Mobility of honey bees (Apidae, *Apis mellifera* L.) during foraging in avocado orchards

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Abstract – The mobility of the honey bee (*Apis mellifera* L.) during foraging has a great influence on the effectiveness of the bees as cross-pollinators. In this work, honey bee mobility was measured in avocado orchards, between neighbouring trees and up to a distance of 15 rows. The average number of bees crossing between adjacent rows in a 10-min period was linearly correlated to bee density, and the corresponding percentage increased with the increase in wind velocity, from 30\% in a light wind (4 km/h) to up to 65\% in a strong wind (45 km/h). The bees tended to travel upwind, and this tendency increased with increasing wind velocity. Consequently, under strong-wind conditions, up to 100\% of the bees travelled to the adjacent upwind row in a 10-min period. The percentage of cross-pollinating bees decreased with increasing distance from the pollen source, following a hyperbolic curve, and reached 1–2\% of the bees at a distance of 10–15 rows.

honey bee / mobility / cross-pollination / *Persea americana* / avocado / wind velocity

1. INTRODUCTION

Pollinator mobility is essential mainly to plants that require, or are benefited by cross-pollination (i.e. pollen transfer between plants of different cultivars within the same species). This need occurs in dioecious crop species (kiwi, some papaya cultivars), in self-incompatible monoecious or hermaphroditic species (almond, cherry), and in crops which are partially self-incompatible (some apple and most avocado cultivars) [32]. In some of these species, such as apple and almond, cross-pollination is performed by honey bees both directly, during the foraging flight, and indirectly, by means of pollen transfer through body contact of bees inside the...
Honey bee mobility during foraging is limited: a single bee usually forages within an area of no more than two or three neighbouring trees [1, 2, 5, 6, 8, 14, 18, 20, 21]. Nevertheless, foragers moving tens, or even hundreds of meters, have been observed. These bees stopped foraging before their loads of nectar or pollen were full, flew above the canopy, and landed elsewhere for continued foraging [4, 35]. This ‘orientation flight’ [13], which was later called ‘sampling behaviour’ [16, 17] or ‘monitoring flight’ [18], was assumed to be made by the ‘scout bees’, which are the only honey bees that perform long-distance cross-pollination during foraging [18].

The purpose of the current research was to measure honey bee mobility during foraging in an avocado (Persea americana Miller) orchard, between adjacent trees and in a larger range, and to correlate this mobility to bee density on the trees, to wind speed and direction, and to the distance from the pollen source.

2. MATERIALS AND METHODS


Honey bee density (BPT = bees per tree) was assessed by counting the bees on a whole tree (five trees per cultivar), while circling it at a distance of about 1 m from the canopy for 1 min, using a manual counter [19, 31]. Calibration counts were performed at the beginning of each day, until the discrepancy among the workers was reduced to less than 10 %.

Wind velocity (WindVel) and wind direction were estimated in an open field beside the orchard. Beaufort scale for field estimation of wind velocity was used, to be later converted to km/h.

Honey bee mobility among adjacent trees was measured on four trees in full bloom: two neighbouring trees in a row and two trees next to them in the adjacent row. At the beginning of each measurement period, wind speed and direction, and bee density were recorded. Later, all the bees that crossed between the observation trees were counted, simultaneously in all directions, by an observer, who sat with his back to the sun, and used a multi-station counter with a marked station for each direction. Using these data, the average number of bees that had crossed in a 10-min period from one tree to the adjacent row (NoMob) was calculated. The percentage of bees which crossed between adjacent rows in 10 min (PrMob) was calculated as:

$$\text{PrMob} = \left( \frac{\text{NoMob}}{\text{BPT}} \right) \times 100$$  \hspace{1cm} (1)

The ratio of wind-direction preference of the bees (UWMP = upwind mobility preference) was calculated for each measurement as:

$$\text{UWMP} = \frac{\text{no. of bees travelling upwind}}{\text{no. of bees travelling downwind}}$$  \hspace{1cm} (2)

Correlations of these variables with both bee density and wind velocity were examined.

The monitoring of honey bee mobility in a range greater than one row was possible owing to the exclusive flowering phenology of avocado. During 4–6 h in the morning, under normal temperature conditions [28], type-A avocado cultivars bear only female-stage flowers, while type-B cultivars carry male flowers exclusively, with a reversal of roles in the afternoon [34]. Therefore, bees that visit flowers of a cultivar in male-stage bloom ‘mark’ themselves by building pollen loads, which render them identifiable and subject to follow-up while crossing to a cultivar in female-stage bloom [27]. Measurements were taken in avocado plots with adjoining blocks of opposite flowering-type cultivars which bloom during the same season. Plots of ‘Hass’ contiguous to ‘Ettinger’ were selected in the orchards of Eilon, Rosh-Hanikra and Kabir, and a ‘Reed’ block bordering with a block of ‘Nabal’ was selected in Rosh-Hanikra orchard. Measurements were performed during the female bloom of type-A
cultivars ('Hass' or 'Reed'), and the pollen-releasing stage of type-B cultivars ('Ettinger' or 'Nabal', respectively), which occur in the morning on warm days and at midday on cool days [28]. At the onset of each measurement, wind direction and velocity and bee density of each cultivar were recorded. Later, pollen-load carrying bees and nonloaded bees were simultaneously counted in several rows by several observers. Each observer walked along one row for 15–20 min and used two counters. Counts were carried out in the two rows of the male-blooming cultivar facing the female bloom, and in several rows of the female-blooming cultivar (nos 1, 2, 4, 5, 7 and 15 away from the male bloom). For each row we performed two to five counts, pooled them and calculated the average percentage of pollen-load carriers, which was marked:

\[ \text{PPM}(0) = \text{percentage of pollen-load carriers on male-bloom trees} \]

\[ \text{PPF}(d) = \text{percentage of pollen-load carriers on female-bloom trees, in 'd' rows away from the male bloom} \]

We assumed that all the pollen-load-carrying bees on the female blooms had arrived from the adjacent male bloom during foraging flight. Also, we assumed that the mobility of pollen-load carriers is similar to that of the nonloaded bees, i.e. that the proportion of the pollen-load carriers among the bees visiting the male bloom is similar to that among the cross-pollinating bees on the female bloom. Therefore, the percentage of cross-pollinating bees in row 'd' of the female bloom, which was designated PCrBee(d), was calculated as:

\[ \text{PCrBee}(d) = \left( \frac{\text{PPF}(d)}{\text{PPM}(0)} \right) \times 100 \] (3)

Take-off and landing directions were observed on three trees in full bloom: two flowering branches (branches which bear inflorescences in each leaf node) per tree were marked, one facing an adjoining tree within the row, and the other facing a parallel tree in the adjacent row. At the beginning of each observation, wind direction and velocity and bee density were measured. Later, all bees visiting the marked branches in a 10-min period were recorded, noting their landing and take-off directions. For improved accuracy, bee-movement directions were recorded by the eight major and secondary compass points. The secondary point counts were later proportionally divided between the adjacent major points. Observations were made by one observer under light wind conditions (1 Beaufort = 3.7 km/h), and by three observers under mild wind conditions (4 Beaufort = 24.1 km/h). Each observer performed three observation periods of 10 min.

Data analysis was performed according to Sokal and Rohlf [33]. The statistical procedures are listed further below.

3. RESULTS

3.1. Mobility between adjacent rows

The number of bees that crossed to the adjacent row in 10 min (NoMob) increased significantly with the increase in BPT, which explained 50 % ($P < 0.0001$) of NoMob variance (figure 1), and increased only slightly (not significantly) with the increase in wind speed (figure 2). NoMob related to BPT and to WindVel by the multivariable regression function:

\[ \text{NoMob} = 0.418 \times \text{BPT} + 0.277 \times \text{WindVel} - 4.02 \] (4)

which explained 51.1 % ($P = 0.0001$) of NoMob variability.

The percentage of bees crossing to an adjacent row in 10 min (PrMob) was found to be hardly influenced by bee density, and was varied around an average of 41% of the bees (figure 1). However, it rose with the increase of wind velocity (figure 2), from 30 % during a light wind to 60–70 % during a strong wind of 44.5 km/h (6 Beaufort, the strongest wind during which we observed bee activity), and wind velocity explained 13 % ($P = 0.042$) of PrMob variance. PrMob related to BPT and to WindVel by the multivariable regression function:

\[ \text{PrMob} = 0.0476 \times \text{BPT} + 0.897 \times \text{WindVel} + 26.2 \] (5)

which explained 13.5 % ($P = 0.073$) of PrMob variability. A parametric transformation of PrMob $[\text{TPrMob} = \arcsin$
Figure 1. Number of honey bees crossing between parallel trees of neighbouring rows in a 10-min period (NoMob), and the corresponding percent (PrMob), as a function of bee density (BPT = bees per tree). Linear regressions are: NoMob = 0.412*BPT – 0.146, r = 0.70, P < 0.0001, n = 26; PrMob = 0.028*BPT + 38.8, r = 0.04, ns, n = 26.

Figure 2. Number of honey bees crossing between parallel trees of neighbouring rows in a 10-min period (NoMob), and the corresponding percent (PrMob), as a function of wind velocity (WindVel, in km/hr). Linear regressions are: NoMob = 0.147*WindVel + 21.6, r = 0.07, ns, n = 26; PrMob = 0.882*WindVel + 29.1, r = 0.36, P = 0.042, n = 26.
(PrMob/100)^{1/2} \ [33] related similarly to these variables ($r^2 = 0.13$, $P = 0.081$).

3.2. Preference for the upwind direction

In all measurements of honey bee mobility between adjacent trees, more bees travelled upwind than downwind (figure 3). The preference for the upwind direction (UWMP) was found to increase with the increase in WindVel, which explained 43 % ($P = 0.0007$) of UWMP variability (figure 3).

3.3. Mobility to a range greater than one row

The percentage of pollen-load carriers was maximal during pollen shedding, and dropped gradually thereafter. It reached 40–60 % on the male-blooming cultivars, and was much lower on the female bloom: during pollen shedding we recorded up to 8 % pollen-load carriers in rows adjacent to the male bloom, but in more remote rows, and at a later period, only 0–5 % of them were observed (figure 4). The best-fit function of regression of the averages of percentage of cross-pollinating bees on female bloom versus distance ('d' in rows) from the male bloom was:

$$\text{PCrBee} = 12.3/d + 0.323 \quad (6)$$

where 'd' explains 85.9 % ($P = 0.0079$) of PCrBee variability (figure 4).

3.4. Take-off and landing directions

Under light wind conditions, no differences were found among the directions of either take-offs ($P = 0.985$) or landings ($P = 0.521$) (table I). However, at a mild

![Figure 3. Honey bee preference of upwind direction (UWMP = upwind mobility preference), which is the ratio between the number of honey bees crossing to the nearest tree in the upwind direction and the corresponding number in the downwind direction, as a function of wind velocity (WindVel, in km/h). The free linear regression is: UWMP = 0.052*WindVel + 1.08, $r = 0.65$, $P = 0.0007$, $n = 23$, and the forced to [0,1] linear regression is: UWMP = 0.056*WindVel + 1.00, $r = 0.65$, $P = 0.0006$, $n = 23$.](image-url)
wind velocity (about 24 km/h), a clear difference was recorded among take-off directions ($P = 0.028$), with an even greater difference among landing directions ($P = 0.0009$). Landings were mostly directed upwind ($P = 0.0038$), whereas most of the take-offs were directed perpendicularly to the wind ($P = 0.0030$).

4. DISCUSSION

Two foraging strategies can be distinguished among social bees: fixed-course foraging ('traplining'), where the bee gathers food along a route which it returns to in subsequent flights and on subsequent days; and fixed-site-and-species foraging ('species and site constancy'), where the bee collects the food from one species in a small patch (1–3 trees or a similar field area), to which it returns in subsequent flights and on subsequent days [24, 26].

Fixed-site-and-species foraging strategy is typical of honey bees, which sophisticatedly transfer information about food sources among the individual bees [24, 26]. According to this information, 'work groups' are formed in the hive, where all the bees visit the same food source. These workers show a high level of constancy to the food location and to the flower species, and hence their mobility during foraging is limited and their efficiency as cross-pollinators is low. The information gathering is effected by 'scouts', who visit several locations and flower species during a flight [24, 26], and perform efficient cross-pollination. The proportion of scouts among the foraging bees sets the cross-pollination efficiency of the colony [18].

![Figure 4. Percentage of cross-pollinating bees on female-stage blooming trees (PCR Bee), as a function of distance (D, in rows) from the male-stage trees. Honey bees carrying pollen loads and non-loaded bees were simultaneously counted on trees in male-stage and on trees in female-stage bloom. The counts of each row were pooled to calculate the average PCR Bee per row (see Materials and methods). The best-fit function of regression of the averages to D is: PCR Bee = 12.3/D + 0.323, $r = 0.93$, $P = 0.0079$, $n = 6$.](image-url)
Our data show that the proportion of honey bee mobility to an adjacent row is not influenced by bee density (figure 1), which may be a result of zero energetic gain to the food collectors from increasing mobility of this type. Therefore, we assume that the reports about increase in bee mobility with increased bee density [4, 6, 12, 14, 30, 32, 35, 36] refer to growth in the number of bees crossing between adjacent trees, and not in their percentage. However, the percentage of short-range bee mobility seems to increase with an increase in wind velocity (equation (5), figure 2), as has been qualitatively observed previously [14, 23, 39]. This effect may result from the increase in upwind-directed movement of the bees with the increase in wind velocity (figure 3), and perhaps also from an expansion of their foraging area.

The ‘tendency to forage upwind’ [7], which we found to grow with increased wind velocity (figure 3), has been explained as the product of aerodynamic restrictions, since it is easier to take-off and land against the wind [39], or as the result of olfactory search for food [23, 39]. We found that bees tend to land against the wind (table I), but they may change their flight direction beforehand. Nevertheless, strong evidence for the olfactory explanation has been provided [38], and it appears that during foraging of either a food collector or a scout bee, food source location is aided by the sense of smell, and thus motion in the upwind direction is preferred. Another explanation is that the bees choose to forage in an upwind direction while loading, and to fly downwind back to the hive when they are full and heavy (D. Roubik, pers. comm.).

We found an average of 41% of the bees crossing between adjacent rows of avocado medium-size trees in a 10-min period. Because under good avocado-pasture conditions honey bees fill their crop in about 10 min [27], we used this figure to estimate the percentage of bees crossing between adjacent rows during foraging. Both bee-mobility rate and the upwind-direction preference grew with increasing wind velocity (figures 2 and 3), and under a wind speed of about 45 km/h the upwind mobility to the adjacent row reached 100% of the bees. This short-range mobility is higher than has been described before [1, 2, 5, 6, 8, 14, 18, 21], and may explain the high rate of both cross-pollination and fruits of cross-pollination that was found in rows adjacent to the pollen donor, and also the growth in production in these rows, compared to rows further away [2, 3, 9, 15, 20, 25, 27].

Our work indicates that the percentage of cross-pollinating bees stabilizes at about

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**Table I.** Percentages of honey bee taking-off to, and landing from various directions, at two wind speeds.

<table>
<thead>
<tr>
<th>Date</th>
<th>Wind speed</th>
<th>Wind direction</th>
<th>Honeybee activity</th>
<th>n</th>
<th>Direction of honey bee movement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N</td>
</tr>
<tr>
<td>27.4.90</td>
<td>3.7 km/h</td>
<td>East</td>
<td>take-off</td>
<td>91</td>
<td>25.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>landing</td>
<td>114</td>
<td>17.8</td>
</tr>
<tr>
<td>28.4.90</td>
<td>24 km/h</td>
<td>West</td>
<td>take-off</td>
<td>150</td>
<td>12.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>landing</td>
<td>180</td>
<td>16.9</td>
</tr>
</tbody>
</table>

Differences among the directions for each row were tested using a $X^2$ test of homogeneity (see Results).
1–2 % of the workers, at a distance of 10 to 15 rows away from the male bloom. This percentage conforms with the early assumption, that this value is about 1 % [17]. This low percentage of cross-pollinating honey bees should explain the reports of cross-pollination, and cross-pollinated fruit set, at long distances from the pollen source [9, 27, 37]. Nevertheless, a rise in the percentage of scouts among the foraging bees with an increase in competition [18] requires further study. The division of labour between food and information gatherers may be flexible, and, under increased-competition conditions, food collecting honey bees may switch to information gathering. Under such circumstances, an increase in cross-pollination efficiency of the honey bee population is expected.

An inconsistency was encountered with regard to the short-range bee mobility. Direct counts of bees resulted in an average of 40 % of the bees crossing to an adjacent row (figure 1), whereas counts of pollen-load carriers led to only 14 % cross-pollinating bees in the first female-blooming row (figure 4). This difference may stem from a low tendency of the bees that collect pollen and nectar on the male bloom, to cross to the female bloom, which carries nectar only.

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tendance aussi s’est accrue avec la vitesse du vent (figure 3). Ainsi, par vent fort, près de 100 % des abeilles ont volé contre le vent d’une rangée à une autre adjacente en l’espace de dix minutes. Par vent faible, aucune différence n’a été trouvée entre les directions d’envol et d’atterrissage ; mais avec un vent de 24 km/h, les atterrissages se sont faits le plus souvent contre le vent, alors que la plupart des mouvements d’envol étaient perpendiculaires à la direction du vent (tableau I). La mobilité sur une distance supérieure à une rangée s’est effectuée au-dessus de la canopée, apparemment comme une recherche d’autres sources de nourriture. Le pourcentage d’abeilles effectuant une pollinisation croisée à la suite de cette mobilité a diminué selon une courbe hyperbole quand la distance à la source de pollen augmentait, pour s’approcher de 1 à 2 % à la distance de dix à quinze rangées (figure 4). La plupart des butineuses ont fait preuve d’un niveau élevé de constance florale, à la fois à l’espèce de fleur et au lieu de nourriture. Leur mobilité au cours du butinage est donc limitée et leur efficacité en tant qu’agents de la pollinisation croisée est faible. Seules les éclaireuses, qui récoltent à la fois de la nourriture et de l’information, présentent une mobilité élevée et accomplissent avec efficacité la pollinisation croisée. Mais, comme elles ne représentent que 1 à 2 % des butineuses, on peut dire que l’efficacité des abeilles dans la pollinisation croisée de l’avocatier est faible. © Inra/DIB/AGIB/Elsevier, Paris

Avocat / Persea americana / pollinisation croisée / efficacité pollinisatrice / butinage / vitesse vent


REFERENCES


