<u>A Year in the Life of a Honeybee Colony</u>

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0. Abstract:

The Western honeybee is a eusocial species of bee that lives in colonies of several thousand and pollinates many species of plant that humanity relies on for both food and manufacturing. This essay takes the reader through a year in a honeybee colony, from nectar collecting and hive maintenance in summer, to survival activities in autumn and winter, to brood rearing and colony swarming in spring.

Due to human activities, honeybee populations are declining which is is problematic as many food and manufacturing crops are mostly or exclusively pollinated by bees and reductions in these bee population likely means reductions in crop growth. To reduce these declines, it may be necessary to understand how the honeybee colony functions throughout the year.

1. Introduction:

Throughout the world there are over 1600 species of bees, some living solitary lives and others being highly social, but all providing the essential function of pollinating plants[1]. This function appears to be a by-product of natural herbivory, however, as bees make use of pollen and nectar collected from plants in their diets. Therefore, it is advantageous to study the life cycle of bees in order to better understand how to halt and reverse their global decline and aid in the propagation of essential plants such as fruits, vegetables, and fibre crops such as cotton[2]. It is first necessary to distinguish between the two main types of lifestyles held by bees, solitary and eusocial.

Female solitary bees live alone in nests that they construct themselves and typically only interact with another bee during mating. They create a 'cell' within the nest and collect pollen to fill it. Once enough pollen has been collected, she lays an egg in the cell and closes it. This cycle of creating, filling, and closing cells continues for the rest of the female's life[1]. Due to their short life, the mass provisioning of food, and their naturally solitary nature, bees of this kind do not care for or interact with their young[3]. Female eusocial bees, on the other hand, live in colonies comprised of one reproductive queen and several thousand sterile workers who maintain the hive and forage for food. There is an overlap in generations and the young are fed progressively and cared for by other members of the colony[4]. Due to a strong division of labour both between queens and workers and within the worker caste, individual bees are not capable of surviving by themselves outside of the colony which maintains the social nature of these bees. Males of both solitary and eusocial bees do not differ greatly in terms of their function as they are mostly seen as 'reproductive entities' that can generally survive well by themselves.

Although typically seen as two distinct categories, solitary and eusocial lifestyles are actually two ends of a continuum of sociality. It is thought that the solitary lifestyle is the ancestral state and, through evolution, eusociality has been achieved in approximately 6% of bee species not by a single jump but by stepwise acquisition of social traits such as progressive feeding, longer life and generation overlap, division of labour and more[5]. This means that between completely solitary and advanced eusocial, there are several lifestyle types that can be achieved by bees such as subsocial, communal, semisocial, and primitively eusocial[3]. This continuum is important to keep in mind as it adds complexity to our understanding of the life of a bee.

Now that the general lifestyles of solitary and eusocial bees have been discussed, we can turn our attention to the subject of this essay: the honeybee. The Western honeybee (*Apis mellifera*) is one of 11 species of honeybee and is considered advanced eusocial due to its producing colonies of one queen and up to 60 000 workers[2], division of labour, progressive feeding of brood, lack of diapause to cope with unfavourable conditions, swarming to found new colonies[3], and generalist herbivory which causes over 100 different families of plants to be pollenated by individuals of this species[1, 2]. The Western honeybee, hereafter known as the honeybee or simply bee, is a key resource for humans due to its ability to produce honey and pollinate a wide range of plants, and so has been spread from its tropical ancestral home to more temperate areas and is now common throughout the world[2]. However, honeybee populations are declining due to human activities[5] which could have a great effect on crop yields. To understand how to save the honeybee it may be necessary to understand the life of the honeybee. This essay, therefore, takes you through a year in a honeybee colony, from the flourishing life of the hive in the summer to the winter preparations in autumn, the less active and more survival-focused winter colony and finishing with the increase in numbers and the splitting of the colony in spring. I hope to provide you with an appreciation for the complex and ever-changing life of a bee colony, an understanding of which could be crucial to saving these fascinating and important insects.

2. Summer:

Summer is a time of floral abundance and high temperatures so a bee colony must focus on increasing the productivity of the hive to make use of the abundance of nectar and pollen and regulating the temperature of the hive[6].

2.1. Hive productivity and division of labour:

As indicated in the introduction, social insects such as honeybees are partly characterised by a division of labour both between reproductive queens and non-reproductive workers and between different groups within the worker caste, and it is this latter phenomenon that is important for maximising productivity during the summer. Workers within a specific group complete a narrow range of tasks which leads to high specialisation and control over the activities in the hive, ultimately leading to higher productivity and work output[7].

2.1.1. Worker classes:

In honeybee colonies there are four classes of workers specialised to different repertoires of tasks: Cell cleaner, Nurse, Middle-aged bee, and Forager.

2.1.1.1. Cell cleaner:

This is the first class that adult worker bees belong to with most members being between 1 and 4 days old. Due to the developmentally immature nature of newly emerged bees and the requirement for continued development, these individuals are only tasked with the cleaning of cells used for brood rearing and are seen as the least important class within the colony as this task is also carried out by members of other classes[7].

2.1.1.2. *Nurse*:

The next worker class, occupied by bees 4 to 12 days old, is characterised by the feeding and caring of the brood, adult workers, and the queen. As discussed in the introduction, a characteristic of social bees is the progressive feeding of the brood instead of the mass provisioning in solitary bees, so a group of individuals that constantly attend to and feed the growing brood are required for the maintenance of the colony. The requirement for high hive productivity, especially during the summer, means that workers likely require relatively large amounts of nutrition to maintain their output but do not have the time to feed themselves, therefore it may be beneficial for one class of worker to be responsible for feeding her fellow workers. Finally, nurses are important for regulating the behaviour of the queen and spreading her pheromones throughout the nest[7]. Therefore, unlike cell cleaners, nurse bees are essential for the maintenance of the colony and therefore do not have a diurnal activity pattern, i.e. they work constantly night and day[8].

2.1.1.3. Middle-aged bee:

The title held by bees 12-21 days old is necessarily vague as their task repertoire is highly varied with approximately 15 tasks completed by these workers, although all tasks are completed within the hive. Young middle-aged bees take on tasks relatively deep within the hive, such as the building and maintenance of the nest, while older middle-aged bees complete tasks towards the entrance of the hive, such as nectar collection/processing and nest guarding. The number of bees that complete a specific task is highly flexible and changes depending on the other activities in the hive, especially the rate of foraging. As the foraging rate is likely to be high during the summer, most middle-aged bees will be engaged in building comb to store nectar/honey and nectar receiving/processing[7].

2.1.1.4. Forager:

For the rest of a worker bee's lifespan (from 21 until ~38 days old in the summer[4]), they engage in foraging activities outside of the hive. Forager bees typically collect pollen and nectar from the abundant flowers, which they then give to receiving middle-aged bees to be processed into honey or used to feed the colony[9]. However, bees also collect other things such as propolis, used for the maintenance of the hive[10], and water, used for temperature regulation as will be discussed later[7]. Alongside active foraging, forager bees engage in the communication of resource location to their fellow foragers through the characteristic 'waggle dance'. This dance, performed at the hive entrance and always with an audience present[11], consists of the forager running in semi-circles and occasionally in a straight line, waggling the body. Distance and direction of a resource source can be inferred from the duration and angle of the straight run, respectively[12], and the more vigorous and fast the waggling/turns are, the higher quality the resource is[11]. From this dance fellow foragers are able to locate high quality resources quickly and therefore maximise their work output. Because of the reliance of foragers on the sun for locating resources[12], they only work during the day, making foragers the only class of workers that sleep at night[8].

2.1.2. Worker class transitions:

From the above discussion of classes of worker bees, it is tempting to assume that transitions between the different classes are dictated by age-related developmental milestones. This appears to be the case for the transition from cell cleaner to nurse[7], however the other transitions seem to be more complicated.

2.1.2.1. *Nurse to Middle-aged bee*:

As the sole responsibility of nurse bees is to look after the brood, and as these bees are the only ones that complete this task, the ratio of nurse bees to brood is likely a controlling factor regarding the nurse-to-middle-aged bee transition. If the ratio is low, i.e. all nurse bees are busy feeding larva, then no transition out of the nurse class[7] should occur and older bees may even revert back to nursing to fill requirements[8]. However, if the ratio is high, i.e. there are many more nurse bees than required to feed the brood, then the nurses may transition out of this class. This latter scenario tends to occur in summer due to a sudden influx of adult bees after the initial boom in egg-laying in the spring. This influx simultaneously reduces the amount of brood needing to be cared for and increases the number of adult bees within the brood areas of the nest. These new bees tend to push the original nurses towards the edge of the brood area, reducing their exposure to two main pheromones important for the ability to nurse - Brood Pheromone (BP) and Queen Mandibular Pheromone (QMP) – and therefore causing the transition from nurse to middle-aged bee.

BP allows the nurse to feed the brood by stimulating the hypopharyngeal glands, allowing the nurse to feed on pollen. Pollen feeding maintains the high vitellogenin (Vg) levels within the nurse to produce food for the brood and suppress juvenile hormone (JH) levels. QMP more directly suppresses JH which decreases the movement and metabolism of nurses, discouraging them from leaving the brood area. Dopamine is also decreased by QMP, this time leading to low task sensitivity which specialises the nurse only to brood-care duties. When nurse bees are pushed to the outside of the brood area, they are exposed to lower amounts of both of these pheromones with the consequence of increasing levels of JH. This leads to increased activity and reduced specialisation to nursing, leading to an eventual transition to middle-aged bee[7].

2.1.2.2. *Early middle-aged to Late middle-aged bee*:

Although they are considered the same class, the task repertoires between early and late middle-aged bees do appear to be different so there may be a transition between the two sub-classes. This transition can be explained by a continuation of the hormone changes discussed in the previous section. The continued decrease of Vg as a result of reduced BP exposure means that JH production is released from inhibition by Vg[7], leading to the production of enzymes important in nectar processing[8].

2.1.2.3. Middle-aged bee to Forager:

The final transition in a worker honeybee's life is (typically) from middle-aged bee to forager. There are two main theories regarding this transition, and both rely on forager feedback on middle-aged bees. The social inhibition model states that foragers produce an inhibitor, ethyl oleate, which is transferred to nectar receiving middle-aged bees[7]. This inhibitor suppresses JH levels[9] to keep in-hive workers unable to progress to the forager class. During the summer, foraging is high and therefore forager mortality is also high[7], due to both internal and external reasons[13], so the amount of inhibitor present in the hive is reduced. Middle-aged bees therefore begin to increase their JH and subsequently their octopamine levels[9] which allows for the transition to the forager class[14]. However, the capability to forage doesn't necessarily mean that the transition to forager is complete and likely will not do so until the population of foragers or more specifically their foraging rate dips below that of nectar receivers. If there are too many middle-aged nectar receivers relative to the number of active foragers, the oldest middle-aged bees are released from their pre-foraging state and complete their transition to forager[7]. This complex transition includes both a release from inhibition and the input of a 'releaser' which allows for the fine control of relative populations within the colony to maximise work-output and reduce unnecessary population loss, as most foragers die within 10 days of the transition[4].

2.2. Hive Temperature Regulation:

Although most of the time during the summer is taken up with maximising the amount of nectar and pollen collected and processed into food and honey, high temperatures, occasionally in excess of 45°C[5], also requires attention by the colony. To promote growth and development of the brood, the brood nest must be maintained at a temperature of 35°C[9], and during high temperatures, foragers bring water into the hive and spread it throughout the nest, especially on brood cells[5]. Other workers, likely middle-aged bees, then fan their wings in order to cause the evaporation of the water and thereby cooling the nest down[6]. Peripheral areas of the hive fluctuate more greatly than the core brood nest and typically compensate for the reduction of heat in the core, as strict temperature regulation is less important outside brood areas[15].

3. Autumn:

Autumn is perhaps best classified as a transitional season from the highly productive summer to the more survival-focused winter. It therefore makes sense that the main task for bees during this season is transitioning from the highly specialised class system of summer bees to the generalised winter bee state.

3.1. Transition to Winter Bee:

Autumn is associated with reduced ambient temperatures, hours of daylight and abundance of flowering plants leading to a decrease in foraging activity. This decrease has a two-fold effect, both slowing the maturation of in-hive worker bees due to the increased number of foragers within the hive, and the reduction in brood production due to pollen shortages[16, 17]. This drastic reduction in brood production subsequently causes a decrease in nursing and BP which, along with slower maturation, allows nurse bees to build up their Vg stores. High amounts of Vg, and the corresponding low amounts of JH, are characteristic of the Winter Bee physiology and are thought to be particularly important in ensuring slow maturation, consistent nutrition, and long lifespan (up to 8 months[16]) in overwintering bees[9].

In many ways, the winter bee state is similar to the nurse class discussed in the 'Summer' section of this essay. High Vg and low JH combined with an active fat body and high immunocompetence are common to both states. However, as previously discussed, the population of nurses is controlled by the amount of brood present; when there is low brood, nurses transition to middle-aged bees, and Vg is decreased as the now middle-aged bee is no longer responsible for feeding the brood. For winter bees, however, low brood, and therefore low BP exposure, triggers storage of Vg as it is important to build up nutritional stores for the upcoming winter, and the increased inhibition from idle foragers stops any transition out of the nurse class[7].

By the end of autumn, the number of bees within the colony has reduced significantly from its summer highs as males are removed from the hive[9], foragers die and are not replaced[17], and egg-laying and brood rearing are greatly reduced[10]. All of the workers within the hive are now 'winter bees' with the capacity to store great amounts of nutrition and not much else. The colony is now ready to wait-out the winter and do its best to survive until the return of spring.

4. Winter:

The low temperatures, short days, and greatly reduced flower abundance during the winter months means that survival and not productivity is what is most important for the bee colony. Therefore, early winter tasks are mostly related to thermoregulation and late winter tasks include a transition from the winter to summer bee state and starting brood rearing in preparation for the more tolerable conditions of spring[9].

4.1. Hive temperature regulation:

Just as an important task during the summer is thermoregulation of the hive, so it is in winter. However, unlike summer when it is most important to maintain a constant temperature within the brood core of the nest to ensure constant brood growth, during early winter it is more important to maintain peripheral temperatures to ensure the continued survival of the colony[15]. Once the temperature outside of the hive has fallen below a critical threshold (typically around 10°C), the colony will form a 'thermoregulating cluster'[9] and individuals in the centre of this cluster will generate heat by rapidly beating their wings, increasing the temperature within the hive. When temperatures drop further, the core temperature increases due to denser clustering and the heat production through wing vibrations in order to maintain a peripheral temperature of approximately 6°C[15]. Throughout the winter, the cluster will slowly move with surface bees taking the place of core bees in order to maintain individual temperature and take honey from storage cells to fuel themselves for continued survival and thermoregulatory activities[5].

In mid- to late-winter, as will be discussed in the next section, egg laying and brood rearing begins again. To do this, the queen, who remains within the centre of the cluster throughout the winter, starts to be fed from the honey and pollen stores[6] and the thermoregulation strategy changes from ensuring a constant temperature on the surface of the cluster at the expense of a constant core temperature to the maintenance of the core at a temperature conducive to brood growth and development (~33 ^{o}C)[16].

4.2. Initiation of Brood Rearing and Winter-to-Summer transition:

As mentioned above, egg-laying and brood rearing is typically initiated in mid- to late-winter but is regulated by the amount of pollen stored within the hive from the previous summer and autumn. Hives that contain large stores of pollen can feed the queen to induce egg-laying and rear the brood before more pollen can be collected in the spring. Hives that use up all of their pollen for survival purposes during winter must wait until more pollen can be collected in the spring before they initiate brood rearing. This shows how important summer and autumn preparations for winter are as colonies that can increase their population during winter are more capable of surviving throughout the year as they have a ‘head start’ on other colonies when it comes to foraging when conditions are more tolerable[6]. It is thought that the initiation of brood rearing is triggered by increasing day length towards the end of winter[16] however the mechanisms that underly the initiation are generally unknown[9].

To rear the new brood, some winter bees within the brood core must use some of the nutritional resource, specifically Vg, that they stored in the autumn to feed the developing larva. As the environment outside of the hive is still unfavourable, these nutrient stores within the bees cannot be restocked leading to a decrease in the levels of Vg and subsequent increase in JH in these bees[9]. These bees will then begin to naturally move out of the brood nest with there place taken by emerging summer-bees and winter bees that now find themselves within the brood nest. This cycle, along with increasing BP levels[16], cause the transition from the generalist winter to the specialist summer physiologies. As spring approaches, all winter workers die[9] (some aged 280 days[7]), leaving a colony consisting of the queen and a relatively small number of newly emerged summer workers[9].

5. Spring:

Spring is associated with increasing hours of daylight, temperatures, and abundance of flowers. For bees, therefore, this season is perfect for increasing brood to replace those who died in the winter and rearing queens and drones (male bees) for the splitting of the colony that occurs each year towards the end of spring.

5.1. Increasing brood:

As discussed in the previous section, late winter sees the initiation of brood rearing causing a decrease in Vg levels and increase in JH levels in the winter workers. As the days get longer and warmer throughout early spring, brood rearing gradually increases as does JH levels until the division of labour described in the 'Summer' section is achieved. The oldest members of the colony will have the highest levels of JH, therefore becoming foragers, and will leave the hive in order to collect fresh nectar and pollen. This influx of food into the hive increases the rate at which new bees can be reared and so there is an accelerated increase in colony population with a peak population occurring towards the end of spring, further stabilising the division of labour and returning the hive to the productive state discussed in the 'Summer' section[6, 9, 16].

5.2. Rearing queens and drones:

Until this point this essay has mostly confined itself to the activities of female worker bees as throughout most of the year it is this caste that is most important to the activity of the hive. Of course, the queen is necessary for the laying of eggs, but this activity is mostly under the control of the workers and the abundance of pollen as discussed previously. Similarly, male drones are important for the fertilisation of the queen's eggs but as this only occurs in spring and early summer and drones do not contribute to the hive outside of this it has not been necessary to mention them up until this point. However, as spring is a time of increasing brood, mating, and the splitting of the colony, as will be discussed in the next section, it is now prudent to turn our attention to these thus far ignored castes.

Many social insects including honeybees have a haplodiploid system of sex determination. This means that the 'queen' or equivalent reproductive individual can choose whether to lay an unfertilised (haploid) or fertilised (diploid) egg. Unfertilised eggs produce male drones whilst fertilised eggs produce female individuals. Throughout most of the year, the queen will only lay fertilised eggs, and the workers will feed the brood pollen and honey so that only new female workers are produced to serve the important productivity functions of the hive previously discussed. During the spring, however, a few of the fertilised eggs will be fed royal jelly and a small proportion of the total eggs laid by the queen will be unfertilised, leading to the production of female queens and male drones respectively[4]. Queens and drones are reared in order to prepare for the propagation of the colony through mating and the splitting of the colony which is triggered by the crowding of the hive caused by the exponential population increase[6].

5.3. Splitting of the colony:

The increasing brood leads to intense crowding within the colony which culminates in the old queen and approximately half of the colony leaving the hive in a process called 'swarming'. The colony is now split in two with a swarming colony led by the old queen and a stationary colony led by one of the new queens reared in the preceding weeks[9]. Let's first focus on the activities of the swarming colony.

The swarming colony's first task is to find a new home. This is done be a few hundred of the up to 10 000 bees within the swarm leaving the body of the swarm to inspect the environment for suitable nests. Once an individual bee has found a site that she believes to be acceptable, she returns to the swarm and completes a 'waggle dance' similar to the one used to inform foragers of the location of food. This dance is intended to convince other scouts to choose her site and gives information about the location of the site but also its quality as the number of dance circuits performed is proportional to how well the site conforms to the ideal site. Once the bee has completed her dance she will return to the site and then come back to the swarm once again repeating the 'waggle dance' but this time with fewer dance circuits. This cycle continues until no more dance circuits are performed and the bee abandons the site. This action is repeated by all of the scouts and so the last bees dancing will be those who started with the most dance circuits i.e. those committed to the highest quality site, and those who started dancing later i.e. those who were recruited to higher quality sites. Although the dance is important for signifying location and quality of a site, it is the recruitment of bees that is important for the actual process of deciding which site to colonise. Once a threshold number of bees has been spotted at a particular site, this site is chosen as the new nesting site for the swarm and so a consensus is not necessary for a decision to be reached. The decision process usually takes about 3 days to be completed with approximately 16 hours of active dancing, recruiting, and 'voting' involved. Once a decision has been made, the scouts return to the swarm and produce a high-pitched piping signal which acts as a stimulus for the swarm to ready themselves for flight[18]. The swarm will then make their way to the chosen nest and begin to set up their new colony through building combs and cells, rearing brood, and foraging[6].

Now that the swarming colony is set up ready for a productive summer, the stationary colony must rebuild, and this begins with choosing a new queen. Before the old queen left the hive, she laid some unfertilised eggs that became drones and quickly left the hive, and a few fertilised eggs which the workers nurtured slightly differently from the rest, and which therefore became queens. As the hive can only support a single queen, however, all contenders must fight and the one who survives is crowned the queen. The new queen then leaves the hive for mating flights and can mate with between 10 and 30[5] (average of 17[4]) drones before returning to the hive to lay eggs[4]. The stationary colony is now ready to rebuild its population and, like the swarming colony, restart its yearly cycle of activities.

6. Conclusion:

For a honeybee colony, collecting enough nectar and pollen to produce honey in the summer, transitioning to a survival physiology in the autumn, regulating the temperature of the hive and initiating brood rearing as early as possible in the winter, and increasing population and swarming in the spring is paramount to survival and propagation. If the colony is not able to collect enough nectar due to a lack of flowers, for example, nutrient stores in the hive will be low throughout the winter leading to higher rates of death and a later initiation of brood rearing, greatly compromising the colonies capacity to survive throughout even the most favourable months. This doesn't just effect the bee colony, however, as fewer bees means greatly reduced pollination and propagation of plants that are important for humans, both in terms of food crops and manufacturing fibres, some of which are exclusively pollinated by bees. Our great reliance on bees in general, and honeybees specifically, for the continued production of food and fabric fibres especially means that the global declines in honeybees, mostly due to human activity, should be highly concerning. To ensure the continued growth of necessary crops it is likely that this decline will have to be addressed and reversed and it may be that knowledge regarding the life history of the honeybee colony can be used to do this. Understanding how the colony works and how it survives could be essential to figuring out how to save the bees and do a little bit to secure the future of humanity.

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