

A review of impacts of temperature and relative humidity on various activities of honey bees

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Abstract The importance of pollination services by honey bees (*Apis mellifera* L.) and their products is well-known. However, honey bee colonies currently face many challenges. These challenges include both biotic and abiotic factors. In this article, the impacts of abiotic factors (mainly temperature and relative humidity) on honey bee activities are reviewed. The suitable ranges of these two factors and the potential impacts of atypical minimal or maximal limits are presented. Social homeostasis of honey bees, and activities inside and outside the colony that are influenced by these two factors are included, followed by a suggestion of additional studies.

Keywords Honey bees · Activities · Temperature · Humidity · Thermoregulation

Introduction

Honey bees, *Apis mellifera* L., live in colonies that can contain thousands of individuals, ranging from 15,000 to 60,000 bees (Southwick and Heldmaier 1987). These large numbers of individuals provide invaluable pollination services (Breeze et al. 2011). The Western honey bee includes approximately 28 recognized subspecies (Alqarni et al. 2011). Honey bees have internal activities, i.e. within the colony, including brood rearing, food storing, and social homeostasis adjusting internal colony temperature to a suitable range (Southwick and Heldmaier 1987). The external activities include worker foraging and flight activity of queens and drones. Fluctuations in the ecological abiotic factors, i.e. temperature, relative humidity, wind speed, and light, are known to impact activity. In this review, the optimum ranges of abiotic factors (primarily temperature and relative humidity) for honey bee activities (inside and outside the colony activities) are provided with corresponding impacts of high or low levels of these factors as well as the optimum range. Additional studies are then suggested.

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Inside colony activities

Thermoregulation

On the individual level, when temperature rises to more than 36 °C, honey bee brood is likely to be exposed to overheating. To better resist any passive effects, the induction of a heat shock protein is activated even during normal colony conditions in adults (Severson et al. 1990). Worker bees exposed to variable temperatures between 4 up to 50 °C for 1 h showed increased levels of heat shock proteins (Koo

et al. 2015). The normal range of temperature within a honey bee colony ranges from 33 to 36 °C (Kleinhenz et al. 2003; Petz et al. 2004), more precisely 34.5 ± 1.5 °C (Jones et al. 2005). Regarding the ambient climate, bees within beehives maintain their own microclimate (Ohashi et al. 2009). Honey bees attempt to maintain this range as bee brood is very sensitive to changes in hive temperatures (Stabentheiner et al. 2010). When the temperature is above 36 °C, honey bee workers begin to mitigate the heat burden using fanning behavior by rapidly vibrating their wings. Workers take specific positions during fanning to be more effective (Southwick and Moritz 1987). The presence of developing stages, e.g. larvae, impacts fanning behavior by worker bees (Cook et al. 2016). Another mechanism is evaporative cooling, as workers collect water, allowing evaporative cooling inside the colony (Nicolson 2009). According to Southwick and Heldmaier (1987), bees forage for water and distribute small water drops within the hive and on the walls of cells containing eggs or larvae to prevent drying. This results in a decrease in hive temperature. Also, a thin water film on the proboscis is held by worker bees. The evaporation of this water film also contributes to nest cooling. An additional strategy to prevent overheating is vacating the colony and clustering outside the entrance while the in-colony bees continue the ventilation and evaporation tasks. In addition, a heat shielding mechanism was reported by Starks and Gilley (1999), where worker bees protect the honey and brood combs from external heat sources by shielding. Hot internal parts in the beehive's walls are the main target of the shield bees to serve as insulation to protect the wax combs.

In case of temperature less than 33 °C, honey bee workers have to increase the temperature to maintain brood, which is accomplished by increasing bee density on the brood nest (clustering behavior) and increased endothermy on demand (Harrison 1987; Stabentheiner et al. 2010). Endothermy is an essential action to ensure the survival of the bee colonies during cold temperature conditions (Harrison 1987; Stabentheiner et al. 2010; Szopek et al. 2013). Endothermy is solely done by bees older than 2 days, while bees less than this age are observed to visit warm brood nest cells to clean them, and probably to enhance the development of flight muscles (Stabentheiner et al. 2010).

There is a misconception that the drones' role is only queen mating. Drones participate in colony thermoregulation under specific conditions (Harrison 1987). Kovac et al. (2009) found drones heating their thoraces, especially drones older than 2 days, to assist in brood warming at low temperatures. But, according to Fahrenholz et al. (1992), younger drones (less than 2 days old) contributed sufficiently in warming brood due to their abundance (3.5 times higher than that of the oldest drones) on the brood nest. Generally, adult drones exhibit a much higher metabolic

rate than the immature ones, indicating that endothermy of immature drones is also not completely developed after emergence.

Brood temperature is regulated not only by clustering behavior of workers, but also by active heating with thoracic flight muscles. This strategy, according to Kleinhenz et al. (2003), includes: (a) superficial warming of the brood caps while bees are sitting motionless on the caps of brood cells, and (b) warming of brood cells by heating within the cells. In the latter case, bees with heated thoraces (thoracic temperature of 34.1–42.5 °C) enter empty cells (gaps) between sealed brood cells. These bees may remain motionless for up to 45 min to increase brood temperature of adjacent cells by 2.5 °C within 30 min. The heat flow in this case is up to three brood cells away from the heating bee (Humphrey and Dykes 2008). The presence of gaps cannot ensure the maintenance of optimal brood nest temperature, but gaps could reduce the time and energy spent by bees to enhance brood heating (Fehler et al. 2007).

Honey bee subspecies occur over a wide range of climates, from hot and dry to tropical and temperate conditions. Beekeepers can help the colony survive better under extreme hot or cold conditions using specific beehive types. Honey bee colony losses during winter were reported to be close to 19% in Belgium during 2008–2009 (Nguyen et al. 2010), 6–18% in Austria (Brodschneider et al. 2010), from 4 to 15% in Germany in 2004–2005 and 2005–2006 (Genersch et al. 2010), and 22.5% in USA during 2011–2012 (Spleen et al. 2013). Honey bee colony losses can occur both during extreme cold [vanEngelsdorp et al. (2008) in the USA] and hot temperatures [Al-Ghamdi et al. (2016) in Arabian countries]. Alattal and Alghamdi (2015) reported 76% of all honey bee colony losses occurred during severe summer weather (temperature up to 46 °C) in the Kingdom of Saudi Arabia (KSA). Also in KSA, Abou-Shaara et al. (2013) found that colonies provided with insulation boxes had a better survival rate than controls (i.e. standard Langstroth beehives) or other tested beehive types. The indigenous Yemeni honey bee (*A. m. jemenitica* Rutner) reared in beehives provided with ventilation fans and water supplies showed the best colony survival and productivity rates (Erdogan et al. 2009; Omran 2011). Using modified beehives is a promising trend for protecting bees from extreme environmental impacts, mostly unsuitable temperature and humidity.

Brood rearing

Pupae in capped cells are particularly more sensitive to low temperature than eggs or larvae (Groh et al. 2006; Tautz et al. 2003). Li et al. (2016) reported that temperatures of worker brood were higher than of drone brood, and it was regulated more precisely. The brood development showed

strong temperature dependency, and that forces the bees to keep the brood nest warm to ensure proper development (Petz et al. 2004). However, weak colonies or colonies exposed to continuous stress of elevated or low temperatures may fail in this task and are often lost. Dance performance was incomplete in bees raised at 32 °C compared with those raised at 34.5 or 36 °C (Tautz et al. 2003). Brood temperature can also impact the adult brain. The highest number of microglomeruli within the mushroom body was found in bees raised at 34.5 °C compared to those raised at ± 1 °C of this temperature (Groh et al. 2004). Jones et al. (2005) reared honey bee pupae at temperatures of 31–37 °C and 52% relative humidity. They found that rearing temperature (except optimum) affected short-term learning and memory abilities of adult workers due to subtle neural deficiencies. Additionally, brood temperature can impact wing morphology. Himmer (1932) reported malformed wings at low brood temperature. Ken et al. (2005) noticed longer forewings in bees raised at 36 °C in comparison to those reared at 35 or 32 °C. In a physiological *in vitro* 10-days study, ovaries of worker bees developed only at an incubation temperature of 34 °C when fed honey + 50% royal jelly, whereas no development occurred at 20 or 27 °C (Lin and Winston 1998).

Another important factor for brood development is relative humidity (RH) within the colonies. Li et al. (2016) found that RH is regulated largely by workers. RH is particularly important for egg hatching. RH below 50% hindered egg hatching, the optimum RH range for normal hatching was from 90 to 95%. Higher or lower RH significantly reduced the number of normally hatched eggs (Doull 1976). Al-Ghamdi et al. (2014) found that Yemeni honey bee eggs showed higher hatching rates than Carniolan eggs. At 50% RH, egg hatching rates were 39.33 and 52.66%, while at 75% RH, rates were 58.67 and 66.67% for Carniolan and Yemeni honey bees, respectively. No eggs were able to hatch at 30% RH. In case of low RH conditions, bees show specific behavior such as nectar water evaporation and foraging for water collection to increase RH (Human et al. 2006). During elevated RH, fanning behavior can work well to reduce RH to be within the optimum range. It is worth mentioning that for *in vitro* rearing of honey bee larvae, a temperature of 34 °C and RH of 96% (Aupinel et al. 2005; Silva et al. 2009) or RH of 90% (Kaftanoglu et al. 2011) were suggested.

Queen rearing

Normally, there is one queen in a bee colony, but honey bees have to rear queens in case of a dead or lost queen (emergency), weak or old age queen (supersedure), and swarming (natural means of reproduction). Allen (1965) found that the majority of queen cells in colonies were built by the end of

June during summer months. Colonies controlled by young queens (less than 1 year old) showed no queen rearing in comparison to those with older queens. In some cases, queen cells are built in the lower or even in the upper part of the comb away from the center of the brood cells. It is not clear whether queen cells benefit from specific heating strategies or not, but temperatures at the queen cell locations seem to be lower than those at the center of the brood nest. Degrandi-Hoffman et al. (1993a) found that in queenless colonies, workers construct emergency queen cells in the center of the comb with a better chance of emerging when temperatures were low, and on the periphery of the brood area at high ambient temperatures within the colony. In winter, temperatures averaged 32.3–34.9 °C around cells from which queens emerged, and the developmental period of queens ranged from 15.4 to 17.4 days. This study somewhat highlights that bees depend on the inner colony temperature during queen cell building instead of using a specific heating strategy. Queen cells have thicker walls than brood cells, which may play a key role in stabilizing the usually protruding cell, and in protecting immature queens, but a thermoregulation function of the thick wall is doubtful. According to DeGrandi-Hoffman et al. (1993b), the color of emerged honey bee queens is influenced by rearing temperature at 31.1 °C emerged queens were darker than those reared at 34.4 °C. Chuda-Mickiewicz and Samborski (2015) found that the incubation of bee queens at 32 °C delayed the pre-imaginal development by 27 h in comparison to those incubated at 34.5 °C, but emerged queens at both temperatures did not differ in their quality parameters including body weight, ovariole number, volume of spermatheca, and starting of oviposition.

Drone rearing and maturity

Extensive drone rearing activity occurs in spring and early summer, i.e. May, June, and July, and more drones are reared in large colonies than in small ones (Free and Williams 1975). Drone population within colonies slowly decreases throughout the late summer and in fall, and reach zero by winter (Boes 2010). The rearing season impacts semen volume and sperm concentration of drones but not the release of semen (Rhodes et al. 2011). After emergence, drones reach maturity in about 14 days or less (Cobey et al. 2013). Drone maturity is impacted by rearing temperature. At 88 °F (31.1 °C) maturity was found to be incomplete (less advanced), and seriously retarded at 83 °F (28.33 °C) but adding royal jelly in their diet reduced slightly the retarding impact at the latter temperature (Jaycox 1961).

Food storing

There are complex relationships between season, brood rearing activity, availability of bee plants, foraging activity,

and food storing activity. A honey bee colony requires a big amount of food, about 10–26 kg pollen per year (Brod-schneider and Crailsheim 2010). During winter, a honey bee colony consumes a large amount of honey, about 20 kg (Seeley and Visscher 1985). Nectar foragers showed no significant variations in their activity with the level of stored honey, whereas pollen foraging behavior was found to be extremely sensitive to colony state in a study by Fewell and Winston (1996). Neupane and Thapa (2005) found a significant impact of season on stored pollen amount, number of pollen foragers, and brood rearing activity. The highest values were in spring, while the lowest values were in the rainy season.

Outside colony activities

Foraging behavior

Foraging behavior includes bees gathering nectar, pollen, propolis, or water to fulfill colony needs. Foraging takes place within a wide range of temperatures from 10 to 40 °C (as reviewed by Abou-Shaara 2014). Below 10 °C, honey bees reduce foraging trips (Joshi and Joshi 2010). The beginning of foraging activity has been recorded to be at a mean of 6.57 °C, whereas the highest activity was at 20 °C (Tan et al. 2012). In another study, Woyke et al. (2003) found that 10 °C is the temperature at which foraging is initiated. These authors also noticed that the number of foragers increased tenfold when temperature increased to 12 °C. Adversely, at a temperature of 43 °C, the lowest foraging activity was observed (Blazyte-Cereskiene et al. 2010).

Foraging behavior is a great challenge for honey bees as it often occurs in variable environments. Forager bees have specific strategies to regulate their body heat under low ambient temperatures. Foragers use solar heat to do both increase body temperature or save energy. They change between an investment-guided and an economizing energetic strategy, depending on whether they can maximize intake rate by a higher body temperature or not, in the latter case being forced to focus on optimisation of energetic efficiency (Stabentheiner and Kovac 2014). Forager bees have a high ability to manage the balance between intake rate and energetic efficiency in their extremely changeable environment (Stabentheiner and Kovac 2016). During flight under different temperatures, worker bees are able to respond to these variations (Roberts and Harrison 1999; Woods et al. 2005). According to Heinrich (1980), head temperature of honey bees was 7 °C above and 3 °C below ambient air temperature at 17 °C and near 46 °C, respectively. When head temperature reached 46 °C, bees regurgitated nectar as a droplet from their honey crop and

kept it in motion in and out of the body to mitigate head temperatures. Maximum thoracic temperature of water collecting Carniolan bees was 44.5 °C at ambient temperatures from 13.6 to 27.2 °C (Schmaranzer 2000). This author mentioned that the duration of water collection increased linearly from 42 to 110 s with increasing ambient temperature.

Generally, the active time of forager bees is day-related, while the inactive time (sleep) is night-related (Eban-Rothschild and Bloch 2008), but during the day the timing of sleeping can be modified to fit within forage availability (Klein and Seeley 2011). Scout bees mainly use dancing language to orient the reticent bees towards food resources. During dancing behavior, Stabentheiner et al. (1995) showed that Carniolan forager bees follow a strategy of selective heterothermy. Thoracic surface temperature ranged from 31.4 to 43.9 °C inside the beehive, the foragers regulating thoracic temperature as high as 40.7 °C or to a low level (37.9 °C) in case of high sucrose concentration or less profitable food sources, respectively. Using light–dark cycles showed that light-off was the primary environmental cue for the circadian locomotor (walking) rhythms of Italian forager honey bees (Moore and Rankin 1993). During the night period, even in the presence of moon light, there is no out-of-colony activity.

The lifespan of foraging bees ranges from 2 to 17 days (mean 7.7 days; Visscher and Dukas 1997). The continuous exposure of forager bees to elevated temperatures could lead to a short lifespan. Remolina et al. (2007) exposed honey bee workers to 42 °C until death and they found that the lifespan ranged from 31 to 91 h (about 1.29–3.79 days). Similarly, Abou-Shaara et al. (2012) recorded survival periods of 12.67, 5.33, and 1.0 days for Yemeni bees, and 13.67, 2.67, and 1.0 days for Carniolan bees when exposed to temperatures of 35, 40, and 45 °C, respectively. Impact of RH on flight activity was found to be weak (Joshi and Joshi 2010).

Impacts on honey bee adults

Under laboratory conditions, Atmowidjojo et al. (1997) found that feral honey bees were more tolerant to high temperatures than domestic honey bees in the deserts of Arizona, USA. Feral bees were able to tolerate temperatures as high as 50.7 °C, whereas domestic honey bees tolerated lower temperatures only (42.8 °C). Abou-Shaara et al. (2012) found that Yemeni bees survived significantly longer than Carniolan bees at 40 °C, by 2.66 days. Noticeably, Carniolan bees were able to tolerate temperatures of 66 °C, but Yemeni bees could tolerate temperatures as high as 68 °C under high heating rates (1 °C/min). Kovac et al. (2014) observed that Italian honey bees had higher thermal tolerance ability than Carniolan bees. The LT50

(temperature with 50% mortality) 8 h after heat treatment was significantly higher in Italian (51.7 °C) than in Carniolan bees (50.3 °C). Under field conditions, Alattal and Alghamdi (2015) observed the highest colony losses in Carniolan bees (92%), followed by Italian bees (84%) and then Yemeni (indigenous) bees (46%) under the temperature conditions of KSA. Although these authors reported more suitability of Italian bees to such hot regions in comparison with Carniolan bees, the indigenous bees showed the highest suitability. Similarly, Alqarni (2006) found that Yemeni bees are more tolerant to elevated temperatures during the summer period in KSA than Carniolan and Italian bees.

Another abiotic factor, air humidity, probably plays not so much of a role in a temperate climate but is important in dry and hot conditions. At a temperature of 35 °C honey bee workers have been found to survive better at 75% RH, whereas at low RH of 50% to 15% worker survival was negatively impacted, especially at 15% (Abou-Shaara et al. 2012). Feral and domestic honey bees of Arizona showed high body water loss with decreasing RH, especially at 0% RH and 35 °C. The same trend was recorded with increasing temperature (Atmowidjojo et al. 1997). In addition to their higher thermal tolerance, Yemeni bees lost significantly less body weight within 2 h than Carniolan bees during summer conditions in KSA with elevated temperatures and low RH (Alqarni 2006).

Honey bees are able to cope with unsuitable temperatures because of integument characteristics. Cuticular lipids play a role in preserving body water due to their water-proofing properties (Gibbs 1998). Foragers have higher levels of *n*-alkanes (which play a role in body waterproofing) than nurse and newly emerged bees (Kather et al. 2011). Thermal receptors allowing bees to sense ambient temperature differences of at least 0.2 °C have been identified on honeybee antennae (Heran 1952; Lacher 1964; Yokohari 1983). Kohno et al. (2010) identified a specific molecular transient receptor channel (AmHsTRPA) suggested to play a role in temperature sensation, which is expressed in the antennal flagellum and is activated at a temperature threshold of 34 °C.

Queen mating and egg-laying

After maturity, drones start leaving the colony to search for virgin queens. Neves et al. (2011) found that flight activity was impacted significantly by temperature and light conditions. The number of drones that left the colony increased from 4 at 31.2 °C to 18 at 33.8 °C, while no drones left the colony at 26.5, 28.3, or 31.3 °C. Also, the number of drones increased with light intensity, while variations in RH and wind speed indicated no impact on the number of drones leaving the colony. Neves et al. (2011) recorded highest flight activity between 11:00 and 15:00 h. With slower

flight speed, the thoracic temperature of drones was higher than that of workers due to their larger body mass (Coelho 1991).

Mating of queens mainly happens at temperatures below 25 °C (Tibor et al. 1987), so high or low temperatures have a negative impact on queen flying (Heidinger et al. 2014). Besides, rain or strong wind negatively influence mating flights (Lensky and Demter 1985). El-Niweiri and Moritz (2011) found that drone mating frequency ranged from 9 to 23 for *A. m. jemenitica* queens in Sudan. They reported that mating frequency was adversely impacted by rainfall. Other factors can also impact queen mating, including insufficient drones, pests, and diseases (Cobey 2007). The time of year or season also influences queens mating, i.e. queens mated in spring are more vigorous than those mated in autumn (Moritz and Kühnert 1984; Jhaji et al. 1992). Also, the highest number of successful matings was recorded in May, while the lowest one occurred in July and August (Al-Ghzawi and Zaitoun 2008). If queens are caged, the presence of attendants is very important, Gontarz et al. (2005) for example found that adding attendant bees to instrumentally inseminated caged queens increased temperature inside the cage to almost 35 °C or higher within a few hours.

DeGrandi-Hoffman et al. (2007) observed that European queenless colonies accepted introduced queens more often than Africanized ones in fall. The rate of queen supersession was very high during summer introductions compared with the other seasons in Africanized colonies. In Jordan, Al-Ghzawi and Zaitoun (2008) found the highest acceptance rate of virgin queens during spring.

Usually, after mating queens do not immediately start egg-laying (Dunham 1930). On the other hand, egg-laying started up to 3–4 weeks after mating in autumn (Cobey 2007). During summer, a long pre-oviposition period of Syrian queens (*A. m. syriaca* Skorikov) and Italian queens has been observed (Al-Ghzawi and Zaitoun 2008). After artificial insemination, the onset of oviposition was 5.7 days in April and extended to 14.3 days in September (Moritz and Kühnert 1984). In Canada, Tibor et al. (1987) found a wide range of oviposition onset times, starting 4–22 days after queen emergence (mean 10.6 days). They found that after mating within 24 h some queens started egg-laying. It is known that queens reduce egg-laying rates under very cold or very hot conditions. Moreover, low brood nest temperature can affect egg-laying negatively, e.g. weak colonies with small bee numbers delayed egg-laying of instrumentally inseminated queens in Woyke and Jasinski (1990).

Swarming and absconding

Swarming is the natural way of reproduction of bee colonies as the honey bee queen is not able to independently find a

nest and workers are not able to reproduce (c.f. Grozinger et al. 2014). There are different reasons for swarming: in small hives, overcrowding causes swarming, whereas a lack of empty cells for egg-laying does not (Simpson and Riedel 1963). Small hive volume and low ventilation promote swarming, as well as overheating of crowded bee colonies (Lensky and Seifert 1980). Swarming happens mostly during spring to early summer. Honey bee swarms tend to regulate their constant core temperature around 35 ± 1 °C, but within the swarm temperature varies from 17 to 36 °C (Heinrich 1981). Even at low ambient temperature (4.0–16.4 °C), a swarm cluster tends to have a constant temperature of about 34.0 °C (Nagy and Stallone 1976). Bees on the surface of a swarm have a lower body temperature than those inside the swarm. When bees find a suitable location, all swarm bees have a thoracic temperature of at least 35 °C at take-off. The cooler bees on the surface layer warm their bodies in the last 10 min before take-off to achieve a flight muscle temperature allowing proper take-off (Seeley et al. 2003).

European (temperate climate) bees generally have a low probability of absconding. In the case of absconding, honey bees leave their hive and fly to another location (nest relocation). Absconding (migration) mostly happens due to the exposure of bee colonies to unsuitable conditions (e.g. pest attack and continuous disturbance) besides other factors, e.g. bee subspecies and inconvenient season. Schneider (1990) reported that 15% of colonies absconded between October and December in Okavango River Delta, Botswana. In Brazil, Africanized honey bees were observed to abscond during the dry season while colonies inhabiting semiarid areas absconded during the rainy season (Freitas et al. 2007).

Outlook

According to the review above, future studies should include the following aspects: (1) impacts of temperature and relative humidity on morphological (body and wing) characteristics, learning, survival, and physiological parameters (cuticle properties, cuticle thickness, and body water content) of the different recognized subspecies and for different stages (i.e. eggs, larvae, pupae, and adults) and castes (workers, drones, and queens); (2) direct comparisons among honey bee subspecies and their hybrids' tolerance to high and very low temperature or RH, especially considering predicted global climate change; (3) the ability of honey bees at different ages to tolerate harsh conditions; (4) new designs of beehives (e.g. increased insulation or using heating or cooling fans) to help the survival of honey bees under harsh summer or winter conditions; (5) impacts of temperatures and RH on food storing activity under

different ecological conditions; (6) queen rearing and drone maturity under various temperatures and RH; and (7) the impacts of temperatures and RH on foraging, mating behaviors, swarming, and absconding of the recognized subspecies of the honey bees.

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