Grooming behavior by *Apis mellifera* L. in the presence of *Acarapis woodi* (Rennie) *(Acari: Tarsonemidae)*

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Abstract – The role of grooming behavior by the honey bee, *Apis mellifera* L., in limiting the infestation of, or being elicited by, the parasitic mite *Acarapis woodi* was investigated. Grooming behaviors examined included allogrooming and the grooming dance that involves self or autogrooming. Observation hives monitored over 24 h revealed that dancing increased significantly at night while allogrooming decreased. In 32 mite-infested observation hives the percentage of bees infested was positively correlated with allogrooming acts and dances observed. In a third experiment, young marked bees were introduced into three hives with 0, 50 and 70 % tracheal mite prevalence and grooming dances increased significantly in the bees 1-3 d of age in the mite-infested colonies. We postulate that mite movement on young bees elicits the grooming dance. Bees from four different single patrilines that had exhibited different propensities to allogroom or dance were marked and placed into eight mite-infested colonies for 5 d. Dissections of marked bees revealed that the allogrooming line was most susceptible and the dancing line least susceptible to mite infestation. We postulate that the dancing line of bees had a lower threshold for detecting mites on their body resulting in increased dance behavior and autogrooming, which we propose lowered the number of mites that transferred to these bees. This is the first evidence for a mechanism of resistance to the honey bee tracheal mite. © Inra/DIB/AGIB/Elsevier, Paris

*Apis mellifera / Acarapis woodi / grooming / behavior*

1. INTRODUCTION

A colony of honey bees, *Apis mellifera* L., plays host to a variety of organisms from large vertebrate pests such as mice to small obligate parasites [1]. One such obligate parasite of adult bees is the tracheal mite, *Acarapis woodi* (Rennie) [4, 22]. All mite life stages occur within the tracheal system of adult bees and only mated females

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migrate to new host bees [10]. Mites appear to be unable to move off the host onto comb or other structures and then regain access to a bee; no live mites have been found in close inspection of combs from mite-infested colonies; ([15]; Pettis pers. obs.). Mite movement would thus be confined to adult bees. Dispersing females preferentially infest adult bees less than 3 d of age [7, 13], and locate these bees in part by attraction to host cuticular hydrocarbons [21]. Additionally, tracheal mites disperse more at night, or are more successful, compared to daytime dispersal [20].

Bees have been shown to exhibit phenotypic and genotypic differences in the number of mites they acquire when compared to other young bees in the same environment [6, 17]. Two broad mechanisms are possible explanations for the observed differences in mite levels between bees in a common environment: 1) behavioral differences between the bees or the mites toward the bees (e.g. induced by chemical cues), and 2) morphological differences between bees. Physiological differences between bees would likely influence the mite’s success once inside the host. Mite behavior is difficult to observe without placing the subjects in extremely unnatural conditions. However, the host bee is quite easily observed within a glass-walled observation hive. Morphological differences have been proposed and examined in the past with no differences demonstrated [10, 13].

Grooming behavior is a common means of reducing ectoparasites in many organisms. Honey bees have been shown to detect and groom another parasitic mite, Varroa jacobsoni Oudemans from their bodies [3, 19]. A grooming dance by A. mellifera was first described by Haydak [8, 9] and further examined by Milum [14]. Allogrooming normally involves a dancing bee and a bee that responds to the dance by grooming the dancer [8, 14]. Dancing bees will autogroom with their mesothorasic legs in addition to being allogroomed. More recent studies have demonstrated that allogrooming [5, 12] is in part genetically determined. Nothing is known as to the age at which bees perform these behaviors. Particular genotypes are more likely to allogroom given some unknown level of stimuli within a colony. Allogrooming occurs primarily on the thorax and especially around the wing bases [2] where tracheal mites are found during dispersal [23]. Tracheal mite dispersal success increases at night [20] and perhaps grooming behavior may vary day–night if involved in resistance to this parasite.

No factors have been demonstrated which elicit the grooming dance and nothing is known about the age at which bees allogroom or dance. Additionally, no benefits from allogrooming have been demonstrated, except with regard to the exotic parasite Varroa [19]. In the present studies we examined:

1. the frequency of allogrooming and dancing on a day–night basis;
2. the relationship between mite levels and grooming behavior;
3. the frequency and age of worker bees performing allogrooming and dancing in tracheal mite-infested and uninfested colonies;
4. the success of tracheal mite dispersal to selected high and low grooming lines of bees to examine the role of grooming behavior in limiting mite dispersal.

2. MATERIALS AND METHODS

2.1. Experiment I

Four observation hives were used to examine the frequency of grooming behavior in honey bee colonies on a day–night basis. Four observation hives, each consisting of one comb 20.3 x 42.5 cm and the second comb 11.4 x 42.5 cm, were established at Texas A&M University, College Station, TX on 15 April 1991 and allowed 2 weeks to become established
prior to observations. Ten days of observations were performed beginning on 29 April and every third day thereafter until 27 May 1991. Hives were observed six times over a 24-h period at 0400, 0800, 1200, 1600, 2000 and 2400 hours for the number of solitary worker bees performing the grooming dance and the number of allogrooming pairs. Observations consisted of scanning one side of each hive in succession, with five scans made per hive per time interval (scan time = ca 1 min/hive). Scans on the same hive were separated by more than 5 min. Adult bee populations were estimated on 26 May 1992 after sundown by averaging the bee counts of 20 randomly selected 5 × 5-cm squares, and multiplying that mean by the total number of squares present. Following the observations a 30-bee sample was collected from each hive, dissected, and tracheal mite prevalence determined.

Data on the number of bees dancing or allogrooming over 24 h were analysed by ANOVA for potential differences in time of day when the behaviors occurred, and if differences were found then means were separated using a Fisher’s LSD test [25].

2.2. Experiment II

Thirty-two hives were used to examine grooming behavior in honey bees with varying tracheal mite prevalence. Observation hives were established in sets of four from overwintered colonies and allowed 7–10 d to become established. Observations consisted of a scan of each side of the hive (scan time = 3.02 ± 0.32 min X ± SD/hive) at 1000 and 1400 hours over a 3-d period for the number of bees performing the grooming dance or allogrooming. Following the observations a 20-bee sample was collected and later dissected to determine mite prevalence. Thus, observations on grooming behavior were conducted blind with regard to mite prevalence. Thirty-two hives were observed from May-August 1992 at Simon Fraser University, Burnaby, BC, Canada.

The relationships of mite prevalence were tested by correlation with the number of allogrooming events and grooming dances [25]. All counts were log transformed to normalize the data. To determine if grooming behavior varied with time of day or over the 3-d period, data were analysed by ANOVA with repeated measures [25].

2.3. Experiment III

Marked worker bees were monitored from emergence to 19 d of age to examine age related grooming behavior in colonies with varying tracheal mite prevalence. Three observation hives were established with tracheal mite prevalences of 0, 50 and 70 % of workers infested. Two of the hives were established on 15 September 1992 and 1000 newly emerged workers from a single source (colony headed by an open-mated queen) were paint marked and 500 released into each hive on 1–2 October 1992. The third hive with 70 % mite prevalence differed in that 2000 newly emerged bees were marked and introduced and the bees originated from each of four distinct patriline (500 bees/patriline). The four patriline colonies were selected during a pilot study in which a pool of colonies was screened for grooming behavior. Colonies were headed by unrelated queens that had been instrumentally inseminated with semen from a single unrelated drone [18]. Sealed brood combs were removed from each of the four patriline colonies and newly emerged bees were marked on the abdomen with a distinct paint color (Aerogloss, Pactra, Medina, OH) by patriline (500/line) and were 0–16 h old when placed into a single four-frame observation hive on 27 August 1992.

Daily observations were conducted between 1000 and 1200 hours and consisted of five 3-min scans per hive over 19 d, with the number of marked or unmarked bees dancing, allogrooming, or being groomed recorded. Scans were separated by greater than 15 min to avoid repeatedly counting individuals. Total number of marked bees surviving on days 5 and 19 was determined by counting all marked bees in the evening when foraging had ceased. Adult bee populations were estimated on day 19 by counting 20 randomly selected 5 × 5-cm squares and multiplying that mean by the total number of squares present.

Tracheal mite levels were confirmed by dissecting 30 bees from each hive, and external examinations were made for the two external Acarapis species. The observer of grooming behavior was unaware of the tracheal mite prevalence in each colony and thus observations were made blind with respect to mite prevalence. The number of marked bees surviving in the three colonies at days 5 and 19 was compared using the LIFEREG procedure in SAS [24, 25]. The number of marked bees dancing,
allogrooming or being groomed were compared between the first two hives over 19 d to determine if grooming behaviors differed by mite prevalence using a Wilcoxon Rank Sum test [25]. The number of unmarked bees (bees of unknown age) dancing and allogrooming were compared between the two hives to evaluate background grooming levels (Wilcoxon Rank Sum test, [25]).

In the colony containing four patrilines, data on dancing, allogrooming or being groomed were analysed by a Chi-square goodness of fit test by patriline against the null hypothesis that each patriline should perform 25 % of each behavior. To examine potential differences in age of task performance, the total number of occurrences was divided by the 19 d of observation to yield an expected value for each day. The observed values was grouped from days 1–5, 6–10, 11–15 and 17–19 (no observations made on day 16) and then compared to expected values using a Chi-square goodness of fit test [25].

2.4. Experiment IV

Workers from four selected lines of bees, which had exhibited varying levels of grooming behavior in experiment III, were introduced into mite-infested colonies to examine the role of grooming behavior in limiting mite dispersal to young bees. The four colonies represented: 1) high grooming dance behavior (HD), 2) high allogrooming behavior (HG), and 3) two colonies that were intermediate for both traits (I1 and I2). The term 'high' refers to an increased likelihood of performing either dancing or allogrooming in a given environment.

Groups of 50 bees per patriline were marked and placed together into each of the four parent colonies and four unselected colonies. Brood combs from each of the four single patrilines were held overnight in an incubator at 35 ± 2 °C and the following day bees were paint marked by patriline and were 0–16 h old when placed into colonies. All eight colonies were infested with tracheal mites. Marked bees were recovered from the colonies after 5 d, frozen, and later dissected to determine mite levels. Data were analysed by a Chi-square goodness of fit test against the null hypothesis that bees from the four lines should become equally infested and to determine if recovery rates for each patriline were equal [25].

3. RESULTS

3.1. Experiment I

Grooming behaviors varied by time of day within the hive. Grooming dances increased significantly from midnight to 0800 hours compared to daytime levels (figure 1, F = 2.70, 5 df, P = 0.02). In contrast, allogrooming decreased significantly at night (figure 1, F = 3.91, 5 df, P = 0.002). Adult bee populations were estimated to be 3 150, 4 500, 2 080 and 2 200, and tracheal mite prevalence was 80, 07, 05 and 66 % for hives 1–4, respectively.

3.2. Experiment II

There were significant positive correlations between mite prevalence and allogrooming (r = 0.27, P < 0.002, n = 32), and the number of dances observed (r = 0.52, P < 0.001, n = 32) (figure 2). There was a wide range in the number of allogrooming acts (25–275) and dances (10–75) observed. Additionally, mite prevalence in the colonies varied from 10–80 %. Acarapis dorsalis Morgenthaler was present in 13 of 32 colonies with mite prevalence within colonies ranging from 10–50 %. There were no differences in grooming behaviors based on time of observation, morning versus afternoon (F = 0.66, 1 df, P = 0.42). Additionally, no significant differences in grooming behavior were found over the 3 d of observation (F = 1.69, 2 df, P = 0.15).

3.3. Experiment III

The three observation hives had tracheal mite prevalences of 0, 50 and 70 %, and had A. dorsalis prevalences of 20, 10 and 20 %, respectively. No A. externus Morgenthaler were found. No differences in marked bee survival were detected be-
tween colonies #1 and #2 ($P > 0.05$) nor between the survival of the four patrilines within colony #3. The total number of unmarked bees (unknown ages) dancing or allogrooming did not differ between colonies #1 and #2 ($P > 0.05$) nor did unmarked bees increase their dancing behavior over days 1–3. The average number of unmarked workers dancing in the two colonies was very consistent at 41.8 ± 8.7 and 41.4 ± 6.4 (mean ± SD) dances per day for hives #1 and #2, respectively. In contrast, the frequency of dancing by marked bees of known age varied with mite levels and age (figure 3), with more dancing occurring in the first 3 d of a bee’s life in the tracheal mite-infested colony. The marked bees in the colony without tracheal mites did not exhibit increased dancing in the first 3 d (figure 3). Total dancing by marked bees over the 19 d period did not differ between the two hives (figure 3, $P > 0.05$). The average number of marked bees allogrooming and the likelihood of being groomed increased significantly in the colony with tracheal mites (figure 3, $P = 0.04$).

In colony #3 containing the four patrilines, workers showed age-related biases for dancing, allogrooming and being groomed (figure 4, similar to patterns in colonies 1 and 2 in figure 3). Dancing was most pronounced when workers were 1–5 d of age, with 56% of all dancing occurring during the first 5 d (expected 26%). Workers 5–15 d of age were most likely to allogroom or be groomed.

Figure 1. Frequency (mean ± SD) of allogrooming and dancing from four observation hives over a 24-h period. Data for each time interval are from 40 1-min scans (1 scan/hive observed over 10 d of observation, College Station, TX, May 1991). Symbols followed by the same letter are not significantly different between hours for each behavior (ANOVA, Fisher’s LSD test $P < 0.05$).
Greater than 90% of allogrooming and 76% of workers being groomed occurred when workers were between 5 and 15 days of age (expected value of 53% for days 5–15).

Dancing and allogrooming varied significantly by patriline but the likelihood of being groomed did not differ between the four patrilines (Figure 4). The patriline named HD (high dancing) accounted for 48% of all dances ($X^2 = 25.06, 3$ df, $P < 0.001$) while the HG (high grooming) line accounted for 64% of the total allogrooming ($X^2 = 80.1,$...
The likelihood of being groomed did not differ significantly between the four patrilines ($X^2 = 2.09, 3\, df, P > 0.05$).

**3.4. Experiment IV**

Marked bees from the four patrilines exhibited varying mite levels after 5 d of exposure in eight mite-infested colonies (table I). The null hypothesis was that each of the four lines of bees would acquire 25% of the available mites. The high dancing patriline, HD, acquired significantly fewer mites than expected and the high allo-grooming, HG, acquired more mites than expected (figure 5). Recovery rates of marked bees were not significantly different.
Figure 4. Percentage and total number per day of marked bees from four patrilines observed dancing, grooming, or being groomed over their first 19 d as adult bees. Observations consisted of five 2-min scans per day in October 1992, Burnaby, BC. ** Indicates significant differences from expected values of 25 % for each patriline (Chi-square goodness of fit test $P < 0.001$).

Figure 5. Percentage of mites acquired by four lines of bees introduced into eight colonies of honey bees infested with tracheal mites. *, ** Indicate significant differences from expected values of 25 % per patriline $P < 0.05$ and $P < 0.01$, respectively (Chi-square, 3 df).
between patrilines. Mite prevalence in the eight host colonies ranged from 40 to 100% (table I). The number of mites that transferred in the eight colonies ranged from 99 to 363.

4. DISCUSSION

The performance of allogrooming and the grooming dance by worker honey bees varied significantly with time of day, worker age and genotype. We propose that grooming behavior in honey bees is both elicited by, and has an impact upon, tracheal mites as they disperse to young bees. Our findings, that young bees 1–3 d of age increased their dancing behavior in the presence of tracheal mites, is strong indirect evidence of a factor which induces the grooming dance. Additionally, young worker bees that demonstrated high dancing behavior also acquired the lowest number of tracheal mites compared to three other patrilines. We postulate that these bees had a lower dance threshold which was elicited by mite presence on their bodies and that they danced and auto-groomed, thus reducing successful mite transfer into the tracheal tubes.

Day–night variation in both allogrooming and dancing was observed. The increased dancing at night can be associated with increased tracheal mite transfers at night [20] as colonies in the current studies were mite infested. The reduction in allogrooming at night may be in association with the overall decrease in worker activity that occurs at night [20]. Allogrooming should increase with increased dancing at night but may not if allogroomers at night are in a less active state [11]. Monitoring grooming behavior from 32 colonies revealed a positive relationship with mite prevalence within these colonies. Both dancing and allogrooming increased with increasing mite levels. No differences were detected in the time of observation during the day, 1 000 versus 1 400 hours, nor between the three consecutive days of observation.

The age and genotype of a worker influences the timing and likelihood of both dancing and allogrooming. Allogrooming had previously been shown to be

<table>
<thead>
<tr>
<th>Host colony</th>
<th>Colony mite prevalence</th>
<th>Number of mites by patriline</th>
<th>Chi-square (3 df)</th>
<th>P value</th>
</tr>
</thead>
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<tr>
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<td>100</td>
<td>HG 109 I1 90 I2 80 HD 84</td>
<td>1.52</td>
<td>NS</td>
</tr>
<tr>
<td>I1</td>
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<td>I1 110 I1 91 I2 69 HD 54</td>
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<tr>
<td>I2</td>
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<tr>
<td>HD</td>
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<td>HD 53 I1 37 I2 20 HD 21</td>
<td>17.84</td>
<td>0.01</td>
</tr>
<tr>
<td>A</td>
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<td>9.68</td>
<td>0.05</td>
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<tr>
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<td>2.96</td>
<td>NS</td>
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<tr>
<td>C</td>
<td>50</td>
<td>C 37 I1 26 I2 22 HD 14</td>
<td>11.00</td>
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<tr>
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<td>D 33 I1 26 I2 24 HD 19</td>
<td>3.44</td>
<td>NS</td>
</tr>
</tbody>
</table>

*Percent recovery ranged from 78 to 92% and was not significantly different between patrilines, 20 bees per line were dissected.
in part genetically determined [5, 12], and is now shown to be age specific. Workers between 5 and 15 d old are most likely to serve as allogroomers. The present studies indicate that workers of a specific genotype are more likely to dance than other genotypes. Additionally, dancing occurs more frequently in young bees < 5 d old if the hive is infested with tracheal mites, as mites disperse preferentially to bees < 5 d of age [7, 13]. The four patrilines were all groomed equally. Thus, no evidence for preferential allogrooming was observed between the four patrilines. This is in contrast to Frumhoff and Baker [5] who did report preferential allogrooming toward full sisters when only two patrilines were present. In the current studies using four patrilines, increased dancing by patriline HD did not result in an increased probability of being groomed (figure 3).

The hives with and without tracheal mites (0 and 50% prevalence) clearly demonstrated an association between the level and timing of dance behavior and tracheal mites. Workers in the tracheal mite-infested colony danced more in the first 3 d following introduction (similar results were obtained in colony #3 with four patrilines). In contrast, when workers from the same colony source were introduced into a tracheal mite-free colony they danced at a lower level over the first 3 d than their sisters in a colony with tracheal mites. The background dancing in both colonies by bees of unknown age was very consistent over the 19 d, averaging 41 dances/d in both hives. Thus, the increased dancing during days 1–3 can be linked to age and mite levels and not to day to day changes within the hive. The increased dancing in the tracheal mite-infested colony on days 1–3 is strong indirect evidence that mite movement onto these workers is eliciting the dance behavior. Tracheal mites disperse to young bees and their preference for 1–3-d-old bees is mirrored by the increased dancing behavior on these days.

Workers from different patrilines exhibited differences in their propensity to acquire tracheal mites in a 5-d bioassay. Workers that had a low dance threshold acquired the fewest tracheal mites, while workers exhibiting high allogrooming behavior had acquired the highest number of mites. Workers that were intermediate in their grooming behavior were not significantly different from expected values. The high allogrooming line was most susceptible, acquiring 34% of the available mites. The high dancing line acquired the fewest mites which we propose was due to their ability to detect the presence of mites on their body and remove these mites with the autogrooming that occurs during the dance. All dancing bees use their second pair of legs to groom over their thorax as they dance. The raking action of the legs could remove mites that are attempting to disperse to these bees.

Grooming behavior changes with changes in tracheal mite levels within honey bee colonies. We found increasing levels of both dancing and allogrooming as tracheal mite levels increased. Most striking was the increased dancing observed in bees 1–3 d of age in mite-infested colonies that corresponds with the movement of mites onto young bees. No increased dancing was found in young bees in a colony free of tracheal mites. We propose that dancing behavior is elicited by mites on the body of workers and that the autogrooming associated with the dance reduces the number of mites that succeed in transferring. Thus, the grooming dance by worker honey bees is proposed as a resistance mechanism to the honey bee tracheal mite.

Since submitting this manuscript the authors have become aware of research in Baton Rouge, LA (USDA-ARS) with Buckfast bees that demonstrates that auto-
grooming is linked to tracheal mite resistance, which corroborates our findings.

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**Résumé – Comportement de toilettage par *Apis mellifera* L. en présence d’*Acarapis woodi* (Rennie) (Acari, Tarsonomidae).** On a étudié le rôle du comportement de toilettage chez l’abeille *Apis mellifera* dans la limitation de l’infestation par l’acarien des trachées *Acarapis woodi* ainsi que le déclenchement de ce comportement par la présence du parasite. On a relevé le nombre d’abeilles qui soit exécutaient une danse de toilettage (= autotoilettage), soit étaient engagées dans une activité de toilettage mutuel (= allotoilettage), qui consiste à toiletter un congénère ou à être toiletté par lui. La première expérience a porté sur quatre ruches d’observation suivies 24 h sur 24 durant dix jours. Le comportement des abeilles a été mis en relation avec le nychémère : la danse augmentait significativement la nuit alors que l’allotoilettage diminuait (figure 1). Dans une seconde expérience, 32 ruches d’observation ont été suivies durant l’été 1992 à Burnaby, Britsh Columba, Canada. Une corrélation positive a été trouvée entre le pourcentage d’abeilles infestées et le nombre d’auto- ou d’allotoilettages (figure 2). Dans une troisième expérience de jeunes abeilles marquées ont été introduites dans trois ruches ayant un taux d’infestation de 0, 50 et 70 %. Leur comportement de toilettage a été observé chaque jour durant 19 jours. Dans la colonie infestée à 50 % comparée à la colonie non infestée, les danses de toilettage ont augmenté significativement chez les abeilles âgées de un à cinq jours puis ont diminué (figure 3), indiquant que le déplacement de l’acarien sur les jeunes abeilles peut déclencher la danse de toilettage. Dans la colonie infestée à 70 %, des groupes d’abeilles récemment écloses de quatre lignées paternelles uniques ont été marquées et leur comportement de toilettage a été observé durant 19 jours. Les abeilles ont présenté des différences significatives, en fonction de leur lignée paternelle, dans leur propension à danser ou à s’allotoilettier. Une lignée paternelle a rendu compte de 64 % de tout l’allotoilettage, une autre de 48 % de toutes les danses, tandis que les deux autres occupaient une position intermédiaire pour ces deux caractères (figure 4). L’allotoilettage est lié à l’âge, la majeure partie (90 %) ayant lieu quand les abeilles ont entre 5 et 15 jours. Dans une quatrième expérience, des groupes d’abeilles récemment écloses issues de colonies de lignée paternelle unique ont été marquées et placés durant cinq jours dans des colonies infestées, réparties en quatre colonies parentales et quatre colonies d’observation (tableau I). Sur les quatre colonies de lignée paternelle simple, l’une correspondait à des abeilles ayant un comportement d’allotoilettage élevé, une seconde à des abeilles ayant un comportement de danse élevé, les deux autres colonies ayant une position intermédiaire concernant ces deux caractères. La dissection des abeilles marquées a montré des différences cohérentes entre les quatre lignées parentales dans le niveau d’infestation (tableau I). La lignée la plus sujette à l’allotoilettage était la plus sensible à l’infestation par l’acarien (figure 5) ; la lignée qui dansait le plus étant la moins sensible. Ceci peut être dû à la capacité de ces abeilles à détecter la présence de l’acarien sur leur corps et à l’éliminer par l’autotoilettage qui a lieu au cours de la danse. Ces expériences montrent que les abeilles qui ont une prédisposition génétique à effectuer des
danses de toilettage sont susceptibles de détecter les acariens présents sur leurs corps et à s’en débarrasser. C’est la première fois que l’on propose un mécanisme de résistance de l’abeille mellifère à l’acarien des trachées. © Inra/DIB/AGIB/Elsevier, Paris

*Apis mellifera / Acarapis woodi / comportement toilettage / résistance au parasite*


*Apis mellifera / Acarapis woodi / Putzverhalten / Verhalten / Arbeitsteilung*
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