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Washboarding in feral honey bees, *Apis mellifera:* Observations at natural hives

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Worker bees of 15-25 days old perform a stereotyped behavior around the hive entrance termed "washboarding". While washboarding behavior is well documented in domesticated bee hives, there is still no consensus as to what its purpose is, and the behavior has not previously been reported in natural bee hives in forest settings. Many observers suggest that the bees are cleaning the surface, though no one has proposed a possible reason for the head-down, vertical body orientation typical of washboarding. I present observations of washboarding at two feral honey bee hives in cavities of dead trees in a mixed hardwood forest in Douglas County, Kansas, in summer 2016. In addition to the probable surface cleaning of the washboarding activity, I suggest that a primary function of washboarding may be to assist returning foragers in locating the nest entrance through the application of pheromones emitted from the tarsal and Nasonov glands of workers, and that the vertical head-down posture of bees may help to disperse the volatile Nasonov pheromone.

Key words: Honey bees, washboarding, Apis mellifera*, Nasonov pheromones, tarsal pheromone*

Introduction

Foraging honey bees usually travel within several hundred meters from the hive in search of nectar, pollen, water and propolis (plant resins), but may venture up to 6 km, depending upon the quantity and quality of food sources available (Michener 1974). In a large hive foraging bees may make from 14,000 up to 163,000 foraging trips per day (Gary 1967). Honey bees do not have great visual acuity, possessing some 25,000 sensory cells per mm^2, compared with 80 million per mm^2 in the human eye. However, they are able to detect movement of objects much more effectively than humans, with a frame-rate discrimination of 300/second as compared with 15-20/sec in humans. The honey bee eye also has no focusing mechanism (Michener 1974). Bees compensate for a lack of visual prowess by utilizing pheromones for chemical communication and orientation. Detection of chemical odors is accomplished by the antennae (Michener 1974). The contextual use of pheromones is responsible for the coordination of the entire bee colony in terms of reproduction, development, food collection, defense, and overall functioning (Bartolotti and Costa 2014). Michener (1974, p.174) has stated that "olfaction plays a significant role in *Apis* orientation." Michener goes on to say "Odor plays an important role in stimulating bees to settle, as on a flower or perhaps a nest entrance." (Michener 1974, p. 147).

Workers who have matured to the guard/forager age may spend much time at the entrance to the nest. Many of these workers engage in a stereotyped behavior that has been termed "washboarding." This behavior consists of a bee generally placing the middle and rear legs securely on the substrate and rocking the entire body forward and backward while scraping at the surface with the front pair of legs and mandibles. The bee normally orients the body vertically, with the head down and the abdomen up and sometimes raised off the surface. A bee may remain in

one position for minutes, or may shift position after a few seconds and start the behavior again (Gary 1992). Bohrer and Pettis (2006) reported that washboarding is performed by adolescent workers 15-25 days old. They observed washboarding behavior throughout the day and experimentally showed that bees more actively treated rough textures compared with smoother surfaces, such as glass. There has been no consensus as to the function of the washboarding behavior. Many observers speculate that the bees are cleaning the surface around the hive entrance, removing any loose particles, parasites, fungi, or other debris (Gary 1992; Bohrer and Pettis 2006). One researcher suggested that washboarding was seen when food sources in the field were scarce and foragers with nothing else to do were "sweeping the porch" to stay active (Garvey 2012).

Among the many pheromones controlling life in a honey bee colony, bees use certain ones to attract and orient other hive mates to both favorable food sources in the field and to the nest entrance (Bartolloti and Costa 2014; Collins 2015). The Nasonov gland, located at the upper tip of the abdomen, produces a variety of volatile chemicals, including acids and alcohols, that are attractive to other foragers at a distance from the source, depending upon wind dispersal and other microclimate conditions (Pickett et al. 1980). Bees assume a distinct head-down, abdomen raised posture (Fig. 1; see also Topitzhofer 2013) when emitting this pheromone (Free 1987; Bartolloti and Costa 2014).

Bees also possess a tarsal gland which produces a so-called "footprint" pheromone, which is stored in a sac at the base of the last tarsal segment (Collins 2015; Fig. 2). The footprint pheromone also functions as an attractant to foraging bees (Ribbands 1954), but its storage sac is unusual in having no ducts whereby the pheromone can be secreted to the environment. The mode of transfer of the chemical from the storage sac to a substrate is unknown (Bartolloti and Costa 2014), but it

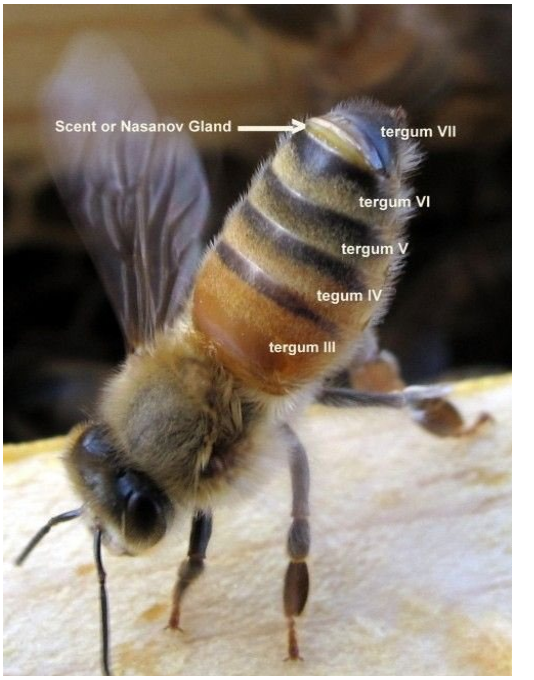

Figure 1. Honey bee posture during emission of pheromone from Nasonov gland at upper tip of abdomen. Photo by Pollinator, April 2003, South Carolina.

has been suggested that the tarsal pheromone may be applied to the surface around the nest entrance by returning foragers as they land and walk around at the surface of the hive before entering (Williams et al. 1981; Butler et al. 1970; Collins 2015). The footprint pheromone is an oily, nonvolatile substance that is thought to exert its influence on other bees within close proximity (Ferguson and Free 1981). Butler et al. (1970) also showed that the attractive influence of the tarsal pheromone on other bees increased in proportion to the number of bees applying it.

Experiments have shown that multiple honey bee pheromones can work in concert to enhance a signaling function, and that the Nasonov and tarsal pheromones together produce a stronger synergistic effect than either pheromone used alone (Breed et al. 1992). Ferguson and Free (1981) suggested that the Nasonov pheromone may exert an attractive influence on more distant foragers

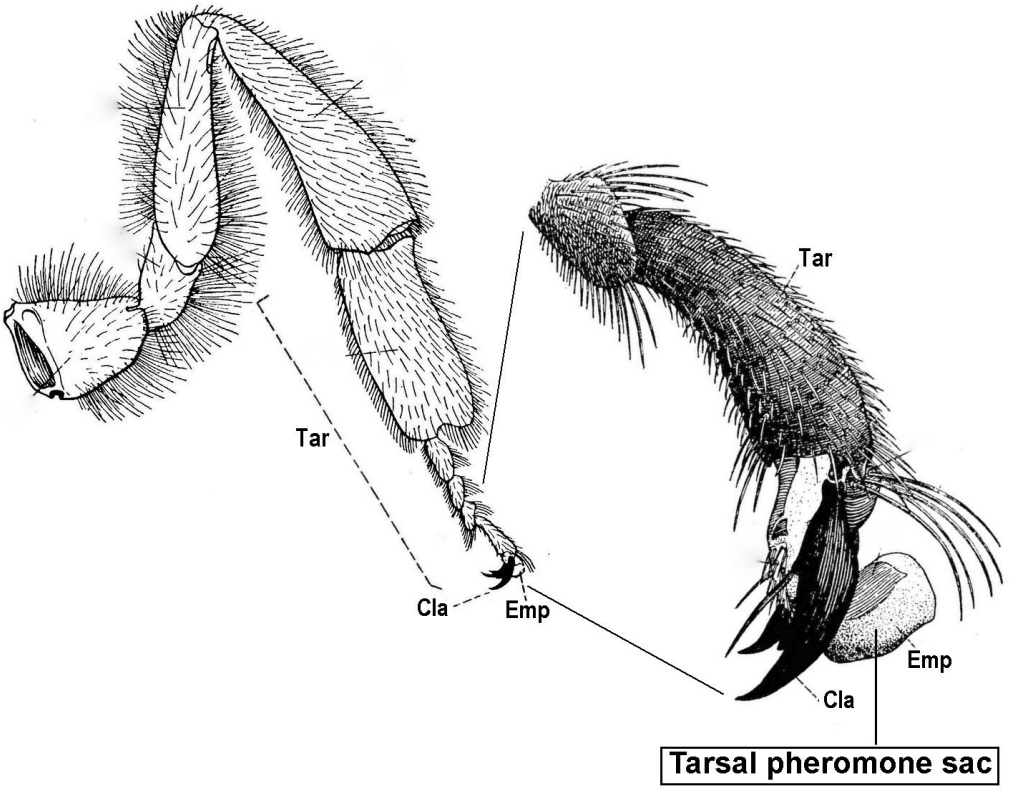

Figure 2. Last tarsal segment, enlarged on right, with arrow indicating storage sac containing tarsal "footprint" pheromone. This sac does not have ducts to the outside and must be rubbed against a surface to transmit the pheromone. Tar = tarsus, Cla = claw, Emp = empodium. Modified from Collins (2015).

with the tarsal footprint scent providing a more proximal signal orienting approaching bees to the specific food source or nest opening.

While washboarding has been widely observed on man-made hives, it has not been described in feral bees nesting in natural tree cavities. In this paper I present observations of washboarding by feral honey bee workers at two natural hives in tree cavities in a mixed hardwood forest and provide hypotheses regarding the possible adaptive functional significance of the washboarding behavior as well as the vertical head-down orientation of most washboarding bees. Because the behavior can only be fully appreciated when observed in action, several figures will take the form of links to YouTube™ video clips illustrating aspects of washboarding discussed here.

Methods and Results

On 29 July 2016 I first observed a feral honey bee colony occupying a cavity 1.5 m above the ground in a dead oak tree of 60 cm diameter in at mixed hardwood forest at the Woodridge Public Use Area at Clinton Lake, KS (UTM 15 S 288737, E 4311679). I subsequently visited this hive on 1 and 6 August. Figure 3 shows the vertical orientation of the bodies of most workers around the nest entrance, with the head down and the abdomen up and raised off the

Figure 3. The first wild honey bee nest observed in a forest snag den at the Woodridge Public Use Area, Clinton Lake, KS, 29 July 2016, 1700 hrs, 30°C (UTM 15 S 288737, E 4311679). Note the vertical orientation of most workers, with the head down and abdomen up and raised off the surface in many bees. These bees were actively exibiting the stereotyped washboarding behavior around the opening to the hive.

surface in many individuals. These bees were actively engaged in the washboarding activity. In order to better illustrate the washboarding behavior I captured a video sequence (Fig. 4) with a small camera attached to a telescoping pole at the first nest site on 6 August 2016 (1800 hrs, 28°C). I visited this nest again on 12 August 2016 and discovered it was abandoned for unknown reasons.

Figure 5 shows the second bee colony observed later in August and September 2016 located 4 m high in a 30 cm diameter snag in the same forest (UTM 15 S 290338, E 4312546). The workers around the nest entrance were actively washboarding, demonstrating the same postures and orientation seen at the first colony. I subsequently visited the second hive on 11 occasions in September, observing

Figure 4. Link to video of washboarding behavior at the first nest site, taken 6 August 2016 (1800 hrs, 28°C). Note the mass of workers actively washboarding an area directly surrounding the nest entrance. [https://www.youtube.com/watch?v=ye534PyIYxE]

washboarding activity by workers around the nest entrance and foragers leaving and returning to the hive on each occasion. Activity at the hive entrance was much reduced on 26 September at 1730 when the ambient temperature was 22.8 °C.

After the first hive was abandoned I was able to closely observe the surface bark surrounding the nest entrance and compare the appearance of the area that had been covered by washboarding bees with the adjacent untreated bark. The entrance area appeared to be very smooth and clean of moss and any loose debris that were present on the rest of the bark surfaces (Fig. 6a). In addition, the bark surface that had been washboarded by the guard bees showed a different purplish tint as well as smooth appearance, compared with the surrounding bark (Fig. 6b).

Further observations at the second hive site yielded additional information on washboarding behavior. Washboarding involves the front legs scraping the surface in a rapid inward motion, which may serve to draw any loose debris or small organisms in toward the mandibles where they can be picked up and discarded (Fig. 7). In addition, washboarding

Figure 5. The second wild honey bee colony located in a mixed hardwood forest at Woodridge Park, Clinton Lake, KS, 8 September 2016, 1700 hrs, 30°C. (UTM 15 S 290338, E 4312546). These bees were also actively "washboarding," most with the head down, abdomen up and raised posture seen at the first site. The Nasonov gland at the tip of the abdomen emits an attractive, volatile set of chemicals that could possibly be better dispersed on the wind by this posture compared with a head-up posture in which some of the chemical might be absorbed by the body of the bee as it rose through the air.

bees will interrupt their activity to repel potential intruders, as well as to interact with other guards or returning foragers (as seen in Fig. 7). They also sometimes change position, moving around the nest entrance, often returning to a previous position to resume washboarding again.

Discussion

My observations of the washboarding activity of bees at two different natural forest hives, along with perusal of the literature, have led me to develop the following hypotheses regarding the functional significance of this behavior. I suggest that an important function of the washboarding activity may be to continuously apply an attractive colony scent to the surface around the entrance to the hive, serving to help orient the returning foragers and allow them to quickly find and enter the hive with their field collections. The continuous scraping of a single small area with the forelegs would seem superfluous if the only function were to clean that spot. But if the repetitive scraping of the front legs deposits and maintains a fresh coating of the tarsal pheromone at the surface around the nest entrance, known to be a non-volatile, oily substance that must be rubbed against the substrate to be transmitted (Goodman 2003), then the nonstop nature of the activity becomes more appropriate. And the fact that the pheromone's attractive effect increases with the number of bees producing it (Butler et al. 1970) further justifies the large number of worker bees massed at the hive entrance continuously performing the washboarding behavior. Further, the vertical posture of washboarding bees may promote effective dispersal of the volatile Nasonov pheromone, which may act as a more distant navigation aid to returning foragers.

The repetitive washboarding behavior, and the head-down, vertical orientation of most washboarding bees, has previously been observed and filmed at box hives. Box hives present a rather unnatural structure on which to observe washboarding bees, and when the activity is performed by a mass of bees spread out on the wall of a box hive above the narrow entrance slit at the bottom of the box, a functional significance of the behavior is not readily apparent (Berlew 2016; http://honeybeesuite.com/washboarding-bees-arockin-and-alickin/).

Many observers have suggested that worker bees around a hive entrance act as guards, identifying returning foragers as colony members and repelling foreign bees (Breed et al. 1992; Arechavaleta-Velasco and Hunt

Figure 6a. At the abandoned first nest site the bark surface around the entrance where honey bees had been actively washboarding appears clean of moss and loose debris compared with surrounding untreated bark; Figure 6b. The surface of bark previously covered by mass of washboarding workers shows a smooth, waxy or oily appearance with a color tint not observed on surrounding untreated bark, suggesting the possibility of a residual presence of a chemical coating applied by the worker guards during their washboarding activity. The tarsal pheromone is described as an oily, non-volatile substance, that must be rubbed against a substrate to transfer the pheromone, and its possible repeated application during long bouts of washboarding around the nest entrance, may result in the difference in bark appearance there.

2003), and that washboarding bees also serve to clean the surface of debris (Bohrer and Pettis 2006). The utility of both the cleaning and guarding functions of washboarding bees is more apparent when the activities are observed at a natural hive compared with worker bees around the entrance to a box hive. The bark area around a natural hive entrance worked by bees is noticeably smoother and cleaner compared to the loose debris and moss that coat the adjacent bark surfaces of a dead tree. The entrance area of a natural tree cavity hive is also regularly visited by numerous other species that might pose a disturbance or threat to the colony, thus confirming the importance of a guarding function of the mass of workers around the hive entrance. Observations of the concentration of the washboarding workers around the single hive entrance of a natural cavity, with returning foragers passing through the center of the mass of washboarding bees as they dart into the hive, are also more suggestive that the workers may be producing attractive orienting pheromones to guide foragers into the entrance, compared with the appearance of a group of washboarding bees spread out on the wall of a box hive, far from the entrance slit at the bottom (Fig. 8).

Though many authors mention the possible function of the Nasonov and tarsal gland pheromones in marking food sources in the field, as well as the nest entrance (Butler et al. 1969; Williams et al. 1981; Bartolloti and Costa 2014), the use of these orienting pheromones has not been previously mentioned in association with the stereotyped washboarding behavior or the vertical orientation of bees around the hive entrance. In addition to a cleaning function, the repetitive scraping of the same spot with the forelegs may serve to maintain a fresh coating of the attractive tarsal pheromone to guide returning foragers back to the hive entrance. The head-down, vertical posture of most washboarding workers may function in assisting dispersal of the Nasonov pheromones, which are known to be volatile chemicals acting as an attractant

Figure 7. Link to video showing detail of washboarding behavior, showing the scraping of the surface by the front legs inward toward the mandibles in the repetitive activity (1700 hrs, 31.7°C). [https://www.youtube.com/watch?v=1CbPYtDhYX4]. The tarsal pheromone sac is known to have no ducts and must be rubbed against a substrate to transfer the attractive pheromone to a surface. In addition to cleaning the site, perhaps this repetitive scraping serves to maintain a fresh layer of the tarsal "footprint" pheromone to aid returning foragers in quickly navigating to the nest entrance.

Also shown is the interruption of washboarding by one worker bee to expel another insect that has ventured too close, then the return of that bee to its previous position and resumption of the washboarding activity. While the washboarding activity appears stereotyped, worker bees may interrupt it at any time to perform other guard duties or to interact with colony mates.

at greater distances depending upon wind dispersal conditions. The Nasonov pheromones may be the first indication to returning foragers that they are approaching the hive, and the tarsal pheromone may provide a final orienting target allowing foragers to quickly find and enter the hive without wasting time searching for it (Ferguson and Free 1981; Blum 1992; Topitzhofer 2013). It has been shown that the Nasonov and tarsal pheromones can operate in conjunction to produce a stronger synergistic effect than either one acting alone (Breed et al. 1992; Bartolloti and Costa 2014).

Figure 8. Link to video showing washboarding worker bees at the entrance to the second hive, with returning foragers quickly darting into the nest past other workers (1700 hrs, 28.9°C). [https://www.youtube.com/watch?v=sGvgYfO-5uE] The tarsal pheromone, which may act as a proximal attractant identifying the nest entrance for returning foragers, might also be strengthened in its effect by the repeated scraping of the forelegs of washboarding bees. This might help explain the incessant, repetitive washboarding by a mass of workers at the hive entrance, which would seem superfluous if cleaning a small patch were the only function. Washboarding activity is also much decreased or absent in cool weather and other times when foraging flights are not taking place.

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