Influence of Nest-Site Characteristics on Honey Bee Colonies

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Abstract

Apis mellifera, the European Honey Bee, is extremely responsive to the environment in which a colony constructs its nest. Given the intricacy of their colonial societies, honey bees have the capacity for observational learning and social immunity, which allows them to adapt to their surroundings rapidly. Characteristics of the nest-site such as its volume, insulation, wall texture, entrances, and distance from other nests each play a role in allowing these insects to survive year round in varying climates. When housed in suboptimal nesting environments, instincts adapted for self preservation are disrupted and the benefits of colonialism are subsequently negated. This review serves to provide a summary of individual effects of several nest-site characteristics in the lives of honey bees.

Introduction

The European Honey Bee, *Apis mellifera,* builds nests of wax combs inside of pre-existing cavities to house a reproductive queen, her brood, together with stores of pollen and honey to sustain the population in seasons of depleted resources. Honey bees reproduce individually as male drones providing semen for a virgin queen during a “nuptial flight”, with which she will return home and begin laying unfertilized drone-bound eggs, and fertilized worker-bound eggs (Engels, 1990). They also reproduce as whole colonies, the process referred to as swarming, when a queen, new or old, and a majority of the colony leave the hive in search of another nest-site (Simpson, 1963). Due to the various mechanisms *A. mellifera* has evolved to diversify its genome, the rate with which its populations can adapt to new environments and pathogens is fairly rapid (Mikheyev, 2015).

The colony’s annual survival is also bolstered by individual’s behavioral responses to the environment, colony members, and potentially threatening organisms, including bees from other colonies. The downfall of a colonial society is the potential risks posed by high population density (Schmid-Hempel, c. 2, 1998). Transmission of pathogens - most commonly through parasites vectoring viruses - can take place through any contact between honey bees. Horizontal transmission occurs between individuals of the same generation, carried between workers, drones, and brood. Vertical transmission occurs between different generations, most commonly from queen to brood. Both instances of transmission can arise within a single colony and spread to other nearby colonies via robbing, swarming, mating, and accidental drift (Fries & Camazine, 2001).

Pressures, such as transmission in dense populations, are managed via behavioral mechanisms of the honey bee: swarming, hostility, disposal of waste and deceased, grooming, resin collection for propolis production, and avoidance of infected individuals and substances. These such behavioral responses have been coined as “social immunity” in a publication of Current Biology by S. Cremer, S. Armitage, and P. Schmid-Hempel (Cremer et al., 2007). The degree by which a colony expresses each aspect of social immunity is dependent upon its genotype in correlation with environmental factors, i.e. location, climate, and seasonality (Uzunov et al., 2014).

Despite the defenses they have acquired, populations of *A. mellifera* have faced global decline due to compounding effects of disease, infestation, and exposure to harmful environmental factors in recent years. The species performs a significant portion of global pollination, and are regarded as the most popular species selected for crop pollination (Garantonakis et al., 2016), responsible for roughly 13% of floral visits to 5% of plant species across all plant networks worldwide (Hung et al., 2018). According to the National Agricultural Statistics Service performed by the USDA, in apiaries with at least five hives, were 2.68 million colonies of honey bees housed in the United States as of 2023 (National Agricultural Statistics Service ([NASS], 2023). From these same colonies, rates of infestation of the endoparasitic mite, *Varroa destructor*, ranged from 39.7-50.9% for the period of January through March of 2023 ([NASS], 2023). Also, 107,630 colonies were lost from symptoms of Colony Collapse Disorder (CCD), showing a 25% increase from the same quarter of 2022 ([NASS], 2023). These substantial losses have been attributed to the stressful living conditions introduced by the commercial beekeeping industry. Namely exposure to toxins via supplemental feeding in addition to chemical treatments to the hive and foraging grounds (Frazier et al., 2015). Poor conditions are exacerbated by the movement of managed colonies during commercial pollination events. One of these is the California Almond Pollination, in which an estimated 89% of all US honey bee colonies are brought to California's Central Valley to pollinate one crop, in the process transmitting any novel pathogens they have encountered on their journey (Fenton et al., 2023; Simone-Finstrom et al., 2016).

In contrast, populations of feral honey bees have, in some cases, developed resistance to the pests they've been exposed to (Harbo & Hoopingarner, 1997; Seeley, 2007). Dr. Thomas D. Seeley - Professor of Biology at Cornell University - has spent his career researching feral honey bees in the forests of New York. His publications include observations of wild colonies before and after the introduction of *Varroa destructor* to the United States in the late 1980s. For his doctoral thesis, Seeley focused on honey bee swarming behavior, the process in which a few bees scout out, debate over, and move the colony to a new nest-site. Observing this behavior revealed the honey bee's natural preference for nest-sites, and the methods they use to analyze each site (Seeley, 1977). Seeley inferred that, given the chance, bees would select nest-sites that complement their evolutionary adaptations.

Seeley remarks (2019), "...there are stark differences between the original environment that shaped the biology of wild honey bee colonies – their environment of evolutionary adaptation (EEA) – and the current living conditions of managed colonies" (p. 278). Managed colonies express the pressures of sub-optimal living environments through their increased susceptibility to parasites and pathogens compared to their feral counterparts. Providing colonies of honey bees with nesting sites more suitable to their needs and local climate could elicit positive behavioral responses. Possibly including increased grooming, propolis hoarding, and swarm production, these behaviors have been adapted to protect colonies from parasites and pathogens.

Nest-Cavity Volume

The space available within a nest cavity seemingly has only one requirement: accommodate the comb, food supply, brood, and adult population of honey bees. However, the space itself dictates the potential growth of the colony within. Since honey bees do not have the capability to alter the dimensions of their nest cavities, the colony must grow to fit inside. When it has reached the full capacity of the nest, the colony will send out a swarm. James Simpson and Inge Riedel of The Rothamsted Experimental Station in Harpenden, England suggest that overcrowding of adult bees stimulates the rearing of new queens to prepare for swarming (1963).

In a swarm, the mother queen will abscond with roughly half of the worker population before her daughter queen(s) emerge and terminate her rivals. The swarm coordinates to form a bivouac at a temporary site, from which scouts begin the search for a new nest-site. Scout bees, first described by Martin Lindauer in 1955, are the older bees with the most experience foraging and navigating the area, making up nearly 5% of the swarm population (Seeley, 1979). At this time, scouts explore potential nest-sites and report back to the swarm to advertise their preferred location for other scouts to evaluate and vote upon.

Studies by Lindauer (1951, 1953, 1955), Seeley and Morse (1976), and Seeley (1977) investigated the architecture of feral nest-sites, showing the same properties and tactics of evaluation by scout bees. By manipulating experimental nest-cavities to deprive specific sensory inputs to scouting bees, Seeley suggested that walking the inner surfaces of a cavity serves as the bees' method of volume perception (1977). The average volume of nest-cavity preferred by scouts ranges from 30 to 60 liters (Seeley & Morse, 1976; Seeley, 1977; Loftus et al, 2016). Smaller hives of 10 to 13 liters are preferred in warmer climates, where honey bees have greater traces of Africanized genetics (Morse et al., 1993). These volumes are vastly different from those found in commercial beekeeping. A standard Langstroth "deep" with 10-frames is roughly 42 liters, to be topped with "supers" to maximize honey production; they can reach up to 160 liters total.

Having a bigger hive to create a bigger colony appears to be an efficient strategy for commercial beekeeping; the colony will grow to fit inside, swarm less, and store more resources. A large colony can result in a bigger honey harvest, but honey is not the only thing being produced within the hive. The endoparasitic mite, *Varroa destructor,* breeds inside the sealed brood cells of a honey bee nest, and more room for brood results in greater numbers of *V. destructor* (Loftus et al., 2016). The need for swarming is suppressed when the colony has more room to spread into, so there is no halt in brood rearing for swarm preparation, allowing *V. destructor* to breed continually in large commercial hives.

To test the effect of this broodless period in small swarming hives, J. Loftus, M. Smith, and T. Seeley at Cornell University compared swarming frequency, *V. destructor* infestation rates, disease incidences, and colony survival between two groups of colonies for two years (2016). One group was housed in small hives of 42 liters and left without swarm-suppression treatments to mimic the behavior of feral colonies. The others were housed in large hives of up to 168 liters and treated to suppress swarming in the manner of commercial colonies. Their results support the conclusion that feral colonies benefit from occupying small nest cavities and swarming frequently. By the end of the study, small hives had about one-third of the *V. destructor* infestation rate of adult bees in large hives (Loftus et al., 2016). None of the small hives showed signs of any disease carried by *V. destructor*, while seven of the twelve large hives displayed symptoms of deformed wing virus (DWV) and subsequently died. Volume of space for the nest-site of *A. mellifera* has been proven to affect the colony’s rate of growth, reproduction, and pathogen resistance.

Nest-Cavity Insulation

Within the allotted volume of the honey bee’s nest-cavity, ambient conditions such as temperature, humidity, and carbon dioxide levels must also be regulated to meet the specific needs of its occupants. Brood development and activity of adult bees are directly related to temperature, therefore, a hive must be optimal for insulation and thermoregulation. Brood nest temperature ranges between 33℃ and 36℃ for rearing, and brood development can be sped up by reaching higher temperatures (Petz et al., 2004). Many differences have been observed in the behavioral performance, memory, and immunity of adult bees reared at abnormal temperatures during larval and pupal development.

Jürgen Tautz and others at the University of Würzburg, Germany (2003), incubated honey bee pupae at 32℃, 34.5℃, and 36℃, which were marked after emergence and introduced into colonies to grow into foraging adults. The only differences observed between the temperature-treated bees and the foster-colony bees were found when foraging from a feeder 200 m from the hive. Those raised at 32℃ completed approximately 20% of dance circuits compared to higher-temperature groups with greater variance in the duration of the waggle phase. They conclude that bees reared at lower temperatures perform poorly at dance communication, and such behavior can result in less nectar inflow for the colony. Poor dance communication may also affect the process of nest-site scouting and deliberation, as it is used to advertise potential nests as well as food sources.

Julia C. Jones and others at the University of Sydney, Australia (2005) sought differences in developmental stability - short and long term memory - in bees reared outside the normal temperature range. Workers, queens, and drones, all offspring of the same queen, were incubated consistently at 32℃, 33℃, 34℃, 35℃, 36℃, and 37℃. The difference in emergence times between bees reared at either end of the temperature range was roughly 48 hours. To test the honey bees' memory, workers were immobilized and trained to respond to a sucrose solution treat containing an odor (limonene) by extending their proboscis. This conditioning was completed once for short-term trials and three times at intervals of 6 minutes for long-term trials. If, upon a final test an hour later for short-term and 24 hrs later for long-term, the bee extended its proboscis after being exposed to the odor without reward, it was deemed a "good learner". Developmental stability was determined by examining fluctuating asymmetry, or variations in bilateral symmetry of individuals.

The results of Jones's study showed noticeable disparities only in the short-term memory of bees reared at 32℃ and 33℃, suggesting that the most important consequence of irregular rearing temperatures are logical deficiencies, not physiological. They also remark upon the different locations of rearing within the nest among individuals. Queens and drones may face greater changes in temperature and subsequent developmental differences because of their placement along the outside of the nest, as opposed to workers reared in the center. Reduced brood rearing temperature has even been correlated to increased susceptibility to infestations of tracheal mites (*Acarapis woodi*), researched by John B. McMullan and Mark J.F. Brown at Trinity College Dublin, Ireland (2004). Comparing the concentration of mites on bees reared at 30℃ and 34℃, infestation increased by a factor of two in the colder-treated colonies (McMullan & Brown 2004).

Honey bees are extremely sensitive to temperature, and require specific climates for different functions within their colony. When inhabiting well-insulated hives that keep warm through the night, foraging bees will emerge earlier in the morning to begin collecting resources. If the hive is too cold in the morning, the bees must wait for the rising sun to warm them before they begin their tasks (Erdoğan, 2019). In a study performed at Bayburt University Apiculture Application and Research Station in Turkey, Yaşar Erdoğan (2019) compared the behavior, development, and efficiency of honey bee colonies housed in hives with varying types of insulation (wood, polystyrene, and composite insulation). The most insulative was the composite hive, which resulted in a brood area development rate 23.99% greater than the wooden and polystyrene hives, and 16.25% the adult bee coverage per frame (Erdoğan 2019). Improved time insulation resulted in 19.03% more "willingness" to work first thing in the morning as opposed to heating or ventilating the hive (Erdoğan 2019).

Regulating the temperature of the hive requires the consumption of stored honey, so wooden hives like those used in traditional beekeeping with poor insulation can result in 34.89% less honey harvested in comparison to well insulated hives. Commercial beekeeping operations sometimes utilize polystyrene hives for ease of transportation, but these are easily damaged by moving, sun exposure, and rodents, and produce 14.23% less excess honey (Erdoğan, 2019). Housing honey bees in nest cavities lacking insulative walls decreases the colony's energy efficiency and can contribute to collapse in extreme climates. In order to actively regulate the nest's temperature, workers must consume excess energy stored as honey, may not initiate foraging before their surroundings warm, and can suffer from developmental deficiencies, ultimately reducing the amount of energy stored to endure winter.

Nest-Cavity Entrances

In order to regulate the ambient climate of the nest themselves, *A. mellifera* has adapted several strategies of thermoregulation and ventilation to control the flow of air through the nest. Adult bees perform best at temperatures between 21℃ and 35℃, but under 14℃, they must form a cluster to preserve heat and cannot move to collect honey or pollen (Abd-Elmawgood et al., 2015). The cluster reduces the area of cooling surfaces of the whole colony, constricting tighter together with cold expanding with heat. Within the cluster, the outermost bees are packed the closest around a more loosely arranged core where individuals have greater room to move. Rapidly moving bees in the centers of clusters are believed to produce more heat than their high metabolisms alone, however these same movements have also been observed in heated hives during summer months, so heat production may not be the intention (Simpson, 1961). Still, special heat producing movements could take place without observable movement, simply by opposing muscular tensions accompanied by increased breathing rates.

In rising temperatures, the cluster is limited by the volume of the nest and cannot expand indefinitely, so the alternative tactic in warmer seasons is ventilation. Bees form chains and clusters inside the hive and collectively fan their wings to move air out of the nest entrance, allowing them to sense upstream nest temperatures and regulate their placement and fanning speeds as needed. Nests with multiple entrances often use convection to move air up through the cavity at the rate of 0.17 liters per second, but bees may also fan at a bottom entrance to move air downward as fast as 1.0 liter per second (Simpson, 1961). In nests with only one entrance, cool outside air and hot inside air must move through the same opening to create turbulence in the nest. This feat is accomplished in two different ways depending on the size of the nest entrance.

Edward E. Southwick and Robin F.A. Moritz (1987) observed “tidal” ventilation in nests with small round entrances (2 cm diameter, 3.14 cm^2 area); resembling slow breathing, bees switch between periods of fanning air inward and outward through the entrance to regulate the nest climate. They recorded an average volume of 0.42 liters of air per minute (0.007 liters per second) moved through the hive during the day with a frequency of 2.9 “breaths” per minute (Southwick & Moritz, 1987). Hives with larger entrances exhibit ventilation behavior that separates the single entrance into an inflow and outflow area simultaneously. Jacob Peters, Orit Peleg, and L. Mahadevan (2018) monitored the positions of fanning bees at their nest entrance in such a hive and the resulting flow patterns under naturally varying conditions, tracking the temperature and total number of fanning bees visible at nest entrances. Fanning bees would remain at the entrance under relatively stable conditions, but numbers would increase and spread in warmer conditions to decrease and condense when conditions became cooler (Peters et al., 2018).

In Seeley and Morse’s first investigations of feral nest-sites in the vicinity of Ithaca, N.Y. (1976), external observations were made on 39 tree nests with 21 being preserved and collected for dissection to describe their natural nest architecture. The majority of nests (70%) had relatively small entrances, the modal entrance area being 10 to 20 cm^2. Knotholes, cracks, and holes among roots served as entrances, most nests (79%) having singular entrances with some (21%) having up to five (Seeley & Morse, 1976). The two regarded the predominance of entrances located at the bottom of nests as highly improbable ($P < 0.002$) had their position been randomly selected, suggesting that this formation was likely advantageous for colonies of honey bees. They also describe some preparation of nest entrances performed by the bees; smoothed areas of bark extending up to 30 cm from entrance holes, being scraped down by young bees and cracks being filled with propolis (Seeley & Morse, 1976). It is surmised that this preparation will improve surveillance and defense of the nest as well as the flow of bees, air, food, and construction materials through the interface between nest and environment.

Seely and Morse conclude that the directional orientation of the nest entrance is of no consequence to colonies, finding no trends among their observed nests (Seeley & Morse, 1976). This conception is opposed in a study performed by William Meikle, Milagra Weiss, and Eli Beren at the Carl Hayden Bee Research Center in Tucson, AZ (2022). 20 hives were separated into random groups facing each cardinal direction and their growth and activity was monitored by automated weighing every five minutes and temperature recording every 30 minutes for over a year. Because temperature and light conditions can be affected by orientation at the entrance to hives, a difference in hive activity was observed in each group. East-facing hives began and ended daily flight activity approximately 50 minutes earlier than other groups and lost less weight each day, 62 grams per day as opposed to 100 grams (Meikle et al., 2022). East-facing hives were also sustained at cooler clustering temperatures, approximately 7℃ less on average, which suggests that their lessened weight loss was due to the reduced need to consume food to sustain thermoregulation (Meikle et al., 2022). The earlier light through the entrances of east-facing hives likely plays a large role in the activity patterns of occupant honey bees, especially in seasons of reduced daylight hours and temperatures. Nest entrances play a large role in energy regulation for honey bees, serving as the conduits for not only essential resources and activities, but information needed for survival.

Nest-Cavity Surfaces

As observed in Seeley and Morse's feral nest-site investigations (1976), *A. mellifera* does undertake some degree of "renovation" to create suitable nesting environments. While they cannot excavate any substantial amounts of material needed to create a nest-cavity, the bees can perform surface level alterations to their nesting environments: the most common example of this behavior is propolis hoarding. Foraging workers will collect plant resins, antimicrobial compounds produced by plants, from their surrounding environments and transport them to the nest in the same fashion as pollen on the corbicula. Resins are unloaded in the nest, not at the nest entrance but near the site of propolis application (Nakamura & Seeley, 2006), and mixed with varying amounts of wax to form a sort of cement used to seal cracks and holes in the nest (Simone et al., 2009).

When residing in tree cavities, feral bees will coat the entire inner surface of their nest cavity in a layer of propolis, generally 0.3 to 0.5 mm thick, to form a "propolis envelope" (Seeley & Morse, 1976). During this process, surface smoothing and propolis deposition is focused around areas where comb is present, leaving the area below combs in a layer of punkwood up to 20 mm thick. This preparation of the cavity is thought to assist in the solid attachment of the combs and to rid the nest of fungal decay. The propolis envelope also serves to repel water from leaking into the nest-interior through cracks and holes, as well as through the capillary ability of end-grain wood. The honey bee's method of applying propolis leaves microscopic gaps in the envelope small enough to allow the passing of water vapor, but prevents the formation of droplets due to surface tension, creating a semi-permeable membrane around the nest to assist with climate control and nectar evaporation ("Propolisforschung," n.d.). Bees can be stimulated to deposit propolis by increasing textural stimuli in hive interiors (Hodges et al., 2019); commercially available plastic propolis traps, sawn kerf marks, or mechanized roughening can be added to manmade hives to emulate the roughness of a tree cavity and increase propolis deposition.

The propolis envelope serves not only as a physical barrier to protect honey bee colonies, but also as an immune barrier. The Honey Bee Genome Sequencing Consortium (2006) found roughly one-third as many genes in 17 gene families responsible for innate immunity in comparison to the genome sequences of *Drosophila* (fruit fly) and *Anopheles* (mosquito). The hypothesis has been proposed that the immune defenses of individual honey bees may be compensated by mechanisms of social immunity, like the formation of the propolis envelope (Evans et al., 2006). The first direct evidence of the effects of the honey bee nest environment on immune-gene expression was discovered by Michael Simone, Jay D. Evans, and Marla Spivak (2009) by treating hives in the field with coatings of propolis extracts along their inner surfaces to mimic the propolis envelope. Significantly lowered expression of two immune-related genes was found in bees from treated hives at only seven days old, as well as decreased bacterial loads within the colony (Simone et al., 2009). The researchers indicate that the treated colonies could invest less energy on immune function due to the decreased bacterial loads. The immune tactic of resin collection, though time intensive (Nakamura & Seeley, 2006), uses only a small proportion of the colony's population and is therefore more energy efficient than all individuals expressing elevated immune-related genes.

Renata Borba and others at the University of Minnesota Agricultural Experiment Station in Rosemount, MN (2015) reproduced the experiment designed by Simone et al. (2009). In this experiment, plastic propolis traps were provided to induce colonies to produce their own natural propolis barrier as opposed to applying less effective propolis extracts (simone et al., 2009). The seasonal bioactivity of the propolis envelope was also tested for the first time in this research. Their results support that of Simone et al. (2009) in regards to reduced immune-gene expression and energy usage, in addition to providing evidence for weakened bioactivity in the propolis envelope during winter while resin foraging and reapplication ceases.

Propolis has even proven to significantly reduce rates of viral and bacterial infection from pathogens within the colony. American foulbrood (AFB), transmitted by the spores of the bacterium *Paenibacillus larvae* in contaminated larval food*,* is one of the most destructive diseases to affect honey bee broods. Renata Borba and Marla Spivak (2017) tested the effects of the propolis envelope as a natural defense against *P. larvae* by measuring the antimicrobial activity of larval food fed to 1-2 day old larvae as well as clinical signs of AFB in inoculated colonies. Comparing the results of colonies with and without natural propolis envelopes, antimicrobial activity of larval food was significantly higher in conjunction with a lower colony-level infection load for two months following the challenge found in colonies with a propolis envelope (Borba & Spivak 2017).

Published the same year, Nora Drescher and others (2017) investigated whether propolis can protect colonies against *Varroa destructor* and its associated diseases. While at least seven viruses have been detected in *V. destructor,* this study tested for black queen cell virus (BQCV), deformed wing virus (DWV), Israeli acute paralysis virus (IAPV), and sacbrood virus (SBV). Two treatment groups were used: a “low level” group having propolis removed regularly and a “high level” group having the excess propolis added to their own envelope. A strong link is known between levels of *V. destructor* and DWV, and DWV titers changed in proportion to *V. destructor* infestations in all experimental colonies unlike other diseases. Colonies in the “high level” treatment group, given additional propolis, experienced a reduced increase in DWV titers with infestation and were significantly stronger in comparison to the "low level" group (Drescher et al., 2017). The studies performed by Borba and Spivak (2017), and Drescher and others (2017) indicate that the propolis envelope serves as an antimicrobial barrier interfering with the dynamics of pathogen infection in honey bee colonies, further emphasizing the importance of propolis for colony health.

Nest-Site Spacing

Reducing individual infection rates within the hive is extremely important for the annual survival of honey bees, as the presence of pests and pathogens in the nest is often unavoidable. Mechanisms of social immunity can control the spread of illness between related individuals of the same colony, but fewer tactics exist to protect bees from members of other colonies. Interactions between separate colonies are often sporadic or accidental to be responded to with hostility, but more frequently occur when nests are spaced densely together, resulting in a greater risk of intercolony transmission. Situations of high host density favor pathogens that exhibit high virulence, the degree to which parasitic infection decreases host survival and reproduction (Fries & Camazine, 2001).

Most common between workers and drones (horizontal transmission), intercolony transmission can also reach reproductive queens (vertical transmission) and spread through her to all offspring. Routes of horizontal intercolony transmission include contact between individuals during accidental drift, resource robbing, and foraging, but also include contact with shared contaminated resources. Vertical intercolony transmission takes place when a queen swarms from an infected colony, comes into contact with infected individuals during her nuptial flight, or drifts during her nuptial or maiden orientation flights (Perez-Sato et al., 2008).

The typical arrangement of apiaries consists of rows of hives spaced approximately one meter apart, all painted the same color and facing the same direction. Clustering hives together is certainly advantageous to beekeepers to shorten harvest and inspection times, as well as to increase a limited area's production, however this organization takes place at the bees' expense. A study by Thomas Seeley and Michael Smith (2015) examined the effects of aggregating honeybee colonies in apiaries*,* spacing identical hives in groups 1 meter apart and 21-73 meters apart. Essentially no drifting of drones was found among colonies in the dispersed group, while approximately 35% of the drones entering crowded colonies were drifting (Seeley & Smith, 2015). Their results illustrate how honeybees living in apiaries with identical hives arranged in rows and spaced close together, no longer inhabit an environment of evolutionary adaptedness and may make errors.

Another study by Dynes and others (2019) designed a "low density, low drift" (LD) apiary configuration and tested its performance in comparison to the common "high density, high drift" (HD) apiary layout when inoculated with *Varroa destructor*, each trial replicated three times. LD apiaries consisted of eight hives arranged in a circle facing outward, 10 meters apart, and at three different heights (6, 200, and 400 cm), each painted different colors with different symbols at each entrance to maximize the bees' ability to visually distinguish between colonies. The HD configuration performed significantly worse than the LD apiaries, with decreased honey production and winter survival rates, and higher levels of drift and *V. destructor* infestation post-inoculation (Dynes et al., 2019). The researchers conclude that beekeepers should consider implementing reduced apiary densities and visually distinctive hives to increase colony productivity, and reduce overwinter mortality and spread of diseases through drift within their own operations.

Conclusion

The traits and needs of honey bees have been naturally selected over the course of millions of years to provide means of year-round survival in vastly ranging climates around the world. Characteristics of the nest-site such as its volume, insulation, wall texture, entrances, and distance from other nests are selected for by honey bees, as each aspect affects the colony's behavior and health differently. However, a majority of common apicultural practices place bees in sub-optimal nesting environments to be bombarded with invasive treatments and manipulations for an expected increase in labor efficiency and production of goods. Traits such as swarming, hostility, and propolis usage, despite being mechanisms of social immunity, are thought to be too inconvenient for commercial beekeeping and are subsequently selected against. Industrialized apiculture exposes honey bees to more environmental stressors than other livestock to the extent that their health and survival is of global concern (Neumann & Blacquière, 2016). Future efforts to enhance honey bee health should take into account the influence of nesting environments on the bees' functions of annual survival and reproduction in apiculture. If given more suitable nesting environments to meet their evolutionary needs, commercial beekeeping operations could reap greater rewards from satisfied bees than in current conditions.

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