Selection and Breeding of Honey Bees for Higher or Lower Collection of Avocado Nectar

OHAD AFIK,[1,2] ARNON DAG,[3] YELENA YESELSON,[4] ARTHUR SCHAFFER,[4] AND SHARONI SHAFIR[1]

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ABSTRACT Intensive activity of honey bees, *Apis mellifera* L., is essential for high fruit set in avocado, *Persea americana* Mill., orchards, but even when hives are located inside the orchard, many bees still search for alternative blooms. We tested for a possible genetic component for a preference of avocado bloom relative to competing bloom. The honey from each hive was extracted at the end of the avocado bloom and the concentration of perseitol, a carbohydrate that is unique to avocado, was analyzed as a measure for avocado foraging. During the first year, five bee strains were compared in three different sites in Israel. Significant differences were found between strains in honey perseitol concentrations, suggesting differences in their efficiency as avocado pollinators, although these differences were site dependent. At two sites, colonies with the highest and lowest perseitol concentrations were selected as parental "high" and "low" lines. Queens were raised from the selected colonies and were instrumentally inseminated by drones from other colonies of this line. During the second and third years, colonies with inseminated queens were introduced to the avocado orchards, together with the selected colonies still surviving from the previous year. Colonies of the high line had greater perseitol concentrations than those of the low line. Selected colonies that survived from the previous year performed consistently vis-à-vis perseitol concentration, in the second year of testing. Heritability value of 0.22 was estimated based on regression of offspring on midparent. The results reveal a heritable component for willingness of honey bees to collect avocado nectar.

KEY WORDS *Apis mellifera*, *Persea americana*, perseitol, pollination

The European honey bee, *Apis mellifera* L., is the most important agricultural pollinator in the developed world. The list of crops that depend on honey bee pollination for commercial yield includes many crops for which honey bees are not natural pollinators (Delaplane and Mayer 2000, Morse and Calderone 2000, Klein et al. 2007). These crops may not be well adapted for pollination by honey bees, a situation that may reduce pollination efficiency. Practices to improve bee pollination under such circumstances include removing competing bloom (Delaplane and Mayer 2000), sequential introduction of bees (Stern et al. 2007), or using alternative pollinators (Velthuis and van Doorn 2006).

One solution that is rarely used is selection of honey bee lines that are better fitted for the pollination of the target crop (Mackensen and Nye 1966, Shimanuki et al. 1967, Gary and Witherell 1977, Dag et al. 2005, Basualdo et al. 2007). For the crops in these studies pollen foragers were the efficient pollinators. The index for colony selection was the percentage of pollen collected from a target crop, estimated by placing a pollen trap at the hive entrance and visually inspecting the pollen pellets in the trap. However, some crops are pollinated mainly by nectar collecting bees. Identifying the nectar sources of the colony is more difficult than identifying pollen sources; therefore, selection for preference of a specific nectar source was never tested before.

Avocado, *Persea americana* Mill., is one example for a crop that is not well adapted for pollination by honey bees but depends on their pollination in modern agriculture (Gazit and Degani 2002). Bees that collect nectar are its main pollinators, because they visit both male and female flowers, whereas pollen foragers visit only male flowers (Ish-Am and Eisikowitch 1993). The need for bee pollination to set fruit is evident, but honey bees tend to prefer competing bloom (Vithanage 1990, Ish-Am and Eisikowitch 1998, Afik et al. 2006a), probably due to the high mineral content of the avocado nectar (Afik et al. 2006b).

Previous work suggested that there is a genetic component to the tendency of honey bees to forage on avocado flowers (Dag et al. 2003; Afik et al. 2006b, 2007, 2008). These findings are based on differences

[1] B. Triwaks Bee Research Center, Department of Entomology, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot 76100, Israel.

[2] Current address: Department of Entomology, University of Georgia, Athens, GA 30602 (e-mail: afikohad@uga.edu).

[3] Institute of Horticulture, Agricultural Research Organization, Ministry of Agriculture and Rural Development, Gilat Research Station M.P., Negev 85280, Israel.

[4] Department of Vegetable Crops, Volcani Center, Ministry of Agriculture and Rural Development, Bet Dagan 50250, Israel.

between bee strains in gathering avocado nectar and on the repeatability of this behavior in the same colonies during consecutive years. Avocado nectar and honey contain perseitol, a unique carbohydrate (Ish-Am 1994, Liu et al. 1995). Therefore, the tendency of a colony to forage on avocado flowers can be assessed by analyzing the perseitol content of the honey that the colony produces (Dag et al. 2003).

Based on these early findings, the purpose of this study was to test whether we could select for greater or lesser avocado foraging. That is, we wanted to evaluate the possibility of establishing a bee breeding program for avocado pollination. For two generations, we performed artificial inseminations of virgin queens from selected colonies with semen of drones from selected colonies to establish bee lines with different preference, high or low, for avocado bloom.

Materials and Methods

Site Description. The experiments were conducted in three sites in Israel. Two sites (S) were in the coastal plain: S1,'HaMa'apil' (32°2′ N, 35°0′ E), an ≈100-ha orchard and S2, 'Negba' (31°4′ N, 34°4′ E), ≈50 ha. One site was in the north: N1, 'Dan' (33°1′ N, 35°4′ E), ≈45 ha. Experiments were conducted in the three sites during 2003 and repeated the following years only in sites S1 and S2. The main avocado varieties in these orchards were 'Hass', 'Ettinger', 'Pinkerton', and 'Fuerte'.

Colony Management. Mated and inseminated honey bee queens were introduced into queenless colonies from September to November of each year. Queens were color marked on the thorax and one wing was clipped, to ensure that only colonies with an introduced queen from a known genetic source were tested. Colonies were kept in an area that was remote (>3 km) from avocado orchards to avoid any possible early conditioning of the foragers to avocado blooms. In early April, at the beginning of the simultaneous avocado and the competing citrus bloom, the colonies were introduced into the orchards. Considering the mild Israeli winter, where foraging never completely ceases, it is assumed that by the time the colonies were introduced into the avocado orchards their population was replaced by daughters of the new queens. After placing the colonies in the orchards a second super was added above a queen excluder. If colonies were too weak to populate a second super, empty marked frames were added into the nest super. Honey frames were collected at the end of April each year, after the citrus and most early avocado cultivars had finished blooming. Honey was extracted from each hive separately and a sample of ≈0.5 kg was kept from each colony for high-performance liquid chromatography analysis of perseitol concentration (for details, see Dvash et al. 2002).

First Generation (P): 2003. Colonies were introduced into sites S1, S2, and N1 (N = 53, 51, and 48, respectively). To increase the potential for genetic-based differences between colonies we used colonies belonging to five different genetic strains: 1) Italian—from a local strain based on *Apis mellifera ligustica* from the Zriffin National Apiary breeding program; 2) Buckfast—from a local breeding program of Buckfast bees; 3) New World Carniolan (NWC)—from Kona Queen Co. in Hawaii (Cobey and Lawrence 1988); 4) Caucasian—daughters of an *Apis mellifera caucasica* mother freely mated with local drones (most probably Italians); and 5) Mellifera—daughters of an *Apis mellifera mellifera* mother freely mated with local drones (most probably Italians). Colonies belonging to all five strains were introduced into sites S1 and N1 and only four strains (excluding the Mellifera) were used in site S2. Between six and 13 colonies from each strain were tested in each site.

Colonies with outstanding high (H) or low (L) honey perseitol levels from sites S1 (1) and S2 (2) were divided into four different parent (P) lines: H1, H2, L1, and L2. Ten colonies were selected for each line without regard to strain. They were kept to test them again the following year. Only colonies that did not replace the original queen were tested for the second year.

Second Generation (F1): 2004. Four colonies from each P line were used as parent colonies for the next generation (F1) queens and drones. Daughter virgin queens (F1) were each instrumentally inseminated with 10 μl of semen from ≈10 drones (brothers) from a different colony belonging to the same parent line, to create four corresponding F1 lines.

The F1 colonies were introduced into sites S1 and S2 (N = 34 and 41, respectively). Colonies were placed in the same site in which their parents had been the previous season. In addition, eight (site S1) and six (site S2) surviving selected colonies from the previous year (P generation) also were introduced into the same sites. At the end of the season, the colonies were tested for their honey perseitol level.

Third Generation (F2): 2005. Colonies (N = 3–5) from each F1 line were selected as parent colonies to create the four corresponding lines of the F2 generation. These were selected according to their performance in relation to their line of selection (i.e., colonies with high perseitol level belonging to a low line or vice versa were not selected). To reduce the risk of inbreeding, we inseminated virgin queens with semen of drones from nonsibling colonies, under the limitations of colony performance, survivorship and the presence of young larvae and drones. The F2 colonies were introduced into sites S1 and S2 (21 and 12, respectively). In addition, 13 (site S1) and seven (site S2) surviving F1 colonies, in which the inseminated queens were still present, also were introduced into the same sites. At the end of the season, the colonies were tested for their honey perseitol level.

Data Analyses. Significance of differences in concentrations of honey perseitol during the first year was tested by two-way analysis of variance (ANOVA) including the experimental site, the bee strain, and their interaction. Differences between bee strains within each site were tested by Tukey–Kramer test. The re-

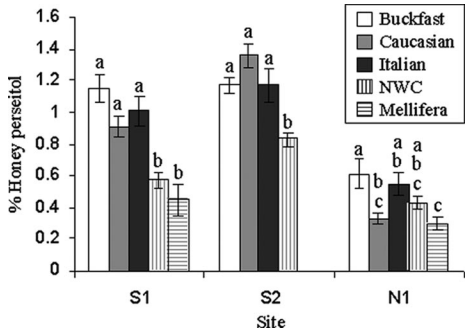

Fig. 1. Mean ± SE perseitol concentration in honey extracted from colonies from five different bee strains during the first year of the experiment (2003). Colonies were placed in three different avocado orchards in Israel during the avocado blooming season. Different letters above columns indicate significant differences ($P < 0.05$; Tukey-Kramer test) between strains in each site.

sults of the second and third years were tested by three-way ANOVA including the experimental site, line of selection ("high" or "low"), queen generation and all the interactions between these factors. ANOVA requirements were tested before each analysis. The arcsine square-root transformation was employed on the 2005 data before analysis (Sokal and Rohlf 1995), and then a normal distribution was achieved. Statistical analyses were performed using JMP 8.0 software (SAS Institute, Cary, NC).

Results

First Generation (P): 2003. Perseitol content in the honey samples ranged from 0 to 1.9% of the total sugar content. The perseitol concentration was affected significantly by both site (Fig. 1; $F = 70.1$; df = 2, 151; $P < 0.0001$) and bee strain ($F = 14.6$; df = 4, 151; $P < 0.0001$). The site × strain interaction was significant ($F = 5.8$; df = 6, 134; $P < 0.0001$) after excluding the Mellifera strain from the statistic model, due to its absence in site S2. All strains had the highest perseitol concentrations in site S2 and the lowest in site N1. The differences between strains were similar in sites S1 and S2, where the NWC and the Mellifera (in site S1) strains had significantly lower perseitol level than the other strains ($P < 0.05$; Tukey–Kramer test). In site N1, the Caucasian and the Mellifera strains had the lowest perseitol concentration, which was significantly lower than that of the Buckfast strain ($P < 0.05$; Tukey–Kramer test). The strains of the colonies from sites S1 and S2 that were selected as parents for the F1 generation are detailed in Table 1.

Second Generation (F1): 2004. Colonies selected for high perseitol concentration had significantly higher perseitol in their honey than colonies selected for low perseitol (Fig. 2; $F = 13.7$; df = 1, 88; $P < 0.001$). The generation effect was not significant ($F = 0.04$; df = 1, 88; $P > 0.05$), indicating that the performance of the F1 colonies was similar to that of the surviving selected colonies from the P generation that were tested for a second year. No site effect was found ($F = 0.5$; df = 1, 88; $P > 0.05$), and none of the interactions were significant.

Table 1. Number of colonies belonging to each strain that were used as parent colonies for each of the F1 lines

Line[a]	Buckfast	Caucasian	Italian	Mellifera	NWC
H1	2	2			
H2		3	1		
L1	1	1		1	1
L2			3		1

H, lines selected for high perseitol content; L, lines selected for low perseitol content. 1 and 2, selection site (S1 and S2).

Third Generation (F2): 2005. The general pattern of the 2005 results was similar to that of 2004. Colonies selected for high perseitol concentration had significantly higher perseitol in their honey than colonies selected for low perseitol (Fig. 3; $F = 5.2$; df = 1, 52; $P = 0.03$). The generation effect was not significant ($F = 0.6$; df = 1, 52; $P > 0.05$), indicating that the performance of the F2 colonies was similar to that of the surviving selected colonies from the F1 generation that were tested for a second year. No site effect was found ($F = 0.3$; df = 1, 52; $P > 0.05$) and none of the interactions were significant.

The regression of offspring on midparent was used to estimate the heritability of avocado nectar collecting behavior. A family was designated as the offspring of all matings that involved drones that were brothers and queens that were sisters (Collins 1986). Only families with more than two surviving offspring colonies were included in the regression. The overall estimate of heritability is 0.22 ± 0.07 ($t = 3.07$; df = 1, 13; $P = 0.01$) when both generations are taken together in the same regression (Fig. 4). However, there are differences in the estimated heritability between the two generations. The regression of F1 on P generation yield h^2 value of 0.45 ± 0.07 ($t = 6.81$; df = 1, 7; $P < 0.001$), whereas the regression of F2 on F1 yield h^2 value of 0.09 ± 0.09 ($t = 1.02$; df = 1, 5; $P > 0.05$), which is not significantly different from zero.

Discussion

Honey bee strains differ in various characteristics (Dietz 1992) that may affect their foraging behavior. However, only limited knowledge exists concerning actual differences in foraging behavior in the field and the efficiency of various strains in pollinating specific crops (Free and Williams 1973, Basualdo et al. 2000), and this is usually restricted to pollen foraging. The current study, in accordance with previous findings (Dag et al. 2003, Afik et al. 2007), demonstrates differences between bee strains in their foraging activity for nectar on avocado flowers. Moreover, we were able to show that this preference for a specific nectar source is heritable and can be manipulated by controlled genetic selection. However, it still remains to be shown empirically that there is in fact a correlation between honey perseitol concentration in a colony, our criteria to estimate the tendency of a colony to

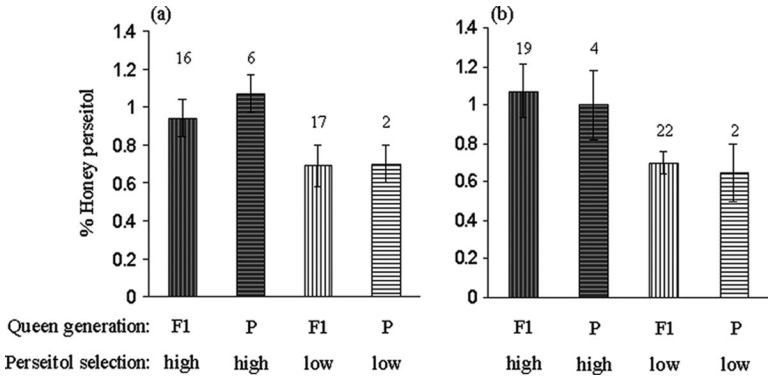

Fig. 2. Mean ± SE perseitol concentration in honey during the second year of the experiment (2004). Colonies were placed in two avocado orchards in Israel: site S1 (a) and site S2 (b), during the avocado blooming season. P queens headed colonies with outstanding perseitol levels in the previous year and survived for a second year of the experiment. Numbers above columns indicate number of colonies of each line.

forage for avocado nectar, and the contribution of that colony to subsequent fruit yield.

Honey perseitol concentrations were up to twice as high in some bee strains relative to others, suggesting that a greater proportion of foragers in these strains collected nectar from avocado (Fig. 1). Because honey bees did not evolve with avocado, any strain-specific differences in preference to avocado are probably the result of differences between the various strains in natural or artificial selection pressures on attributes that are not directly related to avocado. There was also a significant interaction between strain and site, indicating that environmental conditions affect the foraging behavior of different strains differently. This site-dependent behavior may explain why the NWC strain, which was suggested to be better for avocado pollination than the Italian strain in studies conducted in northern Israel and in California (Dag et al. 2003, Afik et al. 2007), was found to store nectar with less perseitol than other strains in the current study, in avocado orchards along the Israeli coastal plain. The only site in which perseitol concentration of NWC colonies was not lower than that of other strains was the northern site that had also been tested in the previous study. The lack of higher avocado fidelity of the NWC bees in this site in the current study may be due to environmental changes in this site during the last few years. A similar interaction between site and strain concerning foraging behavior was also found by Kreitlow and Tarpy (2006), although they did not find significant interactions for any other traits of the bees. The significance of this interaction is that any comparison between bee strains in their efficiency in pollinating a specific crop should also consider the specific environment.

Our selection process of high and low avocado bee lines included hybridization between different strains, to take advantage of the most extreme colonies. This hybridization also enabled us to increase genetic variability in each line, which is important to avoid inbreeding. The selected lines differed in their honey perseitol concentration during the first generation (F1), demonstrating the feasibility of selecting bee lines with improved performance in pollinating a specific crop. The high lines had, on average, 1.4 times higher honey perseitol concentration than the low

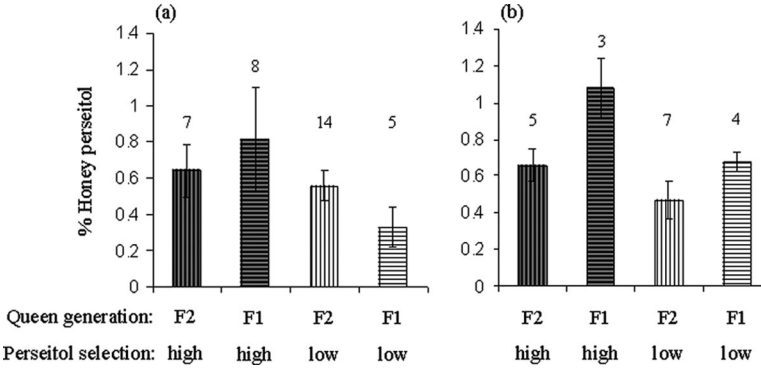

Fig. 3. Mean ± SE perseitol concentration in honey during the third year of the experiment (2005). Colonies were placed in two avocado orchards in Israel: site S1 (a) and site S2 (b), during the avocado blooming season. F1 queens are inseminated queens from the previous year that survived for a second year of the experiment. Numbers above columns indicate number of colonies of each line.

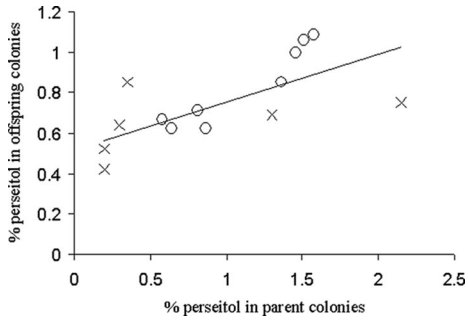

Fig. 4. Regression of offspring average perseitol concentration on midparent results. "O" represents the results of F1 generation on P generation, and "X" represents results of F2 generation on F1 generation.

lines (Fig. 2). Because avocado suffers from insufficient pollination (Gazit and Degani 2002), our results imply that bees from high colonies had higher preference for avocado flowers and may contribute more to fruit set. Our results show a difference between lines in the relative foraging from avocado compared with competing sources among the nectar foragers, which is what our study was designed to test. To achieve lines that forage more from avocado in absolute terms, future efforts would have to combine selection for both an affinity for avocado and for higher honey yields, a trait that can be improved by selection (Kulincevic 1986).

The current study did not include a control average bee line. We have previously shown that colonies with extremely high perseitol concentrations tended to repeat this behavior the following year, whereas colonies with extremely low perseitol concentrations did not differ from the average during the following year (Dag et al. 2003). This phenomenon reflects the greater difficulty in reducing the level of a trait that is already relatively low (Hellmich et al. 1985). Thus, we assume that the performance of the low line would be similar to that of unselected colonies, and that the high selected line is in fact better than average. When comparing the selected F1 high lines with selected colonies from the P generation that survived for a second year, we find that the selection process allowed us to keep a similarly high level of avocado foraging, but we were unable to increase this level to above ≈1% perseitol concentration in the honey (Fig. 2). Because we had previously measured average honey perseitol concentrations of up to ≈2% (Dag et al. 2003) and perseitol concentration in nectar may reach 5% (Ish-Am 1994, Liu et al. 1995), we believe that the trait of avocado foraging may still be improved by means of selection.

We failed to achieve an additional increase in the second generation (F2) of selection (Fig. 3). Our work exemplifies some common problems involved in such a selection program. First, the interaction that was found between site and bee strain indicates that the performance of the selected lines might be limited to specific environmental conditions. These conditions may differ between years even in the same site. In site S1, a nearby citrus orchard was cut and replanted with avocado seedlings between the second and third year of our study. This decreased the bloom that competed with avocado. It did not, however, affect the performance of the surviving F1 colonies. Their perseitol concentrations in 2005 (Fig. 3) were similar to those in 2004 (Fig. 2). Therefore, it seems that the main reason for the decreased differences between the F2 lines, in comparison with the F1 lines, is the effectiveness of our selection process. Second, a whole year elapsed from the insemination of the F1 queens until they were used as parent colonies for the F2 queens and many F1 queens did not survive, a problem that was also reported from another selection program (Gordon et al. 1995). Third, surviving colonies often were too weak to produce drones and sometimes we even failed to raise queen larvae from these colonies. As a result the colonies that were selected as parent colonies, mainly as drone sources, were often not those with the most extreme perseitol concentrations and the potential difference between the high and low lines was not as large as it could have been.

Despite these limitations, the average estimated heritability for avocado nectar foraging in our study was similar to that of pollen hoarding from sunflowers (Basualdo et al. 2007). Such values suggest a potential for selection of honey bees for foraging on specific crops. Heritability estimates are affected by the environment in which they are tested (Collins 1986). The difference in heritability between the 2 yr of our study may reflect environmental variability between years, which may be especially pertinent in a field assay such as ours.

The current study demonstrates for the first time the feasibility of selecting bee lines for the pollination of a specific crop based on nectar foraging behavior. Further research is needed to evaluate the specific behavioral traits that were selected for. A deeper understanding of these traits would enable us to develop more efficient selection processes, to estimate the limitations of selection in improving pollination, and to determine whether the selected bee lines may be appropriate for pollination of other specific crops as well. Selection programs of specialized lines may yet prove to be an efficient tool in pollination management.

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