

Competition between honeybees (*Apis mellifera*) and native solitary bees in the Mediterranean region of Israel—Implications for conservation

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ABSTRACT

The hypothesis that honeybees (*Apis mellifera*) compete for floral resources with native bees was studied mainly in areas outside the original range of the honeybees, i.e., where they are introduced. We studied the effect of honeybees on the foraging behavior of native solitary bees in Israel, within the natural distribution range of the honeybee, by manipulating the presence and absence of beehives in the study sites: Ramat Hanadiv Park and Carmel National Park. We examined the possible degree of competition between honeybees and native solitary bees by observing their foraging on focal nectariferous plants. Temporal introduction of hives increased the visitation frequencies of honeybees to our focal plants and decreased the overall average visitation frequencies of native solitary bees. However, the effect of honeybees varied among native bee species, focal plants, and years. In some cases, honeybees had a negative effect on visitation rates of the other bees, while in other cases we did not find such an effect. The other bees also did not shift to forage on other flowering plants, and did not change their temporal activity pattern as a response to increased foraging by honeybees. The results provide partial evidence for behavioral competition between honeybees and native bees. For this reason, we recommend prohibiting introduction of beehives to all nature reserves in Israel, as a precaution aimed at protecting the native bee fauna. This may help conserve their contribution to biodiversity and pollination of common and rare native plants as well as crops.

Keywords: competition, conservation, honeybee, Mediterranean, native bees

INTRODUCTION

Most (60–70%) plant species depend on bee pollination for their sexual reproduction (Richards and Kevan, 2002). Efficient pollination requires compatibility between the morphologies of the flower and its pollinator (Burd, 1994). Therefore, a change from a diverse native bee to honeybee-dominated fauna may negatively affect fruit and seed set in many plants, including rare and endangered species (Osborne et al., 1991; Tepedino et

al., 1996; Butz-Huryn, 1997; Kato et al., 1999; Richards and Kevan, 2002; Westerkamp and Gottsberger, 2002; Goulson, 2003). Although most flowers are visited by a range of pollinating species, they differ in the quality of the pollination services they provide (Goulson, 2003). Poor pollinators could have a negative demographic effect on specific plant populations.

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“Optimal foraging” theory claims that any animal that forages in an optimal way, or nearly so, maximizes its fitness (MacArthur and Pianka, 1966; Charnov, 1976). Thus, bees are expected to collect the maximal possible amount of nectar and pollen with minimal allocation of time and energy (Pyke et al., 1977; Pyke, 1978; Pleasants and Zimmerman, 1979; Bertsch, 1987; Real and Rathcke, 1988). This holds in an ideal situation when a bee is foraging by itself with no constraints or other co-occurring activities such as mate searching, predator avoidance, or competition. In the presence of a superior competitor, when resources are limited, the inferior one is expected to change its foraging pattern in a way that will minimize the competition. This can lead to a spatial shift to another food resource, or to a temporal shift, namely foraging on the same resource but at times when the superior competitor is less active (Parrish and Bazzaz, 1979; Carothers and Jaksic, 1984). Both responses lead to niche partitioning and a consequent decrease in competition. The superior competitor will forage in a manner close to the optimal way, while the less competitive one will have to forage in a less efficient way.

The nutrition of bees, which are the most important group of pollinators throughout the world (Myers, 1996), depends mainly on floral nectar and pollen, but occasionally other rewards like plant tissues, waxes, heat, or mating place are gained (Kevan and Baker, 1983). Whenever a common floral resource is limited, interspecific competition may occur (Schaffer et al., 1983; Sugden and Pyke, 1991; Sugden et al., 1996; Kato et al., 1999; Steffan-Dewenter and Tschamntke, 2000; Hingston et al., 2001; Paine, 2004). Sharing of such overlapping limited food resources may lead to changes in foraging behavior in which the superior competitive species usually gains the favorable resource while the inferior one may shift to utilizing a less beneficial resource (Begon et al., 1986). When the intensity of the competition is high and its duration long, such changes in foraging behavior may also have consequent negative effects on survival, fecundity, and fitness of the inferior bee species (Goulson, 2003; Paine, 2004; Thomson, 2004; Moritz et al., 2005; Paine and Roberts, 2005; Goulson and Sparrow, 2009). In extreme cases, the fitness and population size of the inferior species may decrease, and eventually this may even result in competitive exclusion (Hardin, 1960).

Honey hunting dates back to prehistoric times. Since then, 26 subspecies of *Apis mellifera* L. have been identified in Africa, Europe, and western Asia. Some were cultivated and transported to all the peopled continents where other *A. mellifera* subspecies are native (Europe, Africa, and western Asia), where other *Apis* species are native (central and eastern Asia), and where there are

no other native *Apis* species (America and Australia) (Winston, 1991; Ruz, 2002; Moritz et al., 2005). As an abundant social and general forager species, honeybees can potentially affect a wide range of both plants and nectar or pollen feeders. Therefore, the expansion and invasion of honeybees worldwide increased the concern of scientists to the possible suppression of local bee faunas, as was already speculated by Darwin (1876). Many researchers who addressed this issue studied the relations between honeybees and various local bees outside the natural range of the honeybee; they used various methods and got contrasting results. A common method is recording foragers' abundance (as a proxy of population size), while looking for negative correlation between honeybees and native bees at the patch level (e.g., Forup and Memmot, 2005). Others used light traps (e.g., Roubik and Wolda, 2001), nesting traps, and counts of nest entrances of ground-nesting bees as measures of population sizes (e.g., Steffan-Dewenter and Tschamntke, 2000). However, correlation alone is not proof of causation, since the abundance of each bee species can change in response to additional factors. A common method is monitoring bee activity at varying distances from a beehive, expecting a decrease in honeybee abundance with increasing distance (e.g., Thomson, 2004, 2006); however, as other factors such as floral resources and bee assemblages may also vary along the distance gradient, this is also inaccurate. A correct method is manipulation of honeybee abundance by introduction and removal of beehives (e.g., Schaffer et al., 1983; Thomson, 2004; Paine and Roberts, 2005; Paine et al., 2005). Other researchers also estimated floral niche breadth for each bee species to estimate the degree of resource overlap, or examined if the resource was a limiting factor, which is a prerequisite for competitive relations (e.g., Minckley et al., 2003; Forup and Memmot, 2005).

Several researchers have found competition between honeybees and local bees (e.g., Schaffer et al., 1983; Pyke and Balzer, 1985; Sugden et al., 1996; Kato et al., 1999; Goulson and Sparrow, 2009), while others did not find evidence for such competition (Butz-Huryn, 1997; Roubik and Wolda, 2001). Moreover, when competition was evaluated in the same systems at different levels (foraging behavior, population density, fecundity, or fitness), different conclusions were obtained (e.g., Roubik, 1978, 1980, vs. Roubik and Wolda, 2001, in the neotropics; Thomson, 2006, in California; and Paine et al., 2005, vs. Paine and Roberts, 2005, in Australia). Consequently, recent reviews vary substantially in their assessment of whether the existing evidence does or does not support negative impacts of honeybees (Goulson, 2003; Paine, 2004; Moritz et al., 2005).

The estimated number of bee species in the world is about 20,000, most of which are solitary (Michener, 2000). The Mediterranean region in general, and Israel in particular, has an extremely rich native bee fauna. More than 1,000 bee species have been identified in Israel (O'Toole and Raw, 1991), while many others are still waiting for scientific description. Thus, the bee fauna is an important component of biodiversity in Israel. Most of the native bees in Israel are of solitary, ground-nesting species, which have an annual life history cycle with highest activity in spring correlated to the peak of the flowering season in the Mediterranean region (Shmida and Dukas, 1990; Dafni and O'Toole, 1994; Potts et al., 2005).

Beehive densities have generally increased during ancient as well as historical and modern times to supply the worldwide growing demand for honey and pollination services (Sugden et al., 1996). The search by beekeepers for nectar foraging grounds in Israel has placed constant pressure on the Nature and Parks Authority to permit introduction of beehives into nature reserves (R. Ortal, pers. comm.).

Our aim was to study the effect of honeybees on the foraging behavior of native solitary bees and feral bumblebees in Israel. By temporal introduction and removal of honeybee hives, we examined the possible existence of competition between honeybees and native solitary bees in Israel. Specifically, we examined whether introducing honeybee hives caused changes in the foraging behavior of the native bees in terms of their visitation frequencies, shifting among nectariferous plants, or changing their temporal activity patterns.

We hypothesized that introducing honeybee hives will: (1) decrease the foraging activity of native bees on flowers where honeybee foraging increased, and (2) change the temporal activity pattern of native bees to times where the activity of the honeybees was lower.

METHODS

Study site and plant species

We performed this research in Ramat Hanadiv Park, (32.74°N, 35.01°E) and in the Carmel National Park, (32.54°N, 34.95°E), both situated on Mt. Carmel in northern Israel (Fig. 1). The climate is typically Mediterranean, with annual precipitation of 500–600 mm. The vegetation in both sites is typical Mediterranean evergreen sclerophyllous disturbed maquis with woody patches, amongst which plenty of herbaceous plants flower in spring. At both sites, no commercial beehives were located within a range of 3 km, so we had full control of the date and duration of hive introduction

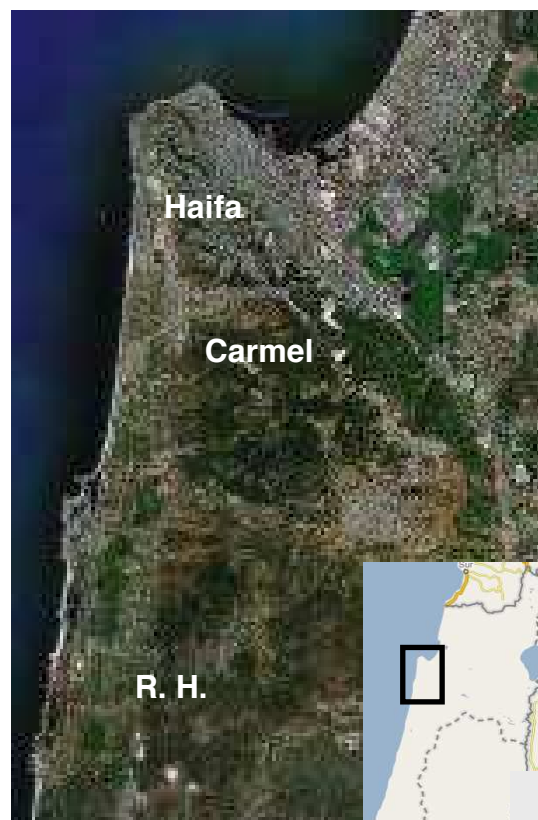


Fig. 1. Map with indication on the location of the study sites: Ramat Hanadiv Park (RH) and Carmel National Park (Carmel).

and removal. Feral honeybee colonies in these areas are extremely rare, if extant at all (D. Eisikowitch, pers. comm.). Observations were made on natural focal plants (*Salvia eigii* Zohary, *S. pinnata* L., and *S. fruticosa* Mill.), which were abundant floral resources utilized by several bee species, and on experimental arrays of potted *Rosmarinus officinalis* L.

Average (\pm SD) floral tube length was $12.8 \pm .13$ mm ($n = 22$) mm for *S. eigii*, 17.4 ± 0.19 mm ($n = 45$) for *S. pinnata*, 11.4 ± 0.33 mm ($n = 18$) for *S. fruticosa*, and 4.88 ± 0.14 mm ($n = 35$) for *R. officinalis*. The average (\pm SD) nectar standing crop for flowers of the focal plants was 0.3 ± 0.20 μ l ($n = 7$) for *S. eigii*, 0.17 ± 0.02 μ l ($n = 83$) for *S. pinnata*, 0.08 ± 0.03 μ l ($n = 30$) for *S. fruticosa*, and 0.12 ± 0.04 μ l ($n = 18$) for *R. officinalis*. The focal plants and native solitary bees that visited them differed among sites and years, as listed in Table 1.

Experimental design and data analysis

We performed this research during two flowering seasons at each site, 2002–2003 in Ramat Hanadiv Park, and 2004–2005 in Carmel National Park. We first ob-

Table 1
The focal observation plants and the species of native solitary bees observed in each site and year ordered by their abundance

Year	Location	Key plants	Bee species
2002	Ramat Hanadiv	<i>Salvia eigii</i> Zohary <i>Salvia pinnata</i> L.	<i>Apis mellifera</i> L. <i>Anthophora dispar</i> Lep. <i>A. dufoureeii</i> Lep. <i>A. rubricans</i> Drs. <i>Eucera</i> sp.
2003	Ramat Hanadiv	<i>Salvia eigii</i> Zohary <i>Salvia pinnata</i> L. <i>Rosmarinus officinalis</i> L. (in pots)	<i>Apis mellifera</i> <i>Anthophora</i> sp. <i>Eucera</i> sp. <i>Synhalonia</i> sp. <i>Osmia</i> sp. <i>Xylocopa</i> sp. <i>Chelostoma</i> sp. <i>Andrena</i> sp.
2004	Carmel	<i>Salvia fruticosa</i> Miller	<i>Apis mellifera</i> <i>Anthophora nigriceps</i> Mor. <i>A. plumipes</i> Pallais <i>A. Heliopolitensis</i> Per. <i>A. biciliata</i> Lep. <i>Eucera</i> sp. <i>Synhalonia</i> sp. <i>Halictus</i> sp. <i>Habropoda</i> sp.
2005	Carmel	<i>Salvia fruticosa</i> Miller	<i>Apis mellifera</i> <i>Anthophora nigriceps</i> Mor. <i>A. plumipes</i> Pallais <i>A. Heliopolitensis</i> Per. <i>A. biciliata</i> Lep. <i>Eucera</i> sp. <i>Synhalonia</i> sp. <i>Halictus</i> sp. <i>Habropoda</i> sp. <i>Bombus terrestris</i> L.

served foraging behavior in the absence of honeybee hives, and then we introduced ten commercial beehives, each with about 10,000 workers, which drastically increased the number of honeybees in the study area. We allowed 3–4 days of acclimation before resuming the observations of foraging behavior of all bees. Each observation session, with and without honeybee hives, lasted for about two weeks, with about three rotations each season. To decrease the effect of possible uncontrolled factors, we haphazardly changed the observation patches, all located at the same sites. All the observation sites were at a distance of 100–500 m from the honeybee hives when present.

We counted the visits of all individual bees of all

species in a patch of focal flowers for sessions of 10 minutes. Each such observation was an independent sampling unit to which the number of samples in the results and the figure relates. We considered a visit only when an observed bee landed and made a “legitimate visit” to the flower, a visit that can cause pollination. An observation patch consisted of the largest possible patch of flowers that still permitted synchronous observation and monitoring of all visiting bees, about 200 flowers. For each observation, we counted the number of all available open flowers in each observation patch, and later calculated the visitation frequencies as the number of visits per flower per hour.

When possible, we identified the bees in the field,

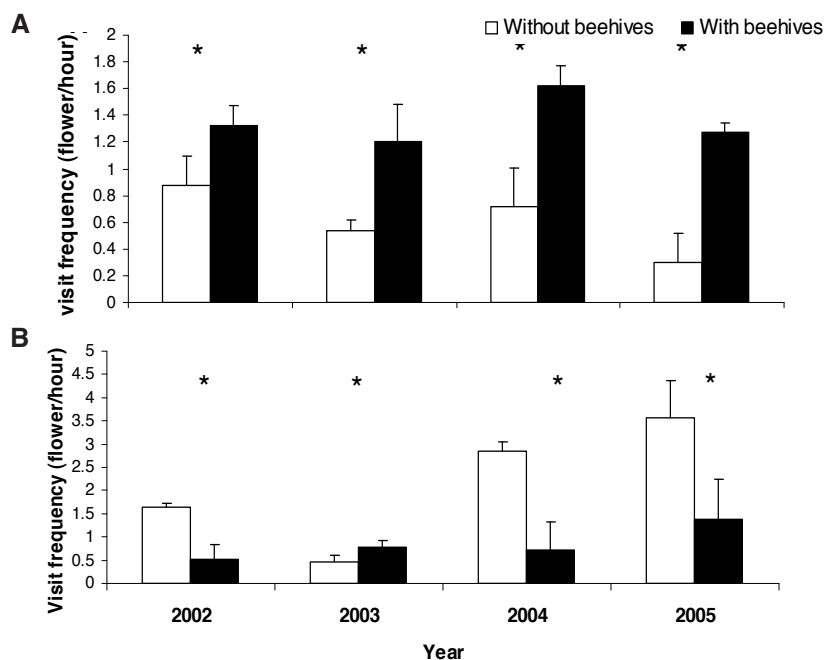


Fig. 2. Average visitation frequencies (per flower per hour) to flowers of all focal plants by honeybees (A) and native bees (B) in the presence of honeybee hives and in their absence during all study years. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$). 2002: $N = 30$; 2003: $N = 54$; 2004: $N = 41$; 2005: $N = 66$.

and captured samples of unidentified bees for later identification to the lowest possible taxonomic level. Final identification of the bees was done by Chris O'Toole, Oxford University, UK. We present the list of all captured bee species in this study in the Appendix.

Unfortunately, because of difficulties in identifying the bees in the field, we grouped several similar genera as "Small bees", which include: *Osmia* spp., *Andrena* spp., *Chelostoma* spp., *Nomada* spp., and *Lasioglossum* spp.

To examine temporal segregation of bees' foraging on flowers of the focal plants we observed their visitation rates at two-hour intervals, from 08:00 to 14:00 in Ramat Hanadiv (2003) and from 08:00 to 16:00 on Carmel (2005). Ambient temperature ranged between 20 and 25 °C for all observations.

The data do not follow a normal distribution, even after transformations. Thus, we used the Wilcoxon signed rank test (Z) to compare visitation frequencies of any given bee taxon on flowers of any given focal plant before and after introduction of honeybee hives, using SPSS 11.0 for Windows software.

RESULTS

As a preliminary test for the effectiveness of our manipulation of honeybee hives, we calculated the average

visitation frequencies of honeybees and native solitary bees to flowers of all the focal plants in the presence or absence of honeybee hives for each study site and year. Average visitation frequency of honeybees to the flowers of all the focal plants was significantly higher in the presence of honeybee hives than in their absence for 2002, 2003, 2004, and 2005 (2002: $Z = -2.660$, $p < 0.001$, $N = 30$; 2003: $Z = -2.880$, $p = 0.01$, $N = 54$; 2004: $Z = -1.438$, $p = 0.05$, $N = 41$; 2005: $Z = -4.335$, $p = 0.01$, $N = 66$) (Fig. 2A). The average visitation frequencies of native solitary bees' were significantly lower in the presence of beehives for 2002, 2004, and 2005 (2002: $Z = -3.427$, $p = 0.01$, $N = 30$; 2004: $Z = -1.058$, $p = 0.05$, $N = 41$; 2005: $Z = -3.879$, $p = 0.01$, $N = 66$). In 2003, visitation frequencies by solitary bees were significantly ($Z = -2.890$, $p = 0.01$, $N = 54$) higher in the presence of honeybee hives than in their absence (Fig. 2B). N represents the number of independent observation pairs (with and without honeybee hives).

Ramat Hanadiv

In Ramat Hanadiv, the average visitation rate of honeybees to flowers of *Salvia pinnata* tended to be higher in the presence of beehives than in their absence in 2002 ($Z = -1.129$, $p = 0.258$, $N = 21$) (Fig. 3B) and significantly higher in 2003 ($Z = -1.93$, $p = 0.05$, $N = 16$)

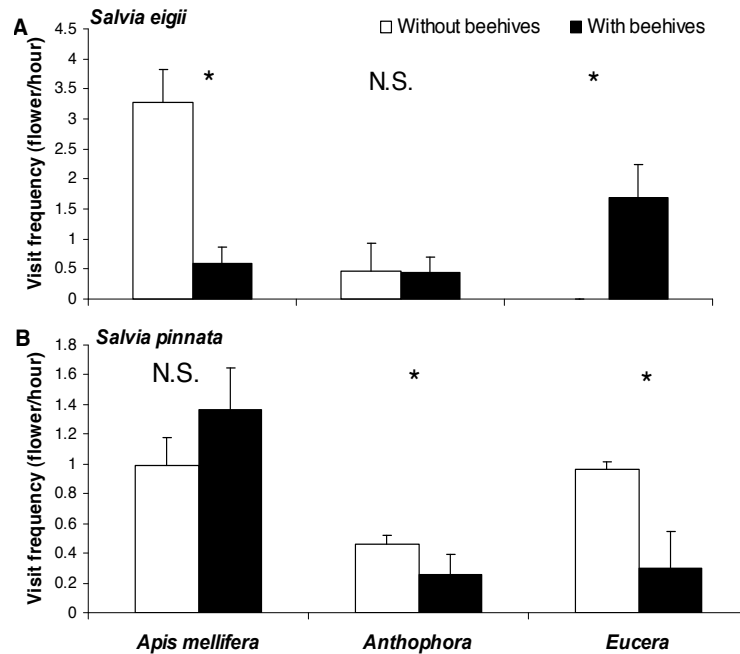


Fig. 3. Average visitation frequencies (per flower per hour) of honeybees and of the visitation frequencies of the native solitary bees *Anthophora* sp. and *Eucera* sp. to flowers of the focal plants *Salvia eigii* N = 9 (A) and *Salvia pinnata* N = 21 (B) in Ramat Hanadiv during 2002 in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

(Fig. 4B). Honeybee visits to flowers of *R. officinalis* in 2003 tended to be higher after introduction of beehives than before introduction ($Z = -1.855$, $p = 0.06$, $N = 37$) (Fig. 4A). However, the honeybee visitation rate to flowers of *Salvia eigii* was significantly ($Z = -2.457$, $p = 0.01$, $N = 9$) lower in the presence of beehives in 2002 (Fig. 3A).

The average visitation rates of the two native solitary bee genera, *Anthophora* sp. and *Eucera* sp., to flowers of *S. pinnata* was significantly lower in the presence of beehives in 2002 (*Anthophora* sp. $Z = -2.532$, $p = 0.01$, $N = 21$, *Eucera* sp. $Z = -2.616$, $p = 0.01$, $N = 21$) (Fig. 3B), but the difference in 2003 was not significant (*Anthophora* sp. $Z = -0.803$, $p = 0.421$, $N = 16$, *Eucera* sp. $Z = -0.676$, $p = 0.4989$, $N = 16$) (Fig. 4B). In contrast, visitation rates of the *Anthophora* sp. to flowers of *R. officinalis* were significantly higher in the presence of honeybee hives than in their absence, when no visits were recorded ($Z = -4.015$, $p = <0.01$, $N = 37$) (Fig. 4A). The opposite tendency occurred for *S. eigii*, namely the differences were significant for visitation rates of *Eucera* sp., but not for *Anthophora* sp. (*Anthophora* sp.: $Z = -0.674$, $p = 0.5$, $N = 9$; *Eucera* sp.: $Z = 2.522$, $p = 0.01$, $N = 9$) (Fig. 3A).

Carmel

Honeybees, *Eucera* spp., and “small bees” were the

major visitors to *Salvia fruticosa* flowers in Carmel in 2004 in the absence of beehives. Visitation frequencies of *Anthophora* sp. and *Halictus* sp. were significantly lower in the presence of beehives (*Anthophora* sp.: $Z = -2.201$, $p = 0.027$, $N = 41$; *Halictus* sp.: $Z = -2.022$, $p = 0.043$, $N = 41$), while that of *Habropoda* sp. was significantly higher ($Z = -2.022$, $p = 0.043$, $N = 41$) (Fig. 5A). In the presence of honeybee hives the visitation frequencies of honeybees and small bees tended to be higher, but not significantly so (Honeybees: $Z = -1.437$, $p = 0.15$, $N = 41$; Small bees: $Z = -1.445$, $p = 0.148$, $N = 41$) (Fig. 5B).

Small bees, *Synhalonia* sp., and *Eucera* sp. were the major visitors to *S. fruticosa* flowers in Carmel in 2005 in the absence of beehives (Fig. 6A,B). In the presence of beehives only the visitation frequencies of honeybees were significantly higher ($Z = -4.33$, $p = <0.01$, $N = 66$), while the visitation frequencies of the small bees, *Synhalonia* sp., and *Habropoda* sp. were significantly lower (small bees: $Z = -3.157$, $p = 0.01$, $N = 66$; *Synhalonia* sp. $Z = -3.183$, $p = 0.01$, $N = 66$; *Habropoda* sp.: $Z = -2.19$, $p = 0.028$, $N = 66$). Those of *Eucera* sp., *Anthophora* sp., and *Bombus terrestris* tended to be lower, while those of *Halictus* sp. tended to be higher (*Eucera* sp.: $Z = -1.51$, $p = 0.13$, $N = 66$; *Anthophora* sp.: $Z = -1.82$, $p = 0.068$, $N = 66$; *Bombus terrestris*: $Z = -1$, $p = 0.317$, $N = 66$) (Fig. 6A,B).

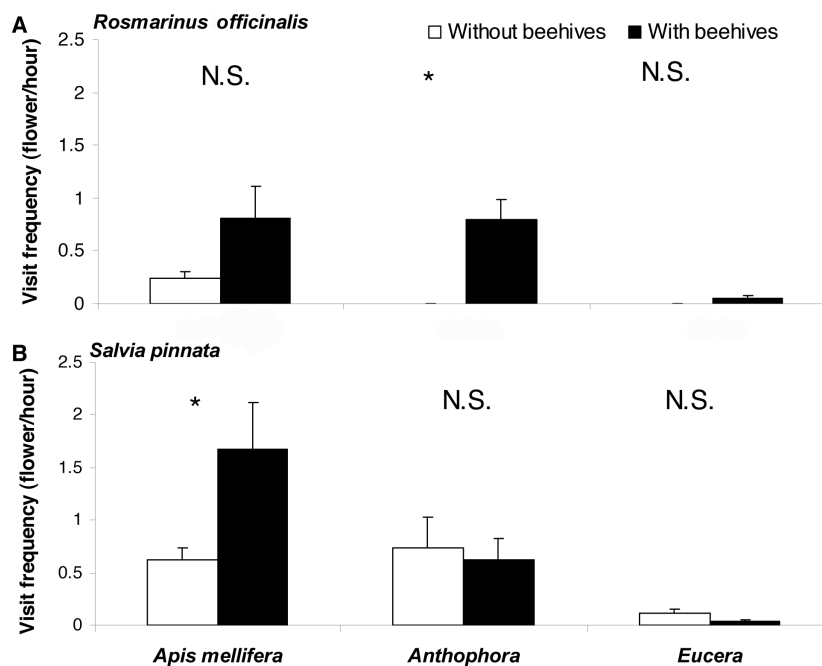


Fig. 4. Average visitation frequencies (per flower per hour) of honeybees and the visitation frequencies of the native solitary bees *Anthophora* sp. and *Eucera* sp. to flowers of the focal plants *Rosmarinus officinalis* N = 37 (A) and *Salvia pinnata* N = 16 (B) in Ramat Hanadiv during (2003) in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

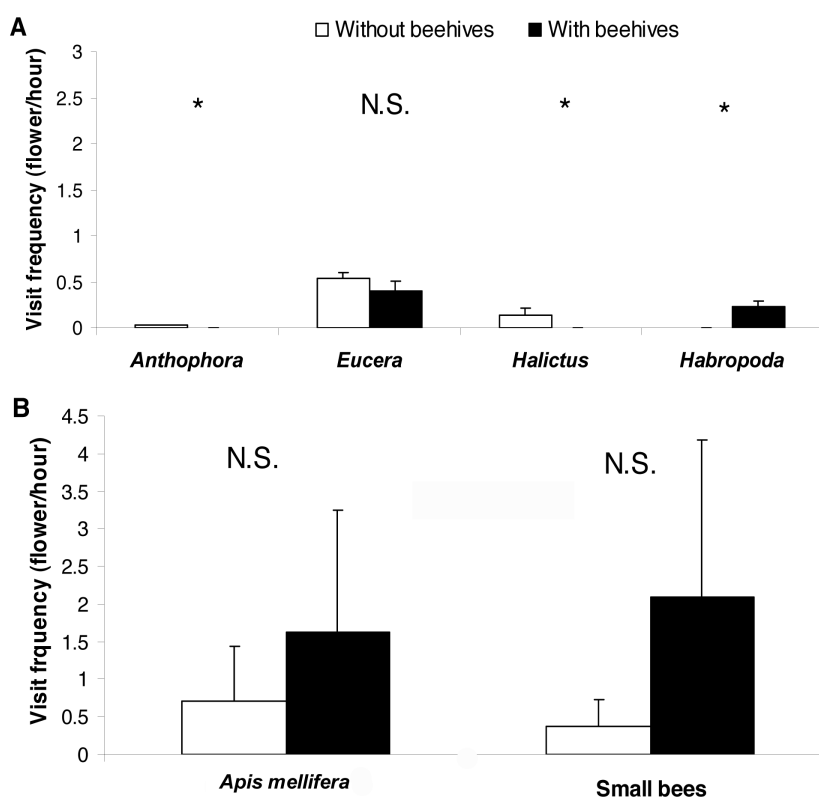


Fig. 5. Average visit frequencies per flower per hour of honeybees and the native solitary bees: *Anthophora* sp., *Eucera* sp., *Halictus* sp., and *Habropoda* sp. (A) and *Apis mellifera* and small bees (B) on *Salvia fruticosa* flowers, N = 41, in Carmel during (2004) in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

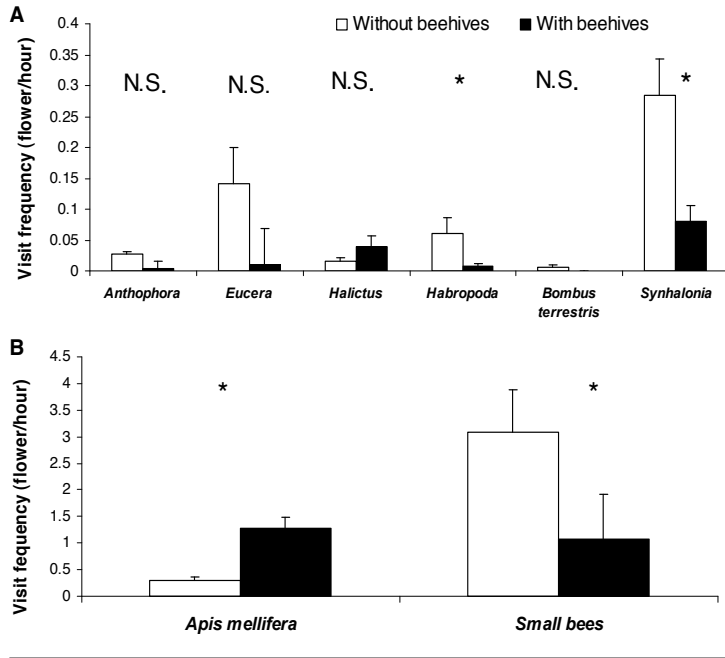


Fig. 6. Average visit frequencies per flower per hour of honeybees and the native bees: *Anthophora* sp., *Eucera* sp., *Halictus* sp., *Habropoda* sp., *Bombus terrestris*, and *Synhalonia* sp. (A) and *Apis mellifera* and small bees. (B) on *Salvia fruticosa* flowers, N = 66, in Carmel (2005) in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

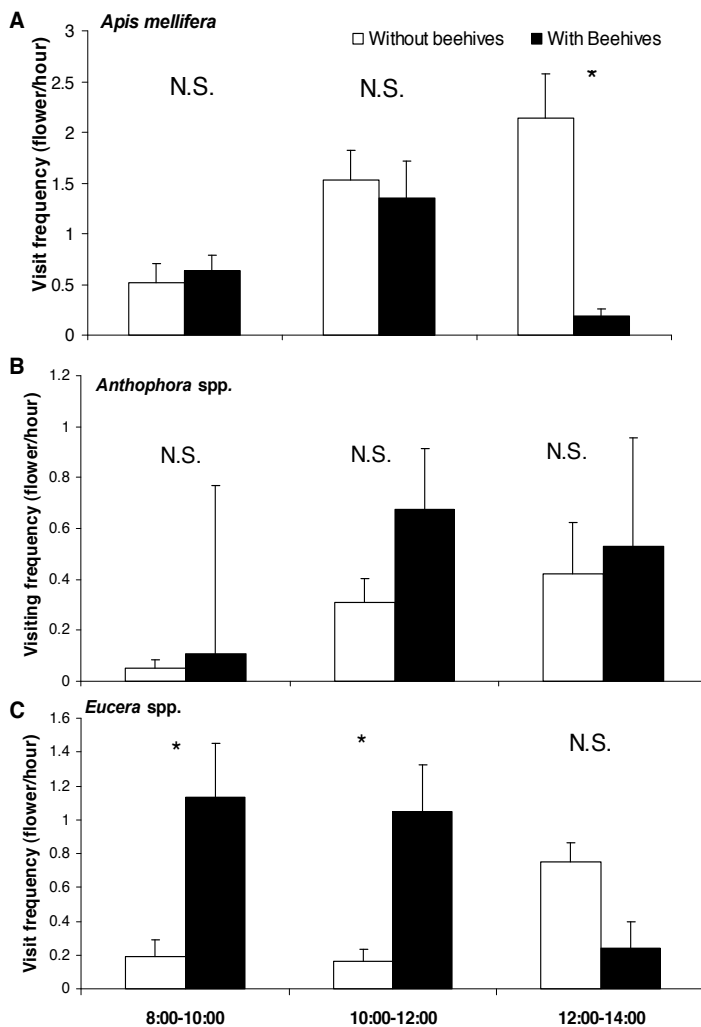


Fig. 7. Average visit frequencies per flower per hour of honeybees (A) and the native bees: *Anthophora* sp. (B) and *Eucera* sp. (C) during daily hours: 08:00–10:00 (N = 5), 10:00–12:00 (N = 7), and 12:00–14:00 (N = 5) to *S. pinnata* flowers in Ramat Hanadiv (2002), in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

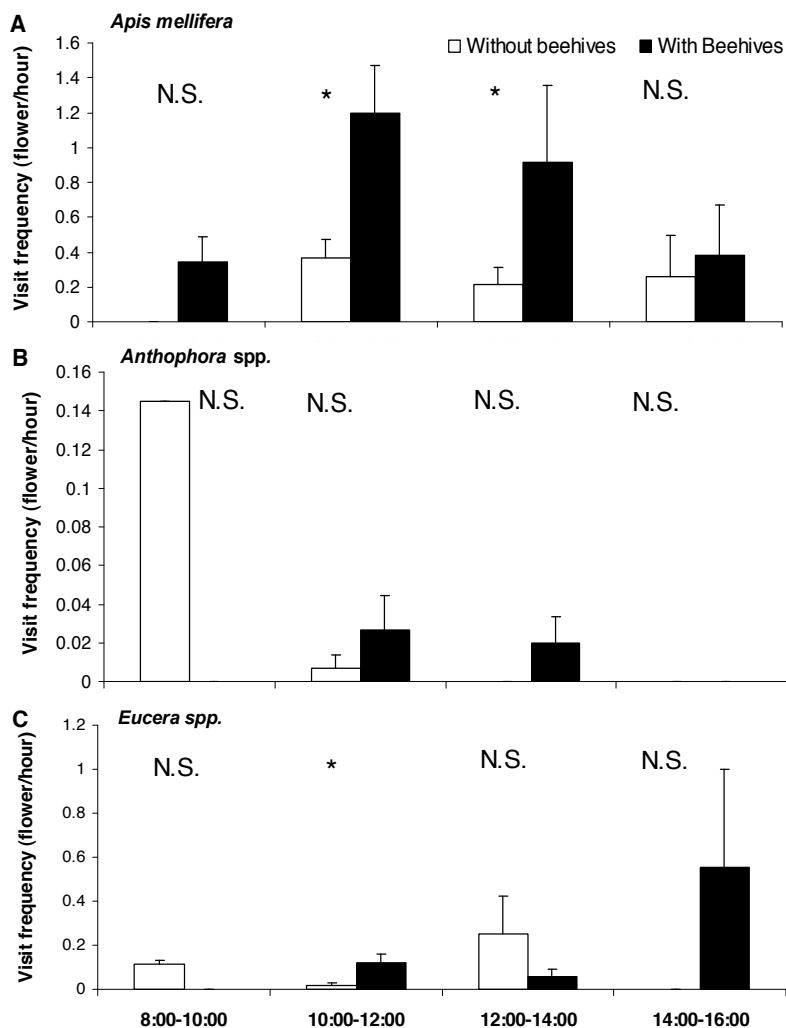


Fig. 8. Average visit frequencies per flower per hour of honeybees (A) and the native bees: *Anthophora* sp. (B) and *Eucera* sp. (C) during daily hours: 08:00–10:00 (N = 4), 10:00–12:00 (N = 32), 12:00–14:00 (N = 22), and 14:00–16:00 (N = 8) to *S. fruticosa* flowers in Carmel (2005), in the presence of honeybee hives and in their absence. The vertical bar indicates one SE, and *, a significant difference (Wilcoxon signed rank tests, $p < 0.05$).

Temporal segregation

Temporal segregation (morning, noon, and afternoon) of the foraging activity of honeybees and native solitary bees was analyzed for each site, focal plant, and year, in the presence of honeybee hives and in their absence. The introduction of hives did not cause any clear segregation in the temporal activity pattern among honeybees and native solitary bees. For illustration, we present two typical temporal analyses, for Ramat Hanadiv 2003 (Fig. 7) and for Carmel 2005 (Fig. 8).

DISCUSSION

Many earlier studies that tested the competition between foraging behavior of honeybees and other bees

were performed along a distance gradient away from a honeybee hive to achieve a parallel gradient in honeybee activity (e.g., Steffan-Dewenter and Tschardtke, 2000). A gradient of honeybee activity is expected along such a gradient, but other factors such as floral species composition and abundance, as well as in non-*Apis* bee species composition and abundance may co-occur. Consequently, if differences in foraging behavior of native bees occur, they could be a response to one or more of these factors. To avoid such a situation, following earlier researches (e.g., Schaffer et al., 1983; Thomson, 2004; Paini and Roberts, 2005; Paini et al., 2005), we have manipulated the presence of honeybee hives and observed bee foraging in the same sites before and after introduction of honeybee hives. The observations were

made within one to two weeks to minimize temporal changes in the composition and abundance of floral and bee species.

Introduction of honeybee hives increased the average visitation frequency of honeybees (Fig. 2), as well as average visitation frequencies on each focal plant species except for *S. eigii* (Fig. 3). This result demonstrated the success of our treatment, and enabled us to analyze its effect on the foraging behavior of the native bees.

Supporting our first hypothesis, introduction of honeybee hives decreased average visitation frequency of native bees (Fig. 2), indicating a negative effect of the honeybees on the native bees. However, examination of the effects of honeybees on specific native bees on each of the focal flowering plants, at both study sites and during the total research period, reveals an ambiguous picture. In nine plant-year-site combinations, we observed a significant decrease in the visitation rates of the native bees; in four cases, a significant increase, and in seven cases there was no significant effect (Table 2). Our focal flowers varied in their floral tube length and their nectar production. We expected that under high honeybee density, smaller bees with short tongue would shift to flowers with shorter floral tubes while larger bees with long tongue will shift to flowers with longer tubes, but such a shift did not occur.

In contrast, with our second hypothesis we also could not detect any clear change in the temporal pattern of native bee activity following introduction of honeybees (Figs. 7,8). Thus, the present results provide only partial evidence for competition between honeybees and native bees in the Mediterranean region of Israel.

There are several possible reasons for the high variability in our results. First, because of the high recruitment rate of the honeybee, the introduced bees may have

preferred to forage on distant rich flowers and avoided our focal plants. Second, despite the short time interval between our observations (5–14 days), natural fluctuations of floral resources and of native forager densities and interactions among non-*Apis* species might have occurred. Third, inadequate sampling for generally low densities of foragers and errors in species identification might have marginal effects.

Although the nectar standing crop of a single flower was low (0.1–0.35 μ l for our focal flowers), the massive spring flowering in the Mediterranean region produces ample amounts of nectar (Bosch et al., 1997; Potts et al., 2003) that may minimize the competition between honeybees and native bees in spring. However, the competition between the honeybees and native bees is probably more severe at the beginning and the end of the flowering season, when floral resources are limited.

Apis mellifera is a native species in the Mediterranean region, but because of pests common in beehives, such as *Varroa*, natural or feral swarms are rare in nature today, as they are in Europe (Moritz et al., 2005). The native bee fauna in western Asia has a long history of interaction with wild, feral, or domesticated honeybees. This could have led to development of mechanisms that allowed their coexistence. However, the extreme density of honeybees in Israel, about 90,000 beehives scattered in 6,300 locations with an average area of 1.5 km² for any beehive location (Israel Honey Council web site), produces heavy pressure on the floral resources, and thus may negatively affect the native bee fauna, mainly during drought years or seasons when floral resources are limited.

Moreover, because of the high honeybee hive density, Israeli beekeepers exert constant pressure to increase the number of hives in each location, and exert pressure for permits to locate beehives within the boundaries of

Table 2

Summary of the responses of native bees' visitation frequencies to focal plant species following introduction of honeybee hives in Ramat Hanadiv and Carmel, by bee positive significant response +; positive but insignificant trend (+), no clear response 0; negative significant response –; negative but insignificant trend (–). Wilcoxon test for significant differences ($p < 0.05$)

Location	Year	Plants	Bees						
			<i>Halictus</i>	SB	<i>Synhalonia</i>	<i>Anth.</i>	<i>Bombus</i>	<i>Euc.</i>	<i>Habropoda</i>
Ramat Hanadiv	2002	<i>Salvia eigii</i>				(+)		+	
		<i>Salvia pinnata</i>				–		–	
	2003	<i>Rosmarinus officinalis</i>				+		(+)	
		<i>Salvia pinnata</i>				0		0	
Carmel	2004	<i>Salvia fruticosa</i>	–	+		–		0	+
	2005	<i>Salvia fruticosa</i>	(+)	–	–	(–)	0	(–)	–

SB = Small bees, *Anth.* = *anthrophora*

nature reserves, which are the only honeybee hive-free areas. The long foraging range of honeybees, up to 10 km (Sugden et al., 1996; Goulson, 2003), and the small size of the nature reserves in Israel makes honeybees common flower visitors in nature reserves (Potts et al., 2003). Even in the heart of Mt. Meiron, the largest nature reserve in northern Israel (10 km across), we commonly observe honeybees. Because of the extreme rarity of feral honeybee swarms, these bees must come from hives located around the boundaries of the nature reserve.

Honeybees are the major pollinator of crops worldwide (Richards and Kevan, 2002). However, the present decline in their density, mainly in the USA and to some extent in Europe, has brought the importance of pollination services provided by native (mainly solitary) bees back into focus (Kremen et al., 2002, 2004). It has been demonstrated that these pollination services are negligible in large and intensive agricultural landscapes, but are important in relatively small areas where the neighboring natural vegetation and native bee diversity is high (Kremen et al., 2002).

To conclude, our data provide circumstantial evidence for a possible negative effect of honeybees on foraging behavior of our native bees at the peak of the flowering season. However, this negative effect is expected to be much more severe in years of drought and in seasons other than spring, when floral resources are scarce. From the agricultural point of view, we need to protect native bees for the sake of their role in pollination of crops, and as an alternative to honeybees in case of future catastrophe (Kremen et al., 2002, 2004). From the conservation point of view, we need to protect the native bees because they comprise an important part of the biodiversity in Israel, and for the sake of the pollination of the native flora, mainly rare and endemic species that may not be properly pollinated by honeybees. There is no unequivocal evidence that competition by honeybees depresses the fitness of other bee species (Sugden et al., 1996; Butz-Huryn, 1997; Paine, 2004; Moritz et al., 2005). There are many papers, however, that do indicate a negative effect of honeybees on the fitness of other bees worldwide (e.g., Schaffer et al., 1983; Pyke and Balzer, 1985; Sugden et al., 1996; Kato et al., 1999; Goulson and Sparrow, 2009). We therefore, as a safety measure, highly recommend keeping the nature reserves in Israel out of bounds for honeybee hives.

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APPENDIX
BEES COLLECTED IN ISRAEL BY OFRIT SHAVIT,
IDENTIFIED BY CHRIS O'TOOLE

Note: the presence or absence of parentheses () around authors' names after insect species names has significance; if there are no parentheses, it means that the species is still regarded as being in the genus it was originally placed in at the time of description; if the author's name is in parentheses, it means that it is no longer placed in its original genus.

The following bee species are arranged according to the two major bee guilds: Small Bee Guild (SBG) and Large Bee Guild (LBG):

SBG—Usually the same size as or smaller than the worker honeybee. These bees are slow flying, have short tongues, and are low-energy bees associated with shallow, open, low-reward flowers.

LBG—These are usually larger than the worker honeybee, are fast-flying, often with a rapid, darting flight, have long tongues, and are high-energy bees associated with deep-tubed flowers with a high-energy nectar source. Some species are oligolectic. In the list below, where an LBG specimen is smaller than a worker honeybee, this is indicated.

A generic name followed by a ? indicates that it has not been possible to identify the specimen to species level.

SBG SPECIES

ANDRENIDAE

Andrena sp. ? female.

HALICTIDAE

Lasioglossum sp. ? female.

MEGACHILIDAE

Chelostoma sp. ? female.

Osmia cornuta (Latr.) male

Osmia sp. ? female

ANTHOPHORIDAE

Nomada sp. ? [Species of this genus are cuckoos in the nests of *Andrena* spp.] male

LBG SPECIES

MEGACHILIDAE

Rhodanthidium sepdempunctatum (Latr.)? male

APIDAE

Xylocopa iris (Christ) female.

Ceratina sp. ? male.

Synhalonia sp. 1 ,? female.

Synhalonia sp. 2 ? female.

Eucera nitidiventris Mocs. male.

Eucera sp. nov. [A manuscript name given for this species by the late D.B. Baker exists, but it has not yet been published, so is unavailable for citation.] female

Eucera sp. 1,? male.

Eucera sp. 2,? male.

Eucera sp. 3,? male.

Eucera sp. 4, ? male.

Anthophora plumipes (Pall.) male. and female.

Anthophora heliopolitensis Pérez. male.

Anthophora nigriceps Mrw. male

Anthophora sp. nov. ["IRAN no. 6" of D. B. Baker] Note: this undescribed species should simply be cited as: *Anthophora* sp. nov., *teste* C. O'Toole] male

Anthophora rubricrus Drs. female.

Anthophora biciliata Lep. female.

Anthophora dufourii Lep. male. and female.

Melecta sp. ? [Species of this genus are cuckoos in the nests of *Anthophora* spp.] female.