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The role of cuticular compounds in the resistance of honey bees (*Apis mellifera*) to tracheal mites (*Acarapis woodi*)

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Abstract. This study examined the migration of tracheal mites (*Acarapis woodi*) into honey bees (*Apis mellifera*) from different colonies and the relative attraction of mites to hexane extracts from the external body surfaces of young bees. Relative resistance of bees from different colonies initially was assessed with a field bioassay that involved tagging newly emerged bees, pooling them in heavily mite-infested colonies, retrieving them 7 days later, and examining them for tracheal mite prevalence and abundance. For those colonies identified as most resistant and least resistant, cuticular chemicals were extracted in hexane from frozen, newly emerged worker bees. These extracts were presented to individual tracheal mites in pairwise fashion in a laboratory bioassay. The results demonstrated that mites prefer extracts of bees from some colonies more than others, however, no consistent differences were demonstrated. Our inability to predict mite responses to extracts based on our initial assessment of relative resistance indicates that other mechanisms of resistance influence mite success in colonizing new host bees.

Key words: honey bees, *Apis mellifera*, tracheal mites, *Acarapis woodi*, cuticular chemicals, mite resistance, hydrocarbons

Introduction

Acarapis woodi, the honey bee tracheal mite, is an obligate parasite found in the tracheae of adult honey bees. It can cause significant damage to honey bee (*Apis mellifera*) colonies, especially during winter (Bailey and Lee, 1959; Guzman-Novoa and Zozaya-Rubio, 1984; Maki *et al.*, 1987; Eischen *et al.*, 1989; Furgala *et al.*, 1989; Otis and Scott-Dupree, 1992; Tomasko *et al.*, 1993). In an attempt to reduce these effects, several research efforts have evaluated or enhanced HBTM-resistance in bees (Gary and Page, 1987; Gary

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et al., 1990; Page and Gary, 1990; Milne *et al.*, 1991; Loper *et al.*, 1992; Danka *et al.*, 1995; Danka and Villa, 1996; Lin *et al.*, 1996; Guzman, *et al.*, 1998; Danka and Villa, 2000; Nasr *et al.*, 2001; van Engelsdorp and Otis, in press). Breeding strategies have included the propagation of surviving colonies in HBTM-infested areas, the artificial selection of *A. woodi*-resistant stocks, and the importation of bee stocks reported to be resistant to mites. All of these studies have documented that bees from different source colonies vary widely in their resistance to *A. woodi*; however, mechanisms underlying this resistance remain poorly understood.

The biology of the honey bee tracheal mite is well known (Bailey and Ball, 1991; Pettis and Wilson, 1996; Sammataro and Needham, 1996). After completing development and mating, a young adult female mite leaves the tracheal system and moves onto the bee's hairs where it assumes a questing position. When it contacts a host, it grabs onto the host's hairs, then determines the suitability of that host and, if suitable, moves towards and enters the prothoracic spiracle of the new host. Numerous studies have confirmed that mites strongly prefer young, newly emerged bees (Morgenthaler, 1930; Lee, 1963; Giordani, 1977; Gary *et al.*, 1989; Phelan *et al.*, 1991). Phelan *et al.* (1991) demonstrated that this preference is influenced by differences in cuticular chemistry. They used hexane to extract chemicals from the cuticle of bees of different ages, then fractionated this extract into various components. Tracheal mites, when placed on a microscope slide midway between extracts taken from newly emerged and older bees, preferentially moved toward the young-bee extract and, specifically, fractions containing saturated and unsaturated hydrocarbons. Because the proportions of branched and saturated hydrocarbons are known to decrease rapidly and predictably during the first few days of a bee's life (Francis *et al.*, 1989), Phelan *et al.* concluded that mites use these hydrocarbons to identify young bees. However, they also noted that nonhydrocarbon cuticular lipids, which increase more than 10-fold over the first 12 days of a bee's life (Francis *et al.,* 1989), could be used by mites to discriminate between young and old hosts. Substances (e.g., vegetable oil) that interfere with or conceal the odor of young bees reduce the colonization of their tracheae by mites (Sammataro and Needham, 1996).

Despite the extensive effort devoted to studying the resistance of bees to tracheal mites, the mechanisms for the variable success of mites in colonizing new host bees from different source colonies remain little studied. Danka and Villa (1998) elegantly demonstrated that self-grooming is a major component of mite resistance, but they concluded that it is not the only factor involved. Pettis and Pankiw (1998) provided evidence that allogrooming also is involved in reducing mite infestations. Another possible mechanism by which

honey bees resist infections of tracheal mites may come from the differential attraction of tracheal mites to bees of different colonies, mediated by cuticular compounds. In our study, the role of cuticular compounds in the resistance of honey bees to tracheal mites was evaluated by examining the movement of mites to hexane extracts of bees determined to be either 'resistant' or 'susceptible' to mites.

Materials and Methods

Evaluation of a population of honey bees for resistant and susceptible colonies

We evaluated worker bees from 34 Ontario colonies of diverse genetic background using a modification of the bioassay developed by Gary and Page (1987). From each colony to be evaluated, a frame containing emerging adult worker bees was sent to the Apiculture Field Lab of the University of Guelph on May 18, 1994. These frames were caged individually and placed in a dark incubator (34°C and approximately 60% RH). The following day, two groups of 15 newly emerged bees (<18 h old) from each frame were collected and individually numbered with thoracic tags. An additional 15–30 bees from each frame were placed in a sterile vial and frozen for subsequent analysis (see below). The marked bees were introduced into two mite inoculation colonies (510 bees per inoculation colony = 34 colonies × 15 bees/colony tested) with mite prevalence of 20 and 26%. Seven days later, when nearly all migration of mites into the tracheae of the test bees would have been completed and before offspring mites could have matured in the tracheae (development from egg to adult requires a minimum of 8 days for males and 10 days for females; Pettis and Wilson, 1996), the tagged bees were removed (mean ± SD: 23.9 ± 0.43 bees retrieved per colony tested) and placed in vials containing 70% ethanol. HBTM prevalence and abundance (*sensu* Margolis *et al.*, 1982) were determined with the cleared thoracic disk method (Shimanuki and Cantwell, 1978; Delfinado-Baker, 1984). Three colonies with bees having high prevalence and abundance ('susceptible' to mites) and another three colonies with completely uninfested bees ('resistant') were identified for further study.

Mite behavior towards cuticular extracts

Following the basic experimental procedure of Phelan *et al.* (1991), extracts containing cuticular compounds from bees of the six selected colonies were prepared by placing 15 frozen, newly emerged bees from each selected colony in 30 ml of hexane for 10 min. After removing the bees, the hexane extract was reduced to 1.5 ml under steady nitrogen flow.

A balanced, incomplete block design was used to compare all six extracts and the hexane control in a two-choice bioassay. The extracts and controls were color-coded by an independent person prior to testing to ensure 'blind' observations. Two Whatman #1 quantitative filter paper disks (1 cm diameter) were placed 4 mm apart on a plastic cover slip, and 10 μl (0.1 bee equivalent) of the appropriate hexane extracts for each comparison were applied to the filter papers. The filter paper 'arenas' were allowed to dry at room temperature for 24 h.

Live mites were obtained by removing the head and pronotum from infested bees to expose the large prothoracic tracheae. With fine-pointed forceps an infested tracheal tube from the spiracle up to and including the first tracheal branch was removed along with some of the surrounding thoracic salivary gland tissue. Placed on a microscope slide, the glandular tissue was allowed to dry for 5 min, thereby affixing the trachea to the microscope slide. Using a 50x Zeiss compound microscope, the trachea was dissected with a human eyelash glued to a dissecting probe. Adult female mites were lifted from the trachea with the eyelash and placed in the center of the experimental arena, midway between the two treated filter paper disks, as described by Phelan *et al.* (1991). The coverslip was placed in a small incubator (33°C, 93% RH) for 5 min. After removal from the incubator, the mite was determined to have moved towards one extract or the other. In all, five complete repetitions of each block in the experimental design were conducted. Data were analyzed using the Durbin statistical procedure (comparison of LSD of ranked values). This procedure compares the number of mites migrating to one extract over another while considering the choices female mites make when presented with other extracts. Thus, relatively few trials allow for statistical differences to be detected.

Results

The modified Page/Gary (1987) bioassay revealed a wide range of 'resistance' among tested colonies (Figure 1). The three colonies that had the highest mite prevalence and abundance values (indicated by the closed circles (•) in the upper right portion of Figure 1) were selected to represent 'susceptible' colonies in the chemical bioassay. No mites were found in the tracheae of bees from five colonies; three of these were randomly selected as 'resistant' colonies (indicated by a closed circle (•) in the lower left portion of Figure 1).

The results of the bioassay evaluating the attractiveness of cuticular extracts are presented in Table 1. Mites nearly always (24 of 30 comparisons) moved toward extracts of bees when compared to hexane-treated (control) filter papers. In other words, tracheal mites preferred bee odor to no odor.

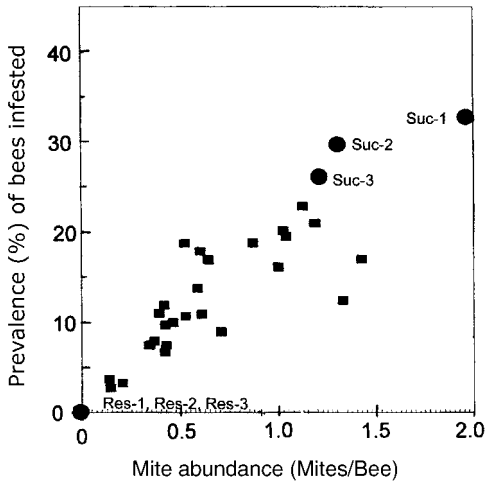

Figure 1. Results of the modified Gary and Page (1987) bioassay for tracheal mite resistance, representing bees from 34 genetically diverse colonies in Ontario. Colonies indicated by closed circles (•) and a colony number were selected for the cuticular extract bioassay. Bees from five colonies had no mites in their tracheae after 7 days of exposure in infested colonies; these are represented by the single • in the lower left corner.

The extracts of bees from Res-1, identified in the colony bioassay as 'resistant', attracted only 4 mites in the 25 pairwise comparisons with extracts from bees of other colonies. Extracts of bees from this colony were more attractive to mites than the hexane controls (attracting four of the five mites tested; Table 1), however the Durbin statistical procedure could not differentiate it from the hexane control because, in total, it attracted a similar number of mites (eight mites in 30 comparisons were attracted to Res-1 and six mites of 30 comparisons were attracted to the hexane control (Table 2). Similarly, 'resistant' colony Res-2 did not show a statistical difference from the hexane control or extracts from Res-1 because mites seemed unable to differentiate between the Res-2 extract and the Res-1 extract (attracting two and three mites, respectively).

At the other extreme, the cuticular extract of bees from 'susceptible' colony Suc-3 was highly attractive to mites. In 21 of 25 pairwise comparisons with extracts of bees from other colonies, mites were attracted to Suc-3. Excluding colony Res-3, extracts of bees of colony Suc-3 were significantly more attractive than those of the other four colonies and the hexane controls ($p < 0.01$, Table 2).

The most anomalous results were obtained from bees of 'resistant' colony Res-3. Although no mites infested the bees of that colony in the HBTM bioassay and it was selected as one of the 'resistant' colonies, extracts from those bees were generally highly attractive to mites (Table 2).

Table 1. Choices of female tracheal mites when presented with extracts of 'resistant' (Res) bees, 'susceptible' (Suc) bees, or hexane controls (Cont)

Extracts used						
Hexane (Cont)	Res-1 (Res)	Res-2 (Res)	Res-3 (Res)	Suc-2 (Suc)	Suc-1 (Suc)	Suc-3 (Suc)
1	4					
0		5				
1			4			
3				2		
0					5	
1						4
	2	3				
	0		5			
	1			4		
	1				4	
	0					5
		1	4			
		3		2		
		3			2	
		0				5
			5	0		
			3		2	
			0			5
				3	2	
				3		2
					1	4

Numbers in a row indicate the number of mites attracted to each extract in pairwise presentations of extracts. All possible pairs of extracts and controls were tested five times.

Discussion

This project confirmed the findings of Phelan *et al.* (1991), that mites strongly prefer bee extracts to hexane controls. This result is expected considering that tracheal mites are obligate parasites of honey bees: any mite should prefer the odor of a bee, even a relatively unattractive one, to no odor.

More importantly, the attractiveness of mites to extracts of bees from different colonies was significantly different. Likely candidate compounds that may mediate differences in attractiveness are hydrocarbons, the major components of the lipid layer on the outer cuticular surface of honey bees (Blomquist *et al.*, 1980) and/or fatty acids (Phelan *et al.*, 1991; Breed, 1998).

Table 2. Differences in mite attraction to hexane (control) and to cuticular extracts of newly emerged bees determined to be 'resistant' (Res) and 'susceptible' (Suc) using a modification of the Gary and Page (1987) bioassay

Number of mites attracted to extract	Increasing degree of attractiveness →						
	Hexane	Res-1	Res-2	Suc-1	Suc-2	Res-3	Suc-3
	6	8	15	16	14	21	25

A total of 30 pairwise comparisons were made with each extract.
*Mite attraction to bees from colonies connected with a bar did not differ significantly ($p > 0.05$, Durbin statistical procedure).

Hydrocarbons of honey bees have been studied extensively, and it is known that newly emerged bees have low levels of hydrocarbons in their surface lipids, a high proportion of branched hydrocarbons, and a high proportion of saturated hydrocarbons (Blomquist *et al.*, 1980; Francis *et al.*, 1989). Over the first 6–9 days of an adult bee's life, all three characteristics change: the total amount of hydrocarbon increases (but decreases again later in the bees life), proportions of branched hydrocarbons decrease rapidly (primarily monomethyl- and dimethyl-substituted alkanes), and proportions of long-chain unsaturated hydrocarbons increase rapidly. Cuticular lipids also increase in the first days of adult life (Francis *et al.*, 1989). The correlation between these chemical changes and the changes in relative attractiveness of bees to mites as they age (e.g., Lee, 1963; Gary *et al.*, 1989) lead to the hypothesis that specific chemicals either serve as attractants to young bees or repellents from older bees. In a similar manner, the chemical signatures of newly emerged bees from different colonies could differ, resulting in bees that differ in attractiveness to migrating mites.

This range in attractiveness has potential implications for mite resistance. At the colony level, if migrating mites could not distinguish between young and old bees, they would, in theory, migrate randomly into older and younger bees. The mites who migrated into older bees would presumably die with their progeny when their host bee died – severally reducing the population growth potential of the mite in the given colony. If this hypothesis were correct, one would predict *a priori* that bees from the three colonies identified as highly 'susceptible' to mites in the preliminary Page/Gary (1987) bioassay (Figure 1) would have considerably more attractive (or less repellent) cuticular compounds than bees from the three 'resistant' colonies. It was unexpected that these two sets of colonies would exhibit a continuum of attractiveness to mites in our cuticular extract bioassay (Tables 1 and 2). Clearly, our results did not consistently support this hypothesis. It seems more likely, therefore, that the resistant bees in this study failed to become infested by tracheal mites because of a resistance mechanism that did not involve the potential host's cuticular composition. For example, self-grooming (Danka and Villa, 1998) and the frequent performance of grooming dances that stimulate allogrooming (Pettis and Pankiw, 1998) are both reported to enhance the resistance of bees to tracheal mites and could have affected the Page/Gary bioassay results.

It is unlikely that the poor match between predicted and observed results was due to a failure of the modified Page/Gary (1987) bioassay. This bioassay has been used for more than a decade to screen honey bee colonies for resistance. Rankings of mite infestations in field colonies are correlated significantly with rankings of resistance of the same colonies as determined with the Page/Gary bioassay (Lin *et al.*, 1996; Nasr *et al.*, 2001). Moreover,

the Page/Gary bioassay has been used to identify mite-resistant colonies and to breed for resistance (Page and Gary, 1990; Danka and Villa, 2000; Nasr *et al.*, 2001). By selecting the colonies whose bees differed the most in mite infestations in our preliminary bioassay (Figure 1), we chose colonies for further study that should have differed strikingly in relative mite resistance.

The results of this study suggest that the attractiveness/repellency of different cuticular compounds play a small role, if any, in honey bee resistance to tracheal mites. For a migrating mite, determination of a suitable host bee is the first step in the behavioral sequence that culminates in successful entry of a new host's trachea. We have shown that the attractiveness of young bees from different source colonies differs significantly. However, the failure of the mites to choose between extracts in the manner predicted from our initial Page/Gary (1987) bioassay indicates that this is not a primary mechanism of resistance. Gary *et al.* (1990) drew the same conclusion, pointing out that although resistance appears to be related to differential attraction of mites in some cases, other cases cannot be explained by this mechanism, and warrant further investigation.

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