureja thymbra</i>	Lamiaceae	Seeder	April–May Synchronized across sites	Self incompatible	Bumblebees, solitary bees
<i>Phlomis viscosa</i>	Lamiaceae	Seeder	April–May Synchronized across sites	Self incompatible	Bumblebees, large solitary bees

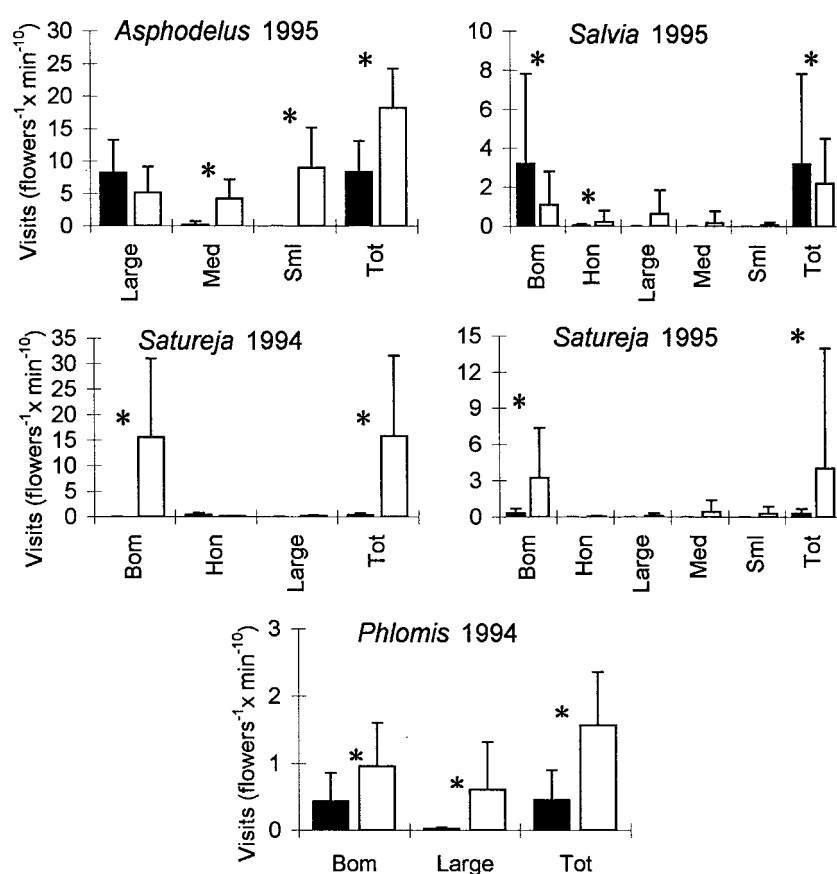


Figure 1. A comparison of flower visitors (Bom = bumble bees, Hon = honey bees, Large = large solitary bees, Med = medium solitary bees, Sml = small solitary bees and Tot = total of all bees) frequency (mean number of visits per flower per 10 min.) in burned (full bars, fire in 1989) and unburned (empty bars) areas for the following species: *Asphodelus ramosus* (in burned $n=9$ and in unburned $n=10$), *Salvia fruticosa* (in burned $n=55$ and in unburned $n=115$), *Satureja thymbra* (in burned $n=9$ and in unburned $n=25$ for 1994 and (in burned $n=23$ and in unburned $n=48$ for 1995) and *Phlomis viscosa* (in burned $n=11$ and in unburned $n=32$). Significant ($P < 0.05$) t -test difference for each taxa between burned and unburned areas is indicated by *, the difference in all other cases is not significant; error bars represent one standard deviation unit.

Materials and methods

Flower visitors and seed production

The observations on all core-species were carried out in spring 1994 and on *Satureja thymbra* also in 1995. A random grid point was assigned within each site from which a 100 m transect was measured along a randomly selected compass direction. For each species different transects were assigned in the burned and unburned areas. All medium and large sized flowering individuals of each core-species along the transect were observed. A flowering plant was the unit of our observations, and the number of observed individuals, for each species, is given in the results (Figure 1). Flower visitors were observed at the peak flowering season for each species, at main insect activity (10:00 to 14:00 and above 18 °C). For each species we counted all individual insects that visited the flowers of the examined plant; counting units were of 10–30 min and a total of about 5–20 h of observation per species. Since the insects were not marked, a visitor was counted regardless of whether it had visited a flower of the same individual plant before. Visit frequency of bees to flowers was calculated as number of visits per flower per 10 min.

Bee samples were caught and identified (by C. O'Toole, University Museum, Oxford). A list of the most common solitary bee visitors for the four experimental plants is given in Appendix 1. In the field, solitary bee species were ranked according to their size into three categories: large (>13 mm in length), medium (12–9 mm, the size of a honeybee) and small (<8 mm). Honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) were counted separately.

Fruits were counted (in 1994, 1995 and 1996) on 10 medium to large individuals that were randomly chosen out of all conspecific plants of each examined species. Fruits were counted on 6 random branches of each individual plant. Fruits were counted at the end of the flowering season and before seed dispersal. Percentage fruit-set was calculated as the percent of fruits out of the number of flowers on each branch. Because each flower in species of the Labiatae (Lamiaceae) potentially can produce 4 nutlets, the percentage of fruit-set for each branch was calculated as % fruit-set = $25 \times$ number of nutlets/number of flowers on each branch.

Plant nomenclature follows Feinbrun-Dotan & Danin (1991).

Data analyses

Bee visitation frequencies of bees to flowers was calculated as the number of visits per flower per 10 min. Average visit frequency was calculated separately according to flower species, visitor taxon and size class, and annually for both the burned and unburned sites. Frequency data were square root transformed before t-test analysis that was used for the comparison between the burned and the unburned area. Average percentage fruit-set was also calculated separately for each species each year for the burned and unburned area. Fruit set proportions were square root arcsin transformed before performing two-way ANOVA to examine the effect of year, fire and their interaction. The a posteriori Bonferroni test served for comparison among the various categories. SYSTAT V.5 for Windows on PC (Wilkinson et al. 1992) was used for all statistical analyses.

Results

Asphodelus ramosus

Solitary bees of all size classes visited flowers in the unburned area but only large solitary bees were active in the burned area with the total number of visits being significantly higher in the burned area (Figure 1). *A. ramosus* flowers in early spring (February–March). Since *B. terrestris* begins its activity on Mt. Carmel only at the end of March (Dafni, Personal. observations), it was not observed visiting the flowers. A list of the most common bee visitors is presented in Appendix 1. Fruit-set was significantly affected by fire and year, and the interaction between year and fire was also significant (Table 2). Fruit-set was higher in the unburned area, but the difference was significant only in 1994 (Figure 2). There is a positive trend between the higher visitation rate and the higher fruit-set in the unburned vs the burned area.

Salvia fruticosa

Bumblebees were the only visitors to the flowers in the burned area, and their visitation frequency was significantly higher than in the unburned area (Figure 1). In addition, honeybees and large, medium and small solitary bees visited the flowers in the unburned area. A list of the most common bee visitors is presented in Appendix 1. Fruit-set was significantly affected by

Table 2. Two-way ANOVA for the effect of the years, fire and their interaction on percentage of fruit-set of four examined key species.

Species	Source	<i>N</i>	<i>R</i> ²	DF	<i>F</i> -ratio	<i>P</i>
<i>Asphodelus ramosus</i>		105	0.250			
	Year			2	8.784	0.004
	Fire			1	25.961	<0.001
	Year*Fire			2	5.084	0.026
<i>Salvia fruticosa</i>		140	0.300			
	Year			2	1.626	0.201
	Fire			1	52.864	<0.001
	Year*Fire			2	3.815	0.024
<i>Satureja thymbra</i>		27	0.867			
	Year			2	39.943	<0.001
	Fire			1	68.969	<0.001
	Year*Fire			2	7.307	0.013
<i>Phlomis viscosa</i>		39	0.740			
	Year			2	7.594	0.002
	Fire			1	77.100	<0.001
	Year*Fire			2	0.415	0.664

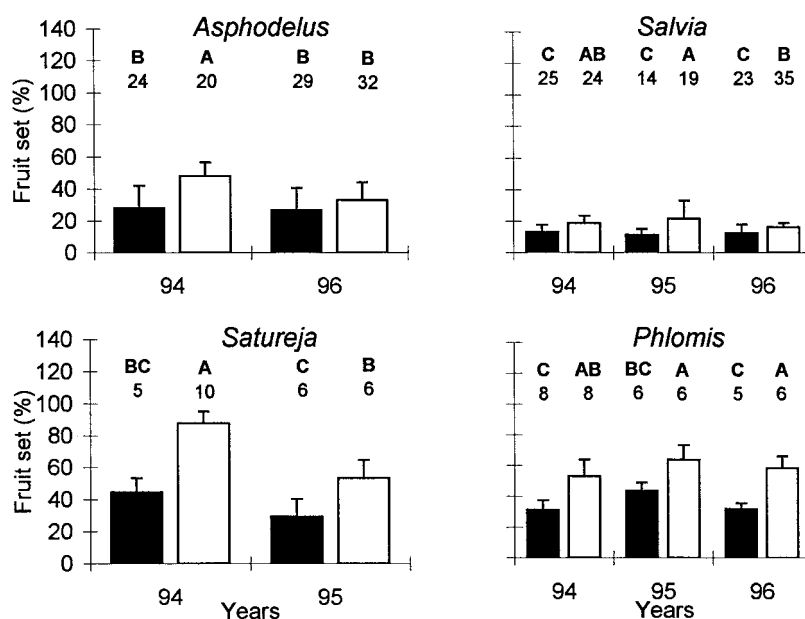


Figure 2. Mean percentage of fruit-set in: *Asphodelus ramosus*, *Salvia fruticosa*, *Satureja thymbra* and *Phlomis fruticosa*, in burned (full bars) and unburned (empty bars) areas during 1994 (94), 1995 (95) and 1996 (96). Bars with similar letters are not significantly different (ANOVA, $P > 0.05$); error bars represent one standard deviation unit and the numbers are sample sizes.

fire but not by year, nor was there a significant interaction between year and fire (Table 2). Fruit-set was significantly higher in the unburned area (Figure 2); this trend is not in accordance with pollinator activity, which was lower.

Satureja thymbra

Bombus terrestris was almost the only visitor to the flowers in 1994, when visits of honeybees and solitary bees were negligible (Figure 1). In 1995 visitation frequency of the bumblebee was much lower, but the visits of the other bees were more frequent than in 1994 (Figure 1). Visits of bumblebees were significantly more frequent in the unburned than in the burned area both in 1994 and 1995, and the same holds also for the total visits of all bees (Figure 1). A list of the most common bee visitors is presented in Appendix 1. Fruit-set was significantly affected by fire and year, and the effect of the interaction between year and fire was also significant (Table 2). Fruit-set was higher in the unburned area (Figure 2); this trend is in accordance with the higher visitation rate.

Phlomis viscosa

Bumblebees and large solitary bees visited the flowers with visits of both taxa being significantly more frequent in the unburned area. Solitary bees were almost entirely absent from the burned area (Figure 1). A list of the most common bee visitors is presented in Appendix 1. Fruit-set was significantly affected by fire and by the year, but the effect of the interaction between year and fire was not significant (Table 2). Fruit-set was significantly higher in the unburned area (Figure 2); this trend is in accordance with the higher visitation rate.

Discussion

All four flowering core-species on Mount Carmel (*A. ramosus*, *S. fruticosa*, *S. thymbra*, and *P. viscosa*) showed a significantly higher seed-set in the unburned area than in the adjacent burned area. In three of these species (*A. ramosus*, *S. thymbra*, and *P. viscosa*) this difference was also associated with a higher total bee visitation frequency. The one exception, *S. fruticosa*, showed higher seed-sets in the unburned habitat with lower overall bee visitation. However, if we consider bee visitation rates in terms of effective pollinators

and not just visitors, the overall pattern is much more consistent.

For *A. ramosus* small solitary bees can be considered as pollen thieves as they collect pollen without actually contacting the stigmatic surfaces and so can not be included as legitimate pollinators (Schuster 1990). Therefore, the significantly higher number of medium sized solitary bees visiting this species, with stigma contact, probably accounted for higher seed production in the unburned area. As this species flowered early in the season prior to the activity period of *B. terrestris*, only solitary bees were recorded. For *S. thymbra*, *B. terrestris* was the only bee in any significant numbers visiting and site differences in visitation rates, in both years, are good candidates for explaining the observed differences in seed-set. Dafni & Shmida (1996) showed that the number of visits per flower was 450 times higher in large plants than in small ones. Therefore, the differences in visitation rate and fruit-set might be because the plants in burned sites tended to be smaller and less attractive for the bumblebees than those in the unburned area (Dafni, unpublished data). The increased presence of *B. terrestris* and large solitary bees, which are both legitimate pollinators, can explain seed-set differences for *P. viscosa*. However, even though *B. terrestris* was more abundant on *S. fruticosa* in the burned area and the total number of bee visitations was also higher, fruit-set was lower. Previous observations showed that bumblebees visited 50 to 200 flowers of a single plant during one foraging bout, which presumably resulted mainly in geitonogamy. Solitary bees, in contrast, visited only 3 to 10 flowers on each plant before moving to another one, performing mainly xenogamy (Kasher 1991; Dafni & Shmida 1996). These facts may explain the inconsistency in our results, because *B. terrestris*, the less effective pollinator, was the main visitor at the burned area, while solitary bees, which are more effective pollinators, were the main visitors in the unburned area.

Mineral nutrition and light regime are better in burned than in unburned areas, resulting in increased growth and flowering magnitude after fire (Rundel 1981). Ash also may improve growth and seed production as tested for alfalfa (Kutiel & Naveh 1987). Therefore, fruit-set was expected to be higher at the burned area. The fact that visitation rates and fruit-set of plants at the burned area was lower than at the unburned area may indicate that pollination and not resources was the limiting factor for fruit-set in the burned area. The observed effects on visitation

patterns and seed-set in the two habitat types could be explained by between-site differences in pollinator foraging preferences rather than fire-induced changes in pollinator density. However, this explanation seems unlikely as pollinator behavior appeared similar in both post-fire habitats, with the only difference being the higher visitation frequency in the unburned area.

Reduction in post-fire abundance of bees, was also found in California chaparral (Moldenke 1979) and may be the result of direct fire-caused mortality. However, many of the solitary bee species are in aestivation in late summer, the season when most wildfires occur, and many of them nest in the soil where temperatures do not reach extreme values. Therefore, it can be assumed that at least a part of the bee population, of several species, can survive fire (Ne'eman, Personal observation). These bees will emerge from their nests in spring into a changed environment. If the new vegetation is rich in annual plant species (Whelan 1995), many of which have nectariferous flowers, the bee populations are expected to recover quickly. However, if the post-fire vegetation is poor in nectar and pollen, a further reduction in the populations of the bees can be expected. In our burned area *Cistus salviifolius*, *C. creticus* and pine seedlings dominated the post-fire vegetation (Schiller et al. 1997). *C. creticus* has pollen but not nectar producing flowers, and *C. salviifolius* has pollen and an average of 0.7 μ l of nectar with 51% of sugar (Potts, unpublished data), which is available only for small to medium solitary bees. However, only high abundance of nectar producing flowers could maintain fire-surviving populations of solitary bees. Small and medium solitary bees have only a short range of foraging flights (Dafni & Shmida 1996; O'Toole pers. comm.) and it is less probable that they will fly long distances crossing non-rewarding areas to reach a patch of a rewarding plant. In contrast, large bees (especially bumblebees) have much longer flight ranges (Wesslering Tschardtke 1995, Dramstad 1996), and therefore are capable of crossing long distances of non-rewarding areas between highly rewarding plants. Under these circumstances large bees are able to reach rewarding plants deep in the burned area, 1–2 km from the unburned area. However, in Britain bumblebees allocated a disproportionately high percentage of their visits to perennial plants of late successional stages, and annual plants of newly disturbed land received relatively few visits (Fussell & Corbet 1992).

Our results show clearly that medium and small bees were absent from the burned area even 7 years after fire, and that large bees probably entered the burned

area from the surrounding unburned area where their activity was higher. It seems that mortality of the pre-fire population and poor rewarding post-fire vegetation are the causes of this situation.

Our conclusion follow for the specific case of the 1989 fire on Mount Carmel may indicate a more general phenomenon in other Mediterranean-type ecosystems where fire is common feature. However, this idea must be more rigorously tested using a series of replicated site in areas comprising of a series of burn times in order to establish the validity of any causal link between pollinator visitation rates and seed-sets in post-fire entomophilous flowering plants.

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Appendix 1. The estimated number of bee species and identification of the most common visitors to each of the four experimental plants (based on C. O'Toole pers. comm.).

Flowering plants	Species number	Primary visitors
<i>Asphodelus ramosus</i>	40	<i>Anthophora nigrifacies</i> , <i>A. dispar</i> , <i>A. biciliata</i> , <i>Chalicodoma parietinum</i> , <i>Habropoda tarsata</i> , <i>Melecta Palestine</i>
<i>Salvia fruticosa</i>	30	<i>Bombus terrestris</i> , <i>Apis mellifera</i> , <i>Synhalonia grandis</i> , <i>Anthophora dispar</i> , <i>A. biciliata</i> , <i>A. nigriceps</i> , <i>A. plumipes</i> , <i>Ceratina cucurbitana</i> , <i>Eucera clypeata</i> , <i>E. nigrifacies</i> , <i>Habropoda tarsata</i> , other small to medium solitary bees (<i>Ceratina</i> , <i>Halictus</i> , <i>Lasioglossum</i> , <i>Melecta</i> , <i>Nomada</i> , <i>Osmia</i>)
<i>Satureja thymbra</i>	38	<i>Bombus terrestris</i> , <i>Apis mellifera</i> , <i>Amegilla quadrifasciata</i> , <i>Anthophora nigriceps</i> , <i>A. orientalis</i> , <i>Eucera demetrius</i> , <i>E. transversa</i> , <i>E. helvola</i> , <i>Chalicodoma sanguinipes</i> , <i>C. parietinum</i> , <i>Megachile giraudi</i> , <i>Synhalonia tricincta</i> , other small to medium solitary bees (<i>Osmia</i> , <i>Andrena</i> , <i>Hoplitis</i>)
<i>Phlomis viscosa</i>	10	<i>Bombus terrestris</i> , <i>Chalicodoma parietinum</i> , <i>Habropoda tarsata</i> , <i>Anthophora sp.</i> , <i>Xylocopa sp.</i>