

REVIEW

Open Access



Current knowledge about behaviors of honey bee queens with highlighting of the importance future studies

Hossam F. Abou-Shaara^{1*} , Nuru Adgaba² and Ahmad A. Al-Ghamdi²

Abstract

Background: There is one queen in each honey bee, *Apis mellifera* L., colony under normal conditions. This queen performs egg laying and pheromonal control in the colony. All genetic characteristics of bee workers and drones depend on the queen. This reflects the importance of bee queen in the colony. In this review, behaviors of honey bee queens are presented and further studies are suggested to fill in gaps in knowledge.

Main body: The major studies about behaviors of honey bee queens either inside or outside the colony were reviewed. Some behavioral aspects especially egg laying pattern, sperm storage and utilization, conflict between queens, and the role of the queens in swarming and absconding have gained relatively few attention. Also, some other points such as the ability of a queen to transmit parasites after mating to her offspring and effects of pesticides on queen rearing and characteristics of emerged queens were highlighted.

Conclusion: This study highlighted the points that require further detailed studies. This review article may stimulate others toward performing specific future studies on bee queens.

Keywords: Honey bees, *Apis mellifera*, Queens, Egg, Ethology, Pheromones

Background

Honey bees are super-organisms live in colonies consist of three castes: one mother queen, thousands of sterile workers, and few hundreds of drones. In very few cases, more than one queen can be existed in the same colony for a short period of time (Butler, 1957). The queen is the main reproductive member of the colony. Specific behaviors are expressed by the queen during her life. Virgin queens, after emergence, fight each other (Fletcher, 1978; Schneider et al., 2001) until the winning of only one queen to be subsequently the mother of the colony. Then, the queen makes nuptial flights outside the colony to mate with many drones (Cobey, 2007; El-Niweiri & Moritz, 2011; Heidinger et al., 2014; Lensky & Demter,

1985; Tibor et al., 1987). After mating flight, the queen stays in the nest to lay eggs (fertilized eggs to give workers and unfertilized eggs to give drones), and to control the behaviors and physiology of the workers using her pheromones. Egg laying and pheromonal control are the main tasks of the queen (Cobey, 2007; Moritz & Kuhnert, 1984; Naumann et al., 1991; Seeley, 1979; Tibor et al., 1987). Basically, the queen does not leave the colony except in case of absconding or swarming (Fell et al., 1977; Grozinger et al., 2014). Herein, these behaviors are described and further studies are suggested. This review paper covers all *Apis mellifera* honey bee subspecies except the Cape honey bees, *A. m. capensis*, because this subspecies has some unique behaviors unlike the other subspecies.

*Correspondence: entomology_20802000@yahoo.com

¹ Department of Plant Protection, Faculty of Agriculture, Damanhour University, Damanhour 22516, Egypt

Full list of author information is available at the end of the article

Main text

Process of queen rearing and conflict between queens

In normal cases, honey bee colony is headed by one queen only. Honey bee workers can rear additional queens at three cases: emergency, supersedure and reproductive swarming. Emergency queens are raised in queenless colonies, while supersedure happens in colonies headed by diseased or aged queens. Reproductive swarming occurs during active seasons. One or more new queens are reared during supersedure (Butler, 1957), and brood perhaps is moved by worker bees into empty queen cells (Butler, 1957; Punnett & Winston, 1983). Supersedure happens mostly during the swarming season (Allen, 1965). In fact, queen infected with *Nosema ceranae* induced the production of supersedure queen by workers (Alaux et al., 2011). More investigations on the impacts of infected queens with diseases on queen rearing activity in bee colonies are needed. The process of queen rearing is regulated by workers that built different numbers of queen cells from different ages of brood (Hatch et al., 1999), and queen age is a significant element over queen quality (Tarpy et al., 2000). During queen rearing, worker bees cooperate to rear queens of similar reproductive potential (Tarpy et al., 2004). Indeed, queen quality traits are regulated by preventing the development of low-quality queens by workers (Tarpy et al., 2016). For research purposes, the queen body weight is utilized as a reliable indicator of potential colony productivity (De Souza et al., 2013). Other indicators for queen quality require additional investigations.

Pesticides can affect queen rearing colonies. The exposure of queen larvae to coumaphos during their development increased the percentage of grafted cell rejection up to 50% and the pre-emergence pupae had low weight (Collins et al., 2004). Moreover, exposure of queen rearing colonies to sub-lethal doses of pesticides (chlorpyrifos and fungicide Pristine) showed less emergence rates of reared queens than control colonies (DeGrandi-Hoffman et al., 2013). Additional studies on the potential effects of pesticides on characteristics of emerged queens would be paramount important.

The emerged virgin queens engaged in a conflict until only one queen becomes the mother of the colony. Virgin queens have specific defense strategies against their rivals. Usually, virgin queens attack other queens prior to their emergence from the queen cells and sting them. Piping of virgin queens in the presence of other queens is considered as activating conflicts (Fletcher, 1978). Virgin queens that vibrate at higher rates can remove more rivals (Schneider et al., 2001). Also, during the conflict, the queen sprays her rectal contents toward the rival queen as a defense strategy (spraying behavior) (Tarpy & Fletcher, 2003). Moreover, fecal materials of virgin

queens have a role in repelling workers and stimulating grooming behavior (Post et al., 1987). Waxy esters composed of 8–14 carbon acids and 6–14 carbon alcohols were detected in feces of queens, and it was suggested that these esters have a role in nest-mate recognition (Breed et al., 1992). Workers play role during the conflicts without killing the queens but may immobilize them (Gilley & Tarpy, 2005). The conflict strategies between honey bee queens in different subspecies need to be investigated well.

Mating flight

The virgin queens, after emergence, stay in the colony for a short period prior to mating. This period depends on the subspecies and climatic conditions such as temperature and rainfall (El-Niweiri & Moritz, 2011; Heidinger et al., 2014; Lensky & Demter, 1985; Tibor et al., 1987) as well as the availability of drones (Cobey, 2007) especially mating which occurs in the air within a few seconds (Gary, 1963). The usual numbers of drones that mate with a queen are between seven to ten (Taber & Wendel, 1985) and up to 45 (Cobey, 2007; Moritz et al., 1996; Neumann & Moritz, 2000). Low-quality queens resulted from older worker larvae and mated with fewer drones (Tarpy et al., 2011). Single insemination resulted in fewer spermatozoa entering the spermatheca than did multiple inseminations (Bolten & Harbo, 1982). It is better for the queens to mate with as much drones as possible because better colony performance was found in colonies headed with queens inseminated with 30 to 60 drones or over 15 drones (Delaplane et al., 2015). However, seven mates at least or more can be considered as sufficient (Tarpy & Pettis, 2013; Tarpy et al., 2012). Queen mating can occur at distances up to 16.2 km (Peer, 1957) but during mating drones select the shortest way to a fast mate (Gries & Koeniger, 1996).

Nuptial flight frequencies of queens depend on mating success in the previous nuptial flights (Schluns et al., 2005). Sperms are stored in the spermatheca after mating. The number of spermatozoa stored in the spermatheca is not impacted by the queen defection before insemination but vice versa with sperm viability (Czakońska et al., 2010). Sperms can stay alive for a long period, and secretions from spermathecal glands of mated queens are essential for viability of sperm (den Boer et al., 2009). Few studies concentrated on the viability of sperms in the spermatheca and the maximum time that sperms can stay alive. Queens fertilize all eggs when receiving 50% fresh semen or more (Collins, 2000). A recent study showed the transamination of deformed wing virus to queens during mating with infected drones (Amiri et al., 2016). Further studies on the possibility of diseases transamination during mating are required. Workers at

one to 11 days old are responsible for feeding the mated queen, and the period of each feed is about 47 s (Allen, 1955). Very few studies were done on queen feeding. The feeding dynamic of mated queens across seasons by the nurse workers requires additional investigations.

The queens can naturally mate during all seasons except in winter in temperate regions but spring was found as the better season over autumn at different regions (Al-Ghzawi & Zaitoun, 2008; Jhaji et al., 1992; Moritz & Kuhnert, 1984). So far, there is no any evidence for the occurrence of queen mating in the hive. However, queens can mate with drones from the same colony and from other colonies or apiaries in the open space. It is possible to control queen mating by using isolated areas, e.g., islands, or by using the artificial insemination (Cobey, 2007; Kaftanoglu & Peng, 1982).

Egg laying

Some physiological and behavioral changes occurred after queen mating (Tanaka & Hartfelder, 2004), and changes in the ovaries happen faster than changes in the brain (Kocher et al., 2008). The newly mated queens take a period prior to the onset of egg laying. This period ranges from 5 days up to 4 weeks (Cobey, 2007; Moritz & Kuhnert, 1984; Tibor et al., 1987). This depends greatly on mating conditions, season, and temperature inside the colonies (Schluns et al., 2005; Woyke & Jasinski, 1990), and distance from the apiary at which mating occurred (Peer, 1957). The queen can lay up to 1500 eggs per day, but this number varies according to many factors including season, colony strength, and diseases prevalence (Moore et al., 2015). The queen normally lays one egg per cell. There are two types of eggs: fertilized (diploid) and unfertilized (haploid). The fertilized eggs are laid in small wax cells (worker cells), while the unfertilized ones are laid in relatively larger cells (drone cells). The sizes of the cells are greatly relying on the bee subspecies. Adding combs with large cells to colonies with small bees in size (e.g., Yemeni honey bees) can disturb the normal egg laying manner of the queens (Abou-Shaara, 2013). The role of cell size in egg laying ability of the queens needs detailed studies. Workers and queens are developed from fertilized eggs unlike drones. The queen has a physiological mechanism to control the fertilization of eggs. All eggs in worker cells are fertilized; hence, they are heterozygous at least on one microsatellite locus, while eggs from drone cells are unfertilized as eggs had a single band at the B124 locus (Ratnieks & Keller, 1998), and the complementary sex determiner gene must be heterozygous for female development (Beye et al., 2003). About one to ten spermatozoa are released per egg (Woyke et al., 1966). The number of sperms released per egg during fertilization worth further studies. The queen determines

the population of drones rearing through regulating drone eggs production (Wharton et al., 2007). So far, there are no available comparisons among bee subspecies, and their hybrids regarding the ability of the queens to control the fertilization of eggs.

Drones are derived from unfertilized eggs. However, fertilized eggs laid in worker cells by inbred queens can produce low survival drone larvae (Woyke, 1964). Diploid drone larvae are mostly eaten alive by the workers instead of carrying them out of the hive (Woyke, 1963). Thus, adult drones from fertilized eggs are not seen in the hive. In very few cases and for temporary period, queens can lay more than one egg in single wax cells (Abou-Shaara, 2013). The pattern of egg laying differs from colony to colony. But in the perfect model, the queen should lay fertilized eggs at the center of the comb, while drone cells, pollen and honey at periphery. The brood pattern of a good queen should be circles of brood with the oldest brood in center while younger brood periphery with few skipped cells (Moore et al., 2015). The young queens lay more worker eggs than drone ones, while the older queens do the vice versa. Some queens could run out their stored sperms earlier than others. This point requires further investigations on bee subspecies.

Egg marking pheromones

The queen marks her eggs with specific signal which known as egg marking pheromone. Such signal is important to guide police workers to discriminate between eggs laid by the queen than those laid by the workers (Ratnieks, 1995). Workers are sterile but they can lay eggs in queenless colonies and in colonies headed by diseased or aged queens. Such workers are called egg laying workers. Large differences in gene expression between queens and sterile and reproductive workers (about 2000 genes) were found in brains as well as between sterile and reproductive workers (221 genes) (Grozinger et al., 2007). In fact, eggs laid by workers represented about 7% of the unfertilized eggs laid in the colonies (Visscher, 1996).

Queen eggs have diversity in the number of hydrocarbons and specific acetates of some fatty alcohols, alkenes and monomethyl alkanes than worker-laid eggs, while linear alkanes is coating all egg types (Katzav-Gozansky et al., 2003). Indeed, mating is not necessary for the queen to produce egg-marking signal (Beekman et al., 2004). Also, dufour gland is larger in queens than egg-laying workers, suggesting its role in reproduction (Abdalla & Cruz-Landim, 2001). Dufour's gland secretion constitutes part of a complex queen signal (Katzav-Gozansky et al., 2001). The correlation between queen age and egg marking pheromones requires further deep investigations.

Pheromonal control

The honey bee queen has many pheromones but the main pheromone is queen mandibular pheromone (QMP) (also known as queen substance). The main component of QMP is 9-keto-2(*E*)-decanoic acid (9-ODA). Mated queens produce 12–400 µg of 9-ODA/day, and retinue bees take the greatest amount (Naumann et al., 1991). The queen substance is surface transmitted by workers over transmission by food exchange, while airborne dispersal is a minor mechanism (Seeley, 1979). The most attractive body part of the queen to the workers is abdomen followed by head, and then thorax (Hazan et al., 1989). QMP is responsible for the ovary-regulating pheromonal capability of queens (Hoover et al., 2003). But pheromones of mandibular gland are not suspected to be as indicators of queen reproductive value (Strauss et al., 2008). Other pheromones are also used by the queen to control the colony beside QMP (Maisonnette et al., 2010). Outside the colonies, the QMP has role in attracting drones to mate with the virgin queens (Butler & Fairey, 1964). Drones can detect queen pheromone from long distances (Loper et al., 1993). 9-ODA is suggested to be responsible for attracting drones from a long-distance (Wanner et al., 2007).

Inside the colony, this pheromone has many roles: preventing queen cell production by workers, control attendance behavior, inhibit ovary development of workers and regulating the work within the colony. QMP can prevent queen cell production completely for a short period (2 days) (Pettis et al., 1995), and beside other signals over 6 days (Winston et al., 1990). The other signals include tarsal secretion (Lensky et al., 1981) and brood-associated signal (Pettis et al., 1997). Queen mandibular gland is more attractive than tergal gland secretions, and secretions mixture of queen tergal gland and mandibular gland (Wossler & Crewe, 1999). Queen replacement can be partially prevented by extracts of queens or 9-ODA, while building of queen cells during the swarming season cannot be reduced by continuous treatment with 9-ODA (Boch & Lensky, 1976).

Another four compounds are account for the retinue attraction by queens beside QMP (Keeling et al., 2003). In fact, QMP allows attendance of the queen (Vergoz et al., 2009). However, attendance behavior perhaps has a genetic basis over linking with response to QMP (Pankiw et al., 1995). As reviewed by Trhlin and Rajchard (2011), queen retinue pheromone (QRP) is a releaser pheromone attracting bees to the queen and is a primer pheromone in inhibiting the ovary development of workers physiologically. On the contrary, QMP did not prevent ovary development in workers at any dose (Willis et al., 1990). Also, the composition of QMP is not related to ovarian development of workers

(Plettner et al., 1993). However, extract of queen mandibular glands and synthetic (*E*)-9-oxo-2-decanoic acid impacted caged queenless workers to the level of queen-right workers (Kaatz et al., 1992). It seems that studies are contradicted in regard to the role of QMP in inhibiting the ovary development of workers. Hence, more experiments are still needed on this specific point.

Various activities in the colony are influenced by the queen pheromones. Colonies with freely moving queens have more comb building activity (Gilley, 2001). Also, the ontogeny of foraging and division of labor of honey bees can be controlled by QMP (Pankiw et al., 1998). Honey bee foragers can be attracted to crops by applying suitable concentrations of QMP (Currie et al., 1992). The role of applying queen-derived pheromones including QMP in activating crops pollination by honey bees requires additional experiments. It is clear that QMP has many roles but still additional studies are required to cover its roles in organizing the activities of workers within the colony especially comb building and foraging behavior.

Swarming and absconding

Swarming is the natural phenomena of reproduction by honey bee colonies (Grozinger et al., 2014). In this particular case, many queen cells up to 20 or more are built up. The queens do not leave their colonies except in case of swarming or absconding. In general, swarming is happened during the active seasons. For example, the majority of swarming happened during the first 2 weeks in June in Ithaca, USA, with virgin queen or a young mated queen (Fell et al., 1977). The intensity of swarming is differed according to colony subfamilies resulted from multiple mating of the queen (Kryger & Moritz, 1997). Queen piping happened prior to colony swarming (Simpson & Cherry, 1969), and bees in one-nest-box started in piping and in takeoff earlier than five-nest-box trials (Seeley & Visscher, 2004). The roles of the mother queen in swarming of the colony needs shading more lights.

All the bees including the queen leave the colony and nesting in another place during absconding. This behavior is very harmful to beekeeping. Absconding happens when the colony is not in a suitable location for staying due to intensive attack of ants, hornets or other bee enemies, exposing the colony to harsh cold or hot conditions or continuous disturbing (Abou-Shaara et al., 2017). Also, the intensive infestation with wax moths may lead to colonies absconding (Tsegaye et al., 2014). Queen behavior during this abnormal situation has not been widely investigated.

Conclusion

This study highlighted the points that require further detailed studies. It is clear that researchers focused on some behaviors especially queen mating and pheromonal control more than other behaviors. Notably, swarming and absconding have gained little attention across honey bee subspecies. The effects of pesticides on queen behaviors are a fertile field for future studies. Also, the transmission of diseases from drones to queens during mating as well as from queen to her offspring requires special attention due to the importance of this topic to honey bee health. This review is likely to be a helpful guide for researchers studying honey bee queens and teaching bee-keeping management.

Abbreviations

QMP: Queen mandibular pheromone; 9-ODA: 9-Keto-2(E)-decenoic acid.

Acknowledgements

Not applicable.

Authors' contributions

HA-S designed and wrote the first draft, and NA and AA-G revised and improved the manuscript. All authors read and approved the final manuscript.

Funding

Not applicable.

Availability of data and materials

All data that support the study are included in the manuscript.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Plant Protection, Faculty of Agriculture, Damanhour University, Damanhour 22516, Egypt. ²Bee Research Unit, College of Food and Agriculture Sciences, King Saud University, P.O. Box 1460, Riyadh, Saudi Arabia.

Received: 24 June 2020 Accepted: 1 September 2021

Published online: 08 September 2021

References

- Abdalla, F. C., & da Cruz-Landim, C. (2001). Size differences in the Dufour gland of *Apis mellifera* Linnaeus (Hymenoptera, Apidae) between and within the female castes. *Revista Brasileira De Zoologia*, *18*, 119–123.
- Abou-Shaara, H. F. (2013). Abnormal behaviors mediated by nest cell size: A case study with Yemeni honey bees. *Egyptian Academic Journal of Biological Sciences*, *6*, 23–27.
- Abou-Shaara, H. F., Owayss, A. A., Ibrahim, Y. Y., & Basuny, N. K. (2017). A review of impacts of temperature and relative humidity on various activities of honey bees. *Insectes Sociaux*, *64*, 455–463.
- Alaux, C., Folschweiller, M., McDonnell, C., Beslay, D., Cousin, M., Dussaubat, C., Brunet, J.-L., & Le Conte, Y. (2011). Pathological effects of the microsporidium *Nosema ceranae* on honey bee queen physiology (*Apis mellifera*). *Journal of Invertebrate Pathology*, *106*, 380–385.
- Al-Ghazawi, A., & Zaitoun, S. (2008). Origin and rearing season of honeybee queens affect some of their physiological and reproductive characteristics. *Entomological Research*, *38*, 139–148.
- Allen, M. D. (1955). Observations on honeybees attending their queen. *British Journal of Animal Behaviour*, *3*, 66–69.
- Allen, M. D. (1965). The production of queen cups and queen cells in relation to the general development of honeybee colonies, and its connection with swarming and supersedure. *Journal of Apicultural Research*, *4*, 121–141.
- Amiri, E., Meixner, M. D., & Kryger, P. (2016). Deformed wing virus can be transmitted during natural mating in honey bees and infect the queens. *Scientific Reports*, *6*, 33065. <https://doi.org/10.1038/srep33065>
- Beekman, M., Martin, C. G., & Oldroyd, B. P. (2004). Similar policing rates of eggs laid by virgin and mated honey-bee queens. *Naturwissenschaften*, *91*, 598–601.
- Beye, M., Hasselmann, M., Fondrk, M. K., Page, R. E., & Omholt, S. W. (2003). The gene *csd* is the primary signal for sexual development in the honeybee and encodes an SR-type protein. *Cell*, *114*, 419–429.
- Boch, R., & Lensky, Y. (1976). Pheromonal control of queen rearing in honeybee colonies. *Journal of Apicultural Research*, *15*, 59–62.
- Bolten, A. B., & Harbo, J. R. (1982). Numbers of spermatozoa in the spermatheca of the queen honeybee after multiple inseminations with small volumes of semen. *Journal of Apicultural Research*, *21*, 7–10.
- Breed, M. D., Stiller, T. M., Blum, M. S., & Page, R. E. (1992). Honeybee nestmate recognition: Effects of queen fecal pheromones. *Journal of Chemical Ecology*, *18*, 1633–1640.
- Butler, C. G. (1957). The process of queen supersedure in colonies of honeybees (*Apis mellifera* Linn.). *Insectes Sociaux*, *4*, 211–223.
- Butler, C. G., & Fairey, E. M. (1964). Pheromones of the honeybee: Biological studies of the mandibular gland secretion of the queen. *Journal of Apicultural Research*, *3*, 65–76.
- Cobey, S. W. (2007). Comparison studies of instrumentally inseminated and naturally mated honey bee queens and factors affecting their performance. *Apidologie*, *38*, 390–410.
- Collins, A. M. (2000). Relationship between semen quality and performance of instrumentally inseminated honey bee queens. *Apidologie*, *31*, 421–429.
- Collins, A. M., Pettis, J. S., Wilbanks, R., & Feldlaufer, M. F. (2004). Performance of honey bee (*Apis mellifera*) queens reared in beeswax cells impregnated with coumaphos. *Journal of Apicultural Research*, *43*, 128–134.
- Currie, R. W., Winston, M. L., & Slessor, K. N. (1992). Effect of synthetic queen mandibular pheromone sprays on honey bee (Hymenoptera: Apidae) pollination of berry crops. *Journal of Economic Entomology*, *85*, 1300–1306.
- Czakońska, K., Chuda-Mickiewicz, B., & Chorbiński, P. (2010). The effect of induced defecation in honey bee queens on the number and viability of spermatozoa in the spermatheca after instrumental insemination. *Journal of Apicultural Research*, *49*, 154–158.
- De Souza, D. A., Bezerra-Laure, M. A. F., Francoy, T. M., & Gonçalves, L. S. (2013). Experimental evaluation of the reproductive quality of Africanized queen bees (*Apis mellifera*) on the basis of body weight at emergence. *Genetics and Molecular Research*, *12*, 5382–5391.
- DeGrandi-Hoffman, G., Chen, Y., & Simonds, R. (2013). The effects of pesticides on queen rearing and virus titers in honey bees (*Apis mellifera* L.). *Insecta*, *4*, 71–89.
- Delaplane, K. S., Pietravalle, S., Brown, M. A., & Budge, G. E. (2015). Honey bee colonies headed by hyperpolyandrous queens have improved brood rearing efficiency and lower infestation rates of parasitic Varroa mites. *PLoS ONE*, *10*, e0142985. <https://doi.org/10.1371/journal.pone.0142985>
- den Boer, S. P. A., Boomsma, J. J., & Baer, B. (2009). Honey bee males and queens use glandular secretions to enhance sperm viability before and after storage. *Journal of Insect Physiology*, *55*, 538–543.
- El-Niweiri, M. A. A., & Moritz, R. F. A. (2011). Mating in the rain? climatic variance for polyandry in the honeybee (*Apis mellifera jemenitica*). *Population Ecology*, *53*, 421–427.
- Fell, R. D., Ambrose, J. T., Burgett, D. M., De Jong, D., Morse, R. A., & Seeley, T. D. (1977). The seasonal cycle of swarming in honeybees. *Journal of Apicultural Research*, *16*, 170–173.

- Fletcher, D. J. C. (1978). Vibration of queen cells by worker honeybees and its relation to the issue of swarms with virgin queens. *Journal of Apicultural Research*, 17, 14–26.
- Gary, N. E. (1963). Observations of mating behaviour in the honeybee. *Journal of Apicultural Research*, 2, 3–13.
- Gilley, D. C. (2001). The behavior of honey bees (*Apis mellifera ligustica*) during queen duels. *Ethology*, 107, 601–622.
- Gilley, D. C., & Tarpy, D. R. (2005). Three mechanisms of queen elimination in swarming honey bee colonies. *Apidologie*, 36, 461–474.
- Gries, M., & Koeniger, N. (1996). Straight forward to the queen: Pursuing honeybee drones (*Apis mellifera* L.) adjust their body axis to the direction of the queen. *Journal of Comparative Physiology A*, 179, 539–544.
- Grozinger, C. M., Fan, Y., Hoover, S. E. R., & Winston, M. L. (2007). Genome-wide analysis reveals differences in brain gene expression patterns associated with caste and reproductive status in honey bees (*Apis mellifera*). *Molecular Ecology*, 16, 4837–4848.
- Grozinger, C. M., Richards, J., & Mattila, H. R. (2014). From molecules to societies: Mechanisms regulating swarming behavior in honey bees (*Apis* spp.). *Apidologie*, 45, 327–346.
- Hatch, S., Tarpy, D. R., & Fletcher, D. J. C. (1999). Worker regulation of emergency queen rearing in honey bee colonies and the resultant variation in queen quality. *Insectes Sociaux*, 46, 372–377.
- Hazan, M. D., Lensky, Y., & Cassier, P. (1989). Effects of queen honeybee (*Apis mellifera* L.) ageing on her attractiveness to workers. *Comparative Biochemistry and Physiology A*, 93, 777–783.
- Heidinger, I. M. M., Meixner, M. D., Berg, S., & Büchler, R. (2014). Observation of the mating behavior of honey bee (*Apis mellifera* L.) queens using radio-frequency identification (RFID): Factors influencing the duration and frequency of nuptial flights. *Insects*, 5, 513–527.
- Hoover, S. E. R., Keeling, C. I., Winston, M. L., & Slessor, K. N. (2003). The effect of queen pheromones on worker honey bee ovary development. *Naturwissenschaften*, 90, 477–480.
- Jhajji, H. S., VChahal, B. S., & Brar, H. S. (1992). Fabrication of queen trap for *Apis mellifera* L. and studies on the pre-mating period. *Indian Bee Journal*, 5, 63–67.
- Kaatz, H.-H., Hildebrandt, H., & Engels, W. (1992). Primer effect of queen pheromone on juvenile hormone biosynthesis in adult worker honey bees. *Journal of Comparative Physiology B*, 162(5), 88–92.
- Kaftanoglu, O., & Peng, Y.-S. (1982). Effects of insemination on the initiation of oviposition in the queen honeybee. *Journal of Apicultural Research*, 21, 3–6.
- Katzav-Gozansky, T., Soroker, V., Ibarra, F., Francke, W., & Hefetz, A. (2001). Dufour's gland secretion of the queen honeybee (*Apis mellifera*): An egg discriminator pheromone or a queen signal? *Behavioral Ecology and Sociobiology*, 51, 76–86.
- Katzav-Gozansky, T., Soroker, V., Kamer, J., Schulz, C. M., Francke, W., & Hefetz, A. (2003). Ultrastructural and chemical characterization of egg surface of honeybee worker and queen-laid eggs. *Chemoecology*, 13, 129–134.
- Keeling, C. I., Slessor, K. N., Higo, H. A., & Winston, M. L. (2003). New components of the honey bee (*Apis mellifera* L.) queen retinue pheromone. *Proceedings of the National Academy of Sciences*, 100, 4486–4491.
- Kocher, S. D., Richard, F.-J., Tarpy, D. R., & Grozinger, C. M. (2008). Genomic analysis of post-mating changes in the honey bee queen (*Apis mellifera*). *BMC Genomics*, 9, 232. <https://doi.org/10.1186/1471-2164-9-232>
- Kryger, P., & Moritz, R. F. A. (1997). Lack of kin recognition in swarming honeybees (*Apis mellifera*). *Behavioral Ecology and Sociobiology*, 40, 271–276.
- Lensky, Y., & Demter, M. (1985). Mating flights of the queen honey bee (*Apis mellifera*) in a subtropical climate. *Comparative Biochemistry and Physiology A*, 81, 229–241.
- Lensky, Y., Slabezki, Y., & More, S. (1981). The inhibiting effect of the queen bee (*Apis mellifera* L.) foot-print pheromone on the construction of swarming queen cups. *Journal of Insect Physiology*, 27, 313–323.
- Loper, G. M., Wolf, W. W., & Taylor, O. R. (1993). Radar detection of drones responding to honeybee queen pheromone. *Journal of Chemical Ecology*, 19, 1929–1938.
- Maisonnasse, A., Alaux, C., Beslay, D., Crauser, D., Gines, C., Plettner, E., & Le Conte, Y. (2010). New insights into honey bee (*Apis mellifera*) pheromone communication. Is the queen mandibular pheromone alone in colony regulation? *Frontiers in Zoology*, 7, 1–8.
- Moore, P. A., Wilson, M. E., & Skinner, J. A. (2015). Honey bee queens: Evaluating the most important colony member. Retrieved March 20, 2017, from <http://articles.extension.org/pages/73133/honey-bee-queens-evaluating-the-most-important-colony-member>
- Moritz, R. F. A., Kryger, P., & Allsopp, M. (1996). Competition for royalty in bees. *Nature*, 384, 522.
- Moritz, R. F. A., & Kuhnert, M. (1984). Seasonal effects of artificial insemination of honey bee queens (*Apis mellifera* L.). *Apidologie*, 15, 223–231.
- Naumann, K., Winston, M. L., Slessor, K. N., Prestwich, G. D., & Webster, F. X. (1991). Production and transmission of honey bee queen (*Apis mellifera* L.) mandibular gland pheromone. *Behavioral Ecology and Sociobiology*, 29, 321–332.
- Neumann, P., & Moritz, R. F. A. (2000). Testing genetic variance hypotheses for the evolution of polyandry in the honeybee (*Apis mellifera* L.). *Insectes Sociaux*, 47, 271–279.
- Pankiw, T., Huang, Z.-Y., Winston, M. L., & Robinson, G. E. (1998). Queen mandibular gland pheromone influences worker honey bee (*Apis mellifera* L.) foraging ontogeny and juvenile hormone titers. *Journal of Insect Physiology*, 44, 685–692.
- Pankiw, T., Winston, M. L., & Slessor, K. N. (1995). Queen attendance behavior of worker honey bees (*Apis mellifera* L.) that are high and low responding to queen mandibular pheromone. *Insectes Sociaux*, 42, 371–378.
- Peer, D. F. (1957). Further studies on the mating range of the honey bee, *Apis mellifera* L. *Canadian Entomologist*, 89, 108–110.
- Pettis, J. S., Higo, H. A., Pankiw, T., & Winston, M. L. (1997). Queen rearing suppression in the honey bee evidence for a fecundity signal. *Insectes Sociaux*, 44, 311–322.
- Pettis, J. S., Winston, M. L., & Collins, A. M. (1995). Suppression of queen rearing in European and Africanized honey bees *Apis mellifera* L. by synthetic queen mandibular gland pheromone. *Insectes Sociaux*, 42, 113–121.
- Plettner, E., Slessor, K. N., Winston, M. L., Robinson, G. E., & Page, R. E. (1993). Mandibular gland components and ovarian development as measures of caste differentiation in the honey bee (*Apis mellifera* L.). *Journal of Insect Physiology*, 39, 235–240.
- Post, D. C., Page, R. E., & Erickson, E. H. (1987). Honeybee (*Apis mellifera* L.) queen feces: Source of a pheromone that repels worker bees. *Journal of Chemical Ecology*, 13, 583–591.
- Punnett, E. N., & Winston, M. L. (1983). Events following queen removal in colonies of European-derived honey bee races. *Insectes Sociaux*, 30, 376–383.
- Ratnieks, F. L. W. (1995). Evidence for a queen-produced egg-marking pheromone and its use in worker policing in the honey bee. *Journal of Apicultural Research*, 34, 31–37.
- Ratnieks, F. L. W., & Keller, L. (1998). Queen control of egg fertilization in the honey bee. *Behavioral Ecology and Sociobiology*, 44, 57–61.
- Schluns, H., Moritz, R. F. A., Neumann, P., Kryger, P., & Koeniger, G. (2005). Multiple nuptial flights, sperm transfer and the evolution of extreme polyandry in honeybee queens. *Animal Behaviour*, 70, 125–131.
- Schneider, S. S., Painter-Kurta, S., & Degrandi-Hoffman, G. (2001). The role of the vibration signal during queen competition in colonies of the honeybee, *Apis mellifera*. *Animal Behaviour*, 61, 1173–1180.
- Seeley, T. D. (1979). Queen substance dispersal by messenger workers in honeybee colonies. *Behavioral Ecology and Sociobiology*, 5, 391–415.
- Seeley, T. D., & Visscher, P. K. (2004). Quorum sensing during nest-site selection by honeybee swarms. *Behavioral Ecology and Sociobiology*, 56, 594–601.
- Simpson, J., & Cherry, S. M. (1969). Queen confinement, queen piping and swarming in *Apis mellifera* colonies. *Animal Behaviour*, 17, 271–278.
- Strauss, K., Scharpenberg, H., Crewe, R. M., Glahn, F., Foth, H., & Moritz, R. F. A. (2008). The role of the queen mandibular gland pheromone in honeybees (*Apis mellifera*): Honest signal or suppressive agent? *Behavioral Ecology and Sociobiology*, 62, 1523–1531.
- Taber, S., Ill, & Wendel, J. (1985). Concerning the number of times queen bees mate. *Journal of Economic Entomology*, 51, 786–789.
- Tanaka, E. D., & Hartfelder, K. (2004). The initial stages of oogenesis and their relation to differential fertility in the honey bee (*Apis mellifera*) castes. *Arthropod Structure & Development*, 33, 431–442.
- Tarpy, D. R., & Fletcher, D. J. C. (2003). "Spraying" behavior during queen competition in honey bees. *Journal of Insect Behavior*, 16, 425–437.
- Tarpy, D. R., Gilley, D. C., & Seeley, T. D. (2004). Levels of selection in a social insect: A review of conflict and cooperation during honey bee (*Apis mellifera*) queen replacement. *Behavioral Ecology and Sociobiology*, 55, 513–523.

- Tarpy, D. R., Hatch, S., & Fletcher, D. J. C. (2000). The influence of queen age and quality during queen replacement in honeybee colonies. *Animal Behaviour*, *59*, 97–101.
- Tarpy, D. R., Keller, J. J., Caren, J. R., & Delaney, D. A. (2011). Experimentally induced variation in the physical reproductive potential and mating success in honey bee queens. *Insectes Sociaux*, *58*, 569–574.
- Tarpy, D. R., Keller, J. J., Caren, J. R., & Delaney, D. A. (2012). Assessing the mating “Health” of commercial honey bee queens. *Journal of Economic Entomology*, *105*, 20–25.
- Tarpy, D. R., & Pettis, J. S. (2013). Genetic diversity affects colony survivorship in commercial honey bee colonies. *Naturwissenschaften*, *100*, 723–728.
- Tarpy, D. R., Simone-Finstrom, M., & Linksvayer, T. A. (2016). Honey bee colonies regulate queen reproductive traits by controlling which queens survive to adulthood. *Insectes Sociaux*, *63*, 169–174.
- Tibor, I., Szabo, I., Mills, P. F., & Heikel, D. T. (1987). Effects of honeybee queen weight and air temperature on the initiation of oviposition. *Journal of Apicultural Research*, *26*, 73–78.
- Trhlin, M., & Rajchard, J. (2011). Chemical communication in the honeybee (*Apis mellifera* L.): A review. *Veterinarni Medicina*, *56*, 265–273.
- Tsegaye, A., Wubie, A. J., Eshetu, A. B., & Lemma, M. (2014). Evaluation of different nonchemical wax moth prevention methods in the backyards of rural beekeepers in the North West dry land areas of Ethiopia. *Journal of Agriculture and Veterinary Science*, *7*, 29–36.
- Vergoz, V., McQuillan, H. J., Geddes, L. H., Pullar, K., Nicholson, B. J., Paulin, M. G., & Mercer, A. R. (2009). Peripheral modulation of worker bee responses to queen mandibular pheromone. *Proceedings of the National Academy of Sciences*, *106*, 20930–20935.
- Visscher, P. K. (1996). Reproductive conflict in honey bees: A stalemate of worker egg-laying and policing. *Behavioral Ecology and Sociobiology*, *39*, 237–244.
- Wanner, K. W., Nichols, A. S., Walden, K. K. O., Brockmann, A., Luetje, C. W., & Robertson, H. M. (2007). A honey bee odorant receptor for the queen substance 9-oxo-2-decenoic acid. *Proceedings of the National Academy of Sciences*, *104*, 14383–14388.
- Wharton, K. E., Dyer, F. C., Huang, Z. Y., & Getty, T. (2007). The honeybee queen influences the regulation of colony drone production. *Behavioral Ecology*, *18*, 1092–1099.
- Willis, L. G., Winston, M. L., & Slessor, K. N. (1990). Queen honey bee mandibular pheromone does not affect worker ovary development. *Canadian Entomologist*, *122*, 1093–1099.
- Winston, M. L., Higo, H. A., & Slessor, K. N. (1990). Effect of various dosages of queen mandibular gland pheromone on the inhibition of queen rearing in the honey bee (Hymenoptera: Apidae). *Annals of the Entomological Society of America*, *109*, 234–238.
- Wossler, T. C., & Crewe, R. M. (1999). The releaser effects of the tergal gland secretion of queen honeybees (*Apis mellifera*). *Journal of Insect Behavior*, *12*, 343–351.
- Woyke, J. (1963). What happens to diploid drone larvae in a honeybee colony. *Journal of Apicultural Research*, *2*, 73–75.
- Woyke, J. (1964). Genetic proof of the origin of drones from fertilized eggs of the honeybee. *Journal of Apicultural Research*, *4*, 7–11.
- Woyke, J., & Jasinski, Z. (1990). Effect of the number of attendant worker bees on the initiation of egg laying by instrumentally inseminated queens kept in small nuclei. *Journal of Apicultural Research*, *29*, 101–106.
- Woyke, J., Knytel, A., & Bergandy, K. (1966). The presence of spermatozoa in eggs as proof that drones can develop from inseminated eggs of the honeybee. *Journal of Apicultural Research*, *5*, 71–78.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article

Submit your next manuscript at ► [springeropen.com](https://www.springeropen.com)
