

# Movement patterns of solitary bees in a threatened fragmented habitat

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**Abstract** – Fragmentation and loss of natural habitats are major threats to many bee species. Large, long-distance flying bees are predicted to be more efficient in utilizing resources and at the same time may function as important pollinators in a fragmented landscape. Using mark-recapture experiments, this study evaluates the movement of bees belonging to the “large, long-tongue” guild in a threatened, fragmented habitat. Bee movement between the sampling plots was limited, despite high recapture proportions within the plots. A maximum likelihood model has estimated a high degree (60 % of all marked bees) of site fidelity to the source plots and a mean traveling distance of 357 m for the bees that left the plots. Additional observations on the bees’ foraging behavior suggest that some anthophorine bee species can be important pollinators in the studied habitat. We suggest that the bees’ site fidelity and flower constancy are the main causes for their observed conservative movement pattern.

solitary bees / habitat fragmentation / movement patterns / foraging behavior / site fidelity

## 1. INTRODUCTION

Loss and fragmentation of natural habitats are main drivers to the decline of communities and the diversity of bees (Biesmeijer et al. 2006; Kearns and Inouye 1997; Kearns et al. 1998; Potts et al. 2010; Winfree et al. 2009) as well as to the plants that they pollinate (Aguilar et al. 2006). The effect of fragmentation on different bee species depends on their ecological traits (Cane et al. 2006; Krauss et al. 2009; Steffan-Dewenter et al.

2006; Westrich 1996; Williams et al. 2010) and is found to be significantly negative on specialized species, such as parasites and floral specialists (oligoleges), and also on other solitary bees (Cane et al. 2006; Krauss et al. 2009).

Higher species’ vagility may permit the utilization of suitable habitat in fragmented landscapes (Westrich 1996) and, on the other hand, can have important consequences on local plant populations via bee contribution to cross pollination (Aizen and Feinsinger, 2003). Therefore, bee foraging ranges and patterns can be important characters in fragmented habitats. Foraging ranges of bees directly correlate with bee body size (Gathmann and Tscharntke 2002; Greenleaf et al. 2007). Thus, large (>10 mm), long-flying bees that can forage over several km (e.g., *Xylocopa*, Pasquet et al. 2008; *Anthophora*, Rau 1929) are more likely to move between various habitat fragments (Beil

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et al. 2008; Cane 2001; Steffan-Dewenter et al. 2006), but foraging distance is subject to interspecific and even intraspecific variation (see in Walther-Hellwig and Frankl 2000). However, small (6–10 mm) solitary bees have generally performed shorter foraging ranges of only 150–600 m (Gathmann and Tschamtké 2002; Zurbuchen et al. 2010b).

Despite the above considerations, potentially long flight ranges cannot always predict the movement of bees in a fragmented landscape (Zurbuchen et al. 2010c). Alternatively, bee movement patterns may largely depend on their foraging behaviors. For example, the females of *Apis*, *Bombus*, and some *Anthophora* species are floral generalist (polylectic), but nevertheless present ‘flower constancy’, i.e., they exhibit floral preference to some degree, and they usually follow a constant spatial pattern. Furthermore, these species display weaker floral specificity while foraging for nectar (Cane and Sipes 2006; Eickwort and Ginsberg 1980). It is therefore expected that the movement of these species will follow the spatial distribution of their favored food plants. Optimal foraging theory suggests a mechanism of foraging behavior based on energetic considerations and predicts that bee foragers are not likely to regularly commute long distances unless the resources within a given patch of flowers are poor. This behavior was observed in the field in social *Bombus* workers (Pyke 1978).

The present study explored the movement patterns and behaviors of solitary bees belonging to the ‘large, long-tongue guild’ (Dafni and O’Toole 1994, see also in “Methods”), viewed as potentially important pollinators in a threatened, fragmented habitat in Israel. The specific objectives of the study were (a) to study and estimate movement patterns of pollinator bees in a fragmented landscape and (b) to characterize their foraging behaviors through observations on flower visitation. We hypothesized that (a) the studied bees, being generalists and long distance flying species, will be able to cross unrewarding landscape matrix and move between habitat fragments and (b) bee species will differ in their movement pattern, based on specific foraging behavior (flower visitation).

## 2. METHODS

### 2.1. The sandy-gravel habitat, study area, and species

The study was performed within a rural landscape of the Sharon coastal plain in Israel, comprising a mosaic of natural, abandoned (seminatural), and actively managed agricultural land use. The study sites were small fragments (12,000–315,000 m<sup>2</sup>) of the sandy-gravel (*Kurkar*) habitat, characterized by highly diverse bee fauna and plant flora (overall ~190 and ~180 species, respectively, authors’ unpublished data) and by high floral endemism (about 24 plant species, Shmida 1984). This unique habitat, which previously formed a thin belt along the central coast (6–8 km wide, MAPI 1995), had already been reduced to 1 % of its estimated original area by the early 1980s (Polak 1984) and, to date, is threatened by ongoing intensive development and urbanization processes.

The studied bees belong to the ‘large, long-tongue guild’ (Dafni and O’Toole 1994), which are large species [body length >12 mm, mainly belonging to the tribes *Eucerini* and *Anthophorini* (Apidae)] and capable of long-distance flight (Greenleaf et al. 2007). These bees are also generalists in terms of exploiting nectar and pollen resources (see bee visitation data in Appendices 1 and 2 in the supplements, though accurate determination of the female’s pollen load is beyond the scope of the present study). Having long mouth parts (proboscis >6 mm), they can obtain nectar from a wide variety of plant species, including tubular flowers as well as open-access flowers (Eickwort and Ginsberg 1980) and therefore may contribute to the pollination of a wide variety of plant species within a fragmented habitat.

### 2.2. Experimental design

In order to follow the movement of the bees, we performed a series of mark-recapture experiments in three study sites, each comprising several natural or moderately disturbed habitat fragments where a relatively high diversity of bees was found in preliminary surveys (authors’ unpublished data). In each of the study sites that we marked sampling plots, each plot representing a separate habitat fragment

(see experiments' description below). We marked the bees using fluorescent powder (Bio Quip Products Inc., USA) mixed with nontoxic, water-soluble glue. Different colors in each sampling plot allowed us to determine the movement of the bees between the plots. Although laborious and distance-dependent, the mark-recapture method suited our purposes insofar as it allows the direct tracking of individuals without manipulation and with minimum intervention.

In each of the experiments, the bees were sampled by the same person for comparable periods of time in each of the sampling plots. All of the bees encountered (both males and females) were caught using insect nets, either while visiting 'focal plants' (see below) or during flight. Dyes were then applied manually to the dorsal part of the bee thorax, using plastic inoculating loop sticks (Plate 1). The handling time was 30–60 s, including determination of the species with the assistance of a pocket microscope (45X, Dealextrime, China). Bee recapture and marking were recorded simultaneously, but if individuals of the same species and sex were found marked, then they were counted only after 30 s from the moment of release in order to exclude returning individuals (especially males practicing territorial behavior). This marking procedure did not seem to alter the behavior of the bees, as individuals frequently continued with the same activity observed prior to our interruption. The dyes markers soon got dry and were found to remain on both males and females for at least one week time from the application (the first day of the experiment), in accordance sampling trials were designed for no longer than six consecutive days with at least 10 days intervals

in each of the study sites. All experiments were performed under favorable conditions for the activity of bees, namely, on sunny days between 0900 and 1600 when the wind velocity was low (<14 m/s) and the weather was warm (20–32 °C).

We focused our sampling efforts on bees visiting selected 'focal plants'. These were abundant plant species that are highly rewarding for bees (e.g., species within the Lamiaceae or Boraginaceae) and which are believed to have prime importance to the pollinator–plant system in the habitat (therefore also referred to as "core species," Dafni and O'Toole 1994).

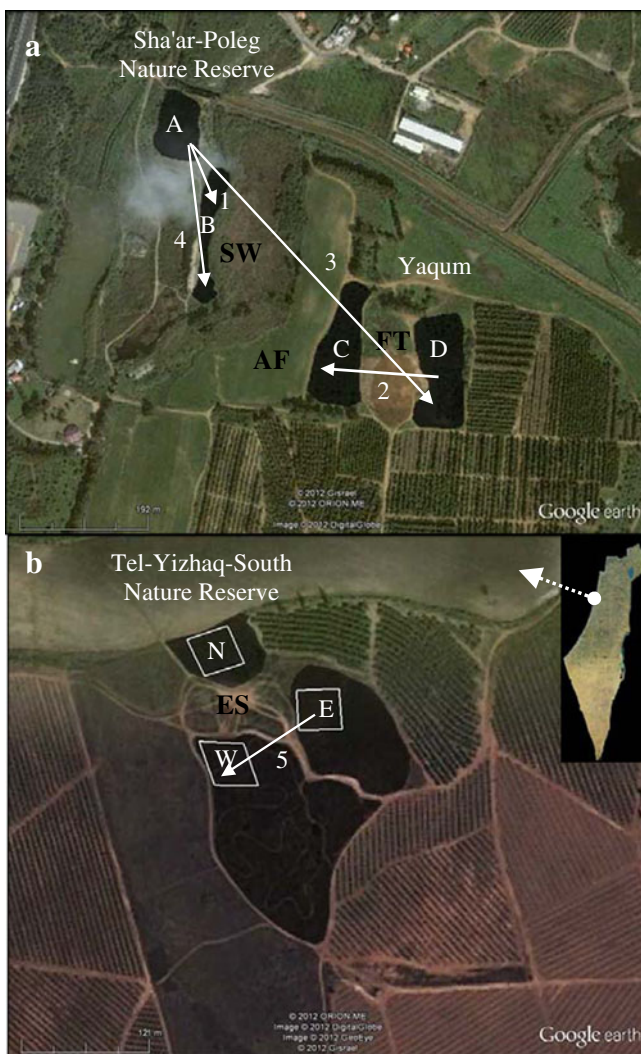
*Experiments' description* The study site in the Tel-Yizhaq-South Nature Reserve (TYS hereafter, coordinates: 22°14'37" N, 24°51'55" E) comprise three habitat fragments, eastern, western, and northern, the former being at least two folds larger than the others (Figure 1b). In order to have comparable replicates we marked in each of the fragments a square sampling plot with an equal area of 1,600 m<sup>2</sup> and with a distance of 50–70 m between them. The plots were divided by eroded land surface, with a maximal altitude difference of 6 m (Figure 1b). We performed two sampling trials: trial 1 during February 2011 took 2 days and 1–3 h in each plot. In sampling trial 2, we marked and recaptured bees simultaneously for five consecutive days, during March 2011, for 2.5 h a day on average in each plot. We alternately sampled the plots, each day starting at random in a different plot and then moving to the next.

Additional samplings were performed in two neighboring study sites, sandy-gravel hills in the Sha'ar-Poleg Nature Reserve (SP hereafter, coordinates: 32°15'30" N,



**Plate 1.** *E. m. sp. nova*. This previously undescribed species (Risch, unpublished data) was found to be the most abundant pollinator in the YYS site, accounting for 37% of the overall bee abundance in three mark-recapture experiments. *Left* Application of dye markers. *Right* Male and female in copulation (photographs by Nicolas J. Vereecken)

**Fig. 1** Map of the study area in the Sharon coastal plain of Israel. The study sites include seven natural fragments (*darkened*) of the threatened sandy-gravel (*Kurkar*) habitat, characterized by highly diverse bee fauna and plant flora. Plots A and B, in Sha'ar-Poleg Nature Reserve, and plots C and D, north to Yaquum represent entire habitat fragments (**a**); three additional fragments in Tel-Yizhaq-South Nature Reserve (**b**) were sampled using eastern (E), western (W), and northern (N), square plots of equal size. The bees moving between the sampling plots were species of the genus *Anthophora* and were found to cover different distances (marked with *white arrows*): 1, *A. plumipes* male, 70 m; 2, *A. agama* male, 180 m; 3, *A. rubricrus* male, 590 m; 4, *A. plumipes* female, 280 m; 5, *A. rubricrus* male, 110 m. *SW* swamp, *AF* agricultural field, *FT* fruit trees, *ES* eroded land surface.



34°50'24" E) and north to Yaquum (coordinates: 32°15' 19" N, 34°50'37" E). Because these sites are located over 2 km away from the TYS site, we treated them as a separate experimental unit. In each of the sites, we used two sampling plots, each representing a separate habitat fragment, along a west to east transect, situated at the hills' west- and east-facing slopes. Plots A and B, with areas of 8,400 and 7,200 m<sup>2</sup>, respectively, within the SP site are 40 m apart and are divided by a narrow dirt road (several meters wide) and disturbed habitat with a maximal altitude difference of three meters (Figure 1a). Plots C and D, with areas of 8,400 and 7,200 m<sup>2</sup>, respectively, in the Yaquum site, are divided by a private park planted with fruit trees at a distance of 90 m. The

two pairs of plots are divided by the Poleg swamp, densely covered with common reed (*Phragmites australis* [Cav.]) and with introduced *Eucalyptus* trees, as well as by an agricultural field strip of seasonal crops, together comprising a distance of 195 m and a maximal height difference of 13 m (Figure 1a). We performed three consecutive sampling trials between February and April 2011, in which we repeatedly marked and recaptured individuals at two to four of the sampling plots simultaneously. Sampling days and hours varied between the plots according to the phenology of the bees and the focal plants. Sampling trial 1 took 4–6 days and 7–10.5 h, sampling trial 2 comprised 1 day and 1.2–3.3 h, and sampling trial 3

entailed sampling plots A and B for 3 days, each plot for 3.5 h, and plots C and D for 6 days and 13–18 h.

*Statistical analysis* In order to evaluate the extent of bee movement among habitat fragments, we applied maximum-likelihood estimation to the following statistical model. Derived from our observations (see in “Results”), we first assume that a fraction  $f$  ( $0 \leq f \leq 1$ ) of all marked individuals exhibit site fidelity to their plot of origin, and therefore, never (during each sampling trial) leave the plot in which they were originally marked. The rest may freely move out of their original plot and are subsequently distributed according to a two-dimensional normal distribution, centered at the plot of origin and having a variance, given by a second parameter,  $V$  (a dispersion pattern expected, based on random walk of individuals). A third parameter,  $q$  ( $0 \leq q \leq 1$ ), determines the recapture success within any resampled area or plot (i.e., the fraction of marked individuals at a given area that are actually recaptured during a single sampling trial).

We combine the data of all plots into a single likelihood model, such that each marked individual contributes a term to the total (log-likelihood function, see Appendix 3 in the supplements for derivations). In that manner, we both increase the power of our statistical tests (by conducting a single analysis with the largest possible sample size, i.e., all marked individuals from all sampling trials in all plots), and take account of the fates of all marked individuals, whether recaptured within the plot of origin, within a different plot, or not recaptured at all.

The site fidelity parameter,  $f$ , also plays the role of measuring how much the actual distribution pattern of the bees deviates from purely random (normally distributed). If the hypothesis  $f=0$  can be rejected, the bees clearly demonstrate a nonzero degree of site fidelity and are therefore not purely randomly distributed. For that purpose, we applied a likelihood-ratio test (Nash and Varadhan 2011, further details in Appendix 3 in the supplements). All analyses were done in GNU R v.2.14.1 (R Development Core Team 2011).

### 3. RESULTS

In the TYS site, we recorded altogether 271 and 245 bees in the eastern and northern plots, respectively, and 22 bees in the western plot (which had lesser sampling effort in sampling trial 2). These were 13 species of the ‘large, long-tongue guild’, mostly from the large genus *Eucera*. Surprisingly, the most abundant species appeared to be a new, previously undescribed species (*E. m. sp. nova*, Risch, unpublished data; see Plate 1 and Appendix 1 in the supplements). The single bee that was recaptured in sampling trial 1 outside the plot of origin was a male from the species *Anthophora rubricrus* Dours moving from the eastern to the western plot to a distance of 110 m (Figure 1b). Despite the considerably high sampling efforts in the eastern and northern plots (>230 marked bees and >0.25 recapture

**Table I.** Number of bees marked and recaptured and bee recapture proportions in mark-recapture experiments ( $n=5$ ) with large, long-tongue bees.

Sampling plot	Sampling plot area (m <sup>2</sup> )	Number of marked bees (range, total)	Number of recaptured bees (range, total)	Recapture proportion (range, total)
SP A	8,400	20–248, 295	1–32, 45	0.05–0.44, 0.62
SP B	7,200	12–122, 157	1–21, 24	0.08–0.17, 0.34
Yaqum C	9,600	13–95, 199	1–11, 20	0.08–0.11, 0.28
Yaqum D	9,600	8–158, 272	4–39, 71	0.17–0.5, 1.04
TYS east	1,600	43–231, 274	26–62, 88	0.26–0.6, 0.87
TYS west	1,600	5–16, 21	1–8, 9	0.2–0.5, 0.7
TYS north	1,600	2–240, 242	1–63, 64	0.26–0.5, 0.76

The sampling plots ( $n=7$ ) represent natural fragments of a sandy-gravel habitat. *SPA/B*- Sha’ar-Poleg Nature Reserve, plots A/B; *Yaqum C/D*- Yaqum, plots C/D; *TYS east/west/north*- Tel-Yizhaq Nature Reserve, eastern/western/northern plots

**Table II.** Richness of large, long-tongue bee species, recorded at focal plants with varying abundance in mark-recapture experiments ( $n=3$ ).

	Bees visiting similar plants	Bees visiting different plants
Common plants	6 species <i>Site fidelity</i>	8 species
Uncommon plants	10 species	19 species <i>Flower constancy</i>

The sampling plots are in Sha'ar-Poleg and Yaqum study sites and represent natural habitat fragments ( $n=4$ ). Values represent number of abundant bee species (>5 % of the total bees) that were visiting similar (*left cells*) as compared to different (*right cells*) focal plants in different plots. The visited plants were labeled either as common (found in 3–4 plots, *upper cells*) or uncommon (found in 1–2 plots and only in one of the sites, *lower cells*). Six bee species are suspected to show site fidelity as compared to 19 species that may demonstrate flower constancy (see “Discussion”)

proportions, see Table I) and the similarity in species composition (see Appendix 1 in the supplements), we did not record a single bee moving between the plots. This result is particularly surprising considering that eroded land surface with a distance of only 50 m was separating between the plots and that many species were marked while visiting the same species of focal plants in the two plots (see Appendix 1 in the supplements).

In the SP and Yaqum sites, we marked a total of 157–295 bee individuals belonging to 14 species, of which 20–71 individuals were recaptured within each of the four sampling plots in three sampling trials (Table I). Bee species that were marked on focal plants in different sampling plots showed variability in floral preference. Table II presents the number of abundant bee species (>5 % of the total bees marked in each of the sampling plots) that were recorded at focal plants of varying abundance. Six bee species were recorded at the same focal plants, in three or in all four of the sampling plots, thus occur in both of the sites (and are labeled as common plants in Table II). These species typically included: *Anthophora plumipes* (Pallas), *Anthophora agama* Radoszkowski, *Eucera cyprina* Alfken, and *Xylocopa iris* (Christ) (see Appendix 2 in the supplements). Relatively more (19) species were recorded at different plants, thus visiting similar plants in only one plot or two plots of the same site (and are labeled

as uncommon plants in Table II). For example, *Megachile sicula* (Rossi) and *Eucera w. sp. nova* (Risch, unpublished data) were recorded mainly at *Bituminaria bituminosa* (L.) only in the two plots in Yaqum (see in Appendix 2 in the supplements).

The recapture proportions within the sampling plots ranged between 0.05 and 0.5 of the individuals marked (Table I), but only four incidents of bees crossing between the plots were recorded. The crossing bees were all species of the genus *Anthophora*, including males from the species *A. plumipes*, *A. agama*, and *A. rubricrus* and a female *A. plumipes*, covering distances of 70, 180, 590, and 280 m, respectively (Figure 1).

Estimation of the statistical model described in “Methods” has revealed a significant and high degree of site fidelity [ $f=0.6\pm 0.036$  (estimate $\pm$ SE); LR statistic=369.9;  $P<10^{-6}$ ]. The remaining estimated 40 % of individuals, which may have moved out of their original plot, are distributed normally with a mean traveling distance of 357 m [95%CI (200 m, 642 m); obtained from the maximum-likelihood estimate of  $V$ ].

Finally, the estimated mean recapture success within any sampled plot is given by  $q=0.36\pm 0.013$ . That is, on average, 36 % of marked individuals present at any sampled area are recaptured. Obviously, realized recapture proportions would be lower because there

are marked individuals outside the sampled plots.

#### 4. DISCUSSION

Movement of bees between the sampling plots was found to be limited in all of our experiments and sites. Altogether, we marked about 1,460 solitary bees belonging to 19 species of which 10–40 % were recaptured at the same plots (the estimated mean recapture success  $q=36$  %). Despite these relatively high recapture proportions, we recorded only five individuals crossing between the plots. The maximum likelihood model has estimated that 60 % of the individuals show site fidelity to their original plot. Therefore, the distribution of bees is far from the one expected by purely random movements of individuals. Instead, bees tended to stay within their plots of origin. Our results are in line with those recorded in mark-recapture experiments with social species of the genus *Bombus* (Bhattacharya et al. 2003 and reference therein). For example, Bhattacharya et al. (2003) recorded similar recapture rates to the ones we observed in solitary bees, with 31 % of the individuals recaptured at the flower patches of origin and with only three bees recorded as crossing between sites. As in the above cited studies, the distances between our sampling plots (40–195 m) were much smaller than the flight ranges of the studied species. In addition, the physical obstructions (e.g., dirt roads, a field strip 70 m long) were smaller than the potential barriers previously reported to be overcome by smaller bee species (Zurbuchen et al. 2010a). Considering the limitations of the mark-recapture method, it is possible that we have underestimated the movement of bees between the sampling plots. In particular, because the density of marked bees quickly decreases with growing distance from the marking point (e.g., according to a normal distribution, as we assumed in our statistical model). Nonetheless in a 5-day sampling trial in the TYS site, in which the distance between sampling plots was short (50–70 m) and the sampling effort was high, we did not observe movement of bees between the

plots. Some solitary bee members of the large, long-tongue guild were able to move between the habitat fragments and the maximum likelihood model estimated their mean traveling distance at about 350 m. But despite our expectations, the bees largely refrained from leaving their source plots. We therefore suggest that high fidelity to site among the studied solitary bees was the main factor shaping their foraging patterns. This same conclusion was reached in the above cited studies on the foraging behavior of *Bombus* (Bhattacharya et al. 2003).

Movement along fixed foraging paths (Heinrich 1976; Thomson 1996) and frequent abstention from otherwise penetrable spatial border lines (Bhattacharya et al. 2003; Kreyer et al. 2004) were reported as foraging features of *Bombus* workers. However, little is known about the foraging behavior among the myriad solitary bee species (Michener 2007, except for several cases like male Euglossine bees since Janzen 1971). The available literature on the foraging behaviors of different solitary bee taxa has commonly reported high fidelity to a flowering patch or tree (Franzén et al. 2009; Gordon et al. 1976; Pasquet et al. 2008), and only when the location of the nests was manipulated, the nesting females commuted to the nearest floral resource (Williams and Kremen 2007). In our experiments, six species were found to be foraging on the same focal plants in different habitat fragments (Table II). These bees, like the bees in the above cited studies, may present site fidelity because they could use the same floral resources in other neighboring plots. In comparison, 19 species were recorded at different focal plants that were restricted to only one or two of the habitat fragments (Table II). Considering these bees as generalist species, they may demonstrate flower constancy rather than site fidelity. Interestingly, the bees moving between the sampling plots were all species of *Anthophora* (four males and one female), which largely belong to the group of bees foraging on the same focal plants in different fragments. The combination of the two characters, a tendency to forage on similar plants in different habitat fragments and the ability to move between

fragments, makes these species potentially important pollinators in a fragmented habitat. The possible contribution of long distance cross pollination by these bees can alleviate genetic and demographic erosion that pose threat to small plant populations in isolated fragments (Ellstrand and Ellam 1993, Groom 1998).

The anthophorines moving between plots were almost exclusively males. Movement patterns and behaviors of male bees depend mainly on their searching strategies for a mate (Alcock et al. 1978; Paxton 2005). Long-distance movement of males will more likely occur in species in which males compete for territory than in those where males practice nonterritorial scramble competition for a mate. Studies with British populations of *A. plumipes* support our results by documenting territoriality of males and movement between habitat fragments only when the competition for mates increases (Stone et al. 1995). Like Stone et al. (1995), we observed territorial behavior among male anthophorines that were guarding specific flowering patches. In contrast, the males of some eucerine species, such as *E. nigrilabris* and *E. kilikiae*, performed mass swarming flights, either over flowering bushes or through the lower vegetation layer, respectively. The difference in search patterns for mates may partially explain the movement of male anthophorines between the sampling plots, possibly in search of territories, as opposed to the movement of male eucerines. As a consequence, the potential contribution of some male bees to cross pollination may be greater than that of females as already suggested in a study with solitary bees (Ne'eman et al. 2006).

Surrounding disturbed (seminatural) and agricultural areas are potentially important for bees in natural habitat fragments by contributing additional food and nesting resources (Westrich 1996). In our study, some of these areas were found to be relatively diverse in both bees and plants (authors' unpublished data), and therefore, we assume that most of the bees that were estimated to leave the source plots (40 % according to the statistical model) were moving into these areas.

In light of the conservative movement patterns and behaviors of the bees in our experiments, we

suggest that efforts should be made to protect maximal natural and seminatural habitats for the conservation of both wild bees and plants. In addition, the foraging behaviors of the particular bee species should be considered as a prime factor for effective conservation management in fragmented habitats. Our results suggest that particularly anthophorine bee species can be important for the conservation of plants in small isolated habitat fragments. This may be true for the highly diverse sandy-gravel habitat along the central coast of Israel, which is seriously being threatened by development and fragmentation processes. It may also be true for many other Mediterranean-type habitats in which large solitary bee (rather than social, multivoltine) species are primary native pollinators.

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### Schéma des déplacements d'abeilles solitaires dans un habitat fragmenté et menacé.

**Abeille solitaire / fragmentation de l'habitat / déplacement / comportement d'approvisionnement / fidélité au site**

### Bewegungsmuster von Solitärbiene in einem durch Fragmentierung bedrohten Habitat

**Solitärbiene / Habitatfragmentierung / Bewegungsmuster / Sammelverhalten/ Ortstreue**

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