Module 6 Honeybee Behaviour

Introduction

This document summarises the study material for BBKA Module 6 produced by members of the Mid Bucks Beekeeping Association.

One of the key issues with studying for the BBKA modules is that common with many things in Beekeeping there is no definitive answer to each item in the syllabus so the reader should treat this document as our understanding of the study material.

The key sources of information are given in the reference table below although the wealth of data available via the internet is vast and varied and sometimes of unknown source.

The reader is welcome to download the document and utilise it as required, however the contributors would appreciate that they are acknowledged if the document is republished.

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Functions of the worker as described by BBKA:


Day 4 - 6. Feeding older larvae (honey + pollen).

Day 7 - 12. Feeding young larvae (brood food).

Day 13 - 18. Processing nectar into honey (water evaporation), wax making, pollen packing, ventilation and temperature control.


Day 21 - 6th week. Foraging for nectar, pollen, water & propolis.

Worker bees often do nothing! Under normal circumstances they spend a lot of time resting and patrolling the colony. Depending upon the state of the colony the worker bee can be dedicated to single tasks as per charts or can carry all activities. Having a pool of resting bees gives the colony the ability to react to incidents such as swarming or increase in nectar/pollen flow.

Duties very much depend on the maturity of the brood glands, wax glands (day 12) & sting gland (day 18) - bees can revert to earlier duties if required. Other duties included ventilation, humidity and temperature control.

Up to the age of 18 days the bees are considered to be house bees. Days 1-3 they will be cleaning cells, capping brood and eating large amounts of pollen. The pollen is required for the development of the hypopharyngeal and mandibular glands which produce brood food and royal jelly which is required for days 3-15. The intake of pollen is also required for the development of the wax glands, peak wax production is 10-18 days.

The hypopharyngeal gland decreases in size and turns to producing invertase and glucose oxidase (2 enzymes required for honey production) this is generally days 16-20.

Younger bees tend to reside in the centre of the brood nest, moving outwards with age to fulfil comb making and food handling activities.

From about day 20 the bee becomes an Outside bee, it transitions to this through ventilation and guard duties within the colony. Before taking on the role of Guard bee the worker must first be able to produce the alarm pheromone through the mandibular glands and the sting pheromones and venom.

From day 5 the adult worker will have been taking orientation flights in preparation of becoming a forager.

Bees will forage for approximately 20 days before dying.

The seasonal variations comprise the early build up and the overwintering of the colony. During colony build up the amount of brood and number of adult bees can reach parity so foraged food is mainly consumed by the young and little honey stores creation is occurring. Over the summer the number of adult bees increases in proportion allowing for stores build up. Going into Autumn the amount of brood declines meaning fewer bees are occupied feeding young. Bees that do not feed young live longer, combined with the increased feeding on pollen the Hypopharyngeal gland returns to brood food generation for the spring build up. The pollen also increases the protein content of the fat body thus extending the life of the bee.

During the season there is flexibility in timing of roles, when there is significant flow house bees will be encouraged to become receivers and honey makers earlier, enabling the foraging population to be serviced. During periods of poor forage there will be less brood management.
If the colony goes queenless the adult bee will exhibit winter tendencies, extending its life and eating pollen in order to feed young at an older age.
6.2 the mating behaviour of the honeybee queen and drone including an account of the pheromones involved and the concept of drone congregational areas;

Queens mature and are ready to mate within days of emerging from the cells, queens are unable to mate 3 - 4 weeks after emerging. Workers will generally ignore a virgin queen although they will become more aggressive towards her as time goes by, this is seen as encouraging the virgin to go on mating flights. Once mated the queen will always be surrounded by a retinue of workers, feeding, cleaning and licking her.

The drone takes 12 - 14 days after emerging to reach maturity for mating, during this period they take daily flights (initially short but getting longer prior to mating). When mature the drones from surrounding apiaries (up to 6 km) will congregate in a Drone Congregation Area (DCA), the routes to the DCAs are known as flyways and are up to 21m high, the DCA is 10-40m above the ground. DCAs are always at least 100m away from the apiary.

The Drones will congregate around the middle of a warm day.

The queen will go on several mating flights and mate with 15 to 20 drones on up to 6 occasions. When within a DCA a pheromone (9-ODA – 9-oxodec-2-enoic) produced by her mandibular glands, this attracts drones up to 50m away forming a drone comet tail. A second pheromone from the tergite gland attracts the drone within 30cm.

A Drone will approach the Queen from below, it hovers above the abdomen and clasps the Queen with all 6 legs. The Queen’s sting chamber is open and the Drone inserts his endophallus within. The Drone becomes paralysed and flips backwards causing the ejaculation to occur and the endophallus to break off remaining in the sting chamber. The Drone falls to the ground and dies.

The remains of the Drone within the Queen’s sting chamber is known as the mating sign and works as a plug to ensure semen does not seep out. A subsequent Drone will go through the same process, first removing the mating sign.

The queen can mate again on the same flight and on subsequent days, the preference is to mate with drones not from her colony.

The DCA is a mystery in that they exist in the same place each year, generally in sheltered but open areas at a height of 10-40m and a radius of up to 100m. Because drones do not survive the winter the DCA needs to be fixed by some method other than learnt knowledge, the theories include:

1. Topographical features - which drones asses by sight and other senses
2. Distance from apiary – usually greater than 100m
3. Magnetic effects – drones develop large quantities of magnetite in their abdomens, this could be affected by the earth’s magnetic field
6.3 the queen honeybee’s egg laying behaviour and its relationship to changing circumstances in hive and external factors relating to climate and season;

Once the queen has mated she soon begins laying eggs. She will walk over the empty and cleaned out cells, looking deeply in and inspecting each one before she will walk passed the cell and back into the cell to deposit the eggs. The queen is very picky and will not deposit an egg into a cell that was not cleaned to her satisfaction.

The queen backs in to the cell and produces a small sticky substance that the egg will adhere to. The egg is laid at the bottom centre of the cell in a standing position. After the egg is laid, the queen moves to the next cell and repeats this process. At the height of the season she will do this more than 1500 times every day. The queen will take short rest periods of 5 or 10 minutes, but generally speaking lays eggs around the clock.

In the queen's body, the eggs and sperm are kept separate from each other. Sperm is kept alive by feeding it protein within the queen's body. The queen actually has a small valve that she can control by restriction, which either allows or prevents a single sperm from being deposited on the egg she lays. If the queen lays an egg in a worker cell, she allows one sperm to attach to the egg, thus producing a worker. If the egg is laid and no sperm is attached, it will develop into a drone.

The workers actually determine what type of egg (drone or worker) the queen will lay, by leading her to two different size cells. The large drone cells are usually found in the corners where the pollen and nectar are stored. Drone cells are larger than worker cells because drones are large, almost twice as big as a worker.

Assuming the queen is young and well mated the rate of lay is dependent primarily upon supply of food and pollen, temperature and swarming state. The colony needs good supplies of pollen in order to create brood food, an over wintered colony will depend upon the pollen stored from the previous season, if this is lacking the colony build up will start later when pollen can be collected from plants. Only in severe winters will a queen stop laying completely, as the winter cluster becomes less compact in spring the queen will lay.

As the spring flow continues the lay rate increases, the increase will only be interrupted by periods of poor weather. The lay rate will peak May-June with concentration of the colony switching to stores build up from July for survival of the coming winter.

If the colony becomes overcrowded during may and June (swarming period) and the colony decides to swarm the queen will be starved in order to reduce her size so that she can fly with the swarm. Swarming is not only determined by crowded state of colony, queen substance and lay rate are other factors that can initiate the queen replacement process.
6.4 the seasonal variations in population size of a honeybee colony and an explanation of such variations

The bee population size of a colony follows an annual cycle in the spring it builds up until the colony swarms, then it builds its population to collect stores to see it through the winter and winter comes it reduces with the cold whilst the colony feeds on the stores.

Winter to Spring

Coming into spring the colony population will be 10-15,000 (can be as low as 5,000) and the queen will be laying few eggs, the colony will be closely clustered (tightening and loosening dependent upon the external temperature).

There will be no foraging only random water collection and cleansing flights, the bees will be living on the stores built up the previous summer.

Spring Expansion

The queens laying rate is governed by the amount of food available, the more forage and specifically pollen available the higher her egg laying rate, up to 1,500 a day by late May. In early April drone eggs will be laid in preparation for swarming season late May through June.

Early Summer

Population will have attained 45 - 50,000 bees and with a continuous supply of new brood. The brood and adult bee population will match.

If the conditions are right (such as old queen or colony congestion) the colony will swarm May – June with the colony population diminishing by up to 50%, more if there are after swarms. Up to 70% of the swarm would be young bees

Summer to Autumn

The egg laying rate of the queen will diminish as the forage dries up, the temperature cools and the autumn arrives. There will be more adult bees than brood which means that stores can be built up rather than focussed on feeding the young.

New queens may lay through to October whereas older queens may stop in August. Over the winter months laying will stop completely.

The worker bee extends its life through building up fat and gorging on pollen, however the winter will still take its toll on the population.
6.5 The social organisation of the honeybee colony including worker policing;

The honey bee is a member of the order Hymenoptera which comprises nearly all the eusocial insects. Eusociality (Greek eu: “good/real” + “social”) is a term used for the highest level of social organization in a hierarchical classification.

The honey bee is a fully eusocial insect species. Colonies of honeybees show the three characteristics of fully eusocial organisation:

- Individuals of the same species cooperate in caring for the young
- There is a reproductive division of labour with more or less sterile individuals, working on behalf of the reproductives. There is a caste division of honeybees into three phenotypes.
- An overlap of at least two generations in which the offspring contribute to colony labour.

Originally the honeybees’ distribution was Africa, Europe and Asia however its current worldwide distribution owes much to the activities of man. Colony sizes can reach tens of thousands and their organisation represents the most complex seen in social Insects.

The advanced nature of the honeybee colony is based on the differentiation (individuals into three castes) for labour along with integration of the community through a communication system.

There are three phenotypic castes within the honeybee colony:

**The Queen:** a diploid reproductive responsible for the production of all the eggs. The honeybee queen has taken this strategy to extremes and does nothing else other than produce eggs.

The queen established the colony after a reproductive flight in which she mated with a male bee called a drone. This is the only mating the Queen will perform and she retains the sperm from this mating, fertilising eggs as required.

**The Workers:** These are female and diploid. The worker is produced by the fertilisation of an egg from the Queen and sperm from the earlier drone mating.

Within a single colony there will be thousands of workers. The life span of a worker is about 40 days. There is further differentiation of task for the workers as they nurse and tend the brood of larva during the early part of their life and then change to foraging in the latter period of their 40 days.

The foraging workers are the Bees that we see searching and gather food for the colony.
**Drones:** Drones are male and haploid. The drones are produced from the unfertilised egg of the queen. Drones as the name implies, contribute little if anything to the care of the colony.

**Integration through communication:**

As eusocial colonies become more complex the ‘power’, the control method shifts form aggressive queen behaviour to the pheromone mediated behaviour typical of honeybee queens. Reproductive control in honeybees is based on inhibitory pheromones exchanged with and between the workers and the developing larvae. 9-oxodec-2-enoic acid (9-ODA) is the main chemical pheromone ‘queen substance’ used to both attract males and also to inhibit the building of queen cells.

Honeybees use a combination of communication forms as already mentioned there is chemical exchange of pheromones but they also use touch and vibration as seen in the different forms of dance.

**Worker Policing**

In queenright honey bee colonies workers normally prevent each other from reproducing by worker policing through workers eating worker-laid eggs and aggression towards laying workers. Worker reproduction is minimal in queenright colonies. Only 0.1% of the adult males are workers’ sons and only 0.01% of the workers have full-sized eggs in their ovaries. This is thought to arise due to the distribution of queen substance and brood pheromone produced by larva to encourage feeding, which prevents the development of worker ovaries. The marking of eggs with a pheromone by the queen at point of lay ensures that eggs resulting from a laying worker which do not have this pheromone can be identified.

The situation is very different in queenless colonies, the absence of queen substances and brood pheromone enables worker ovary development. Worker policing is switched off so that the colony rears a final cohort of workers’ sons before dying due to its dwindling workforce. In a “hopelessly queenless” colony, that is one which has lost its mother queen and has failed to rear a replacement, many workers (5–24%) have fully-active ovaries with full-sized eggs and lay eggs.
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6.6 the methods of communication used by the honeybee including food sharing (trophallaxis), dancing, scenting and vibration;

The main methods of communication from one bee to another are:

- Trophallaxis (food sharing)
- Pheromones
- Dancing
- Vibrations

All the processes combine to make up the communication system and are not to be viewed in isolation, e.g. pheromone and food exchange can occur at the same time.

**Trophallaxis**

Exchange:

- One bee will **beg** from a second bee by pushing its tongue towards the mouth parts of a second bee
- A bee will **offer** food to another bee by opening its mandibles, regurgitating a drop of nectar and pushing it forward on its tongue
- During exchange of nectar antennae of the bees touch passing on scent messages
- Food is also exchanged as part of the wagtail dance

Usually the offering will be from old to young and full crop to hungry (empty crop) bees, although it still occurs between bees with similarly full crops.

It has been shown by using coloured nectar that within 24 hours 50% of a colony will have elements of that nectar within their crop. This means the colony effectively forms a common crop and with the same level of concentration.

A common crop issues a distinct odour helping colony bees to recognise each other by smell.

Bees that have been feeding the queen continue to be big feeders after and thus promote the distribution of queen pheromones.

**Pheromones**

Pheromones have only recently been discovered (since 1950s), the definition is:

Pheromones are substances which are secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction which may be behavioural, developmental or physiological

Interesting facts on pheromones:

- Pheromones are produced in exocrine (ducted) glands
- They are produced continuously by the gland concerned
- Usually released under certain circumstances
- They can have multiple chemical components
- Pheromones do not always work alone, they may depend upon environmental circumstances
- Most pheromones are volatile chemicals e.g. alarm pheromones
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Four example pheromones:

- Nasonov, enables workers to recognise the queen, mark locations and attract drones to queens during mating flights
- Queen Mandibular pheromone, basis of queen substance 9-oxodec-2-enoic acid (9-ODA) which when distributed throughout colony prevents swarming and workers laying. The pheromone is also used to hold swarm together 9-hydroxydec-2-enoic acid (9-HDA), attract drones at long distance.
- Worker Mandibular gland, creates alarm pheromone, used by guard bees to ward off intruders (2-heptanone)
- Alarm pheromone from sting gland, (isopentyl acetate) attracts other bees to sting

Where the effect of the pheromone benefits the receiver it is called kairomone, e.g. smell from drone brood attracts varroa. When it benefits the emitter it is called allomone e.g. sting scent which induces colony to defend.

Dancing

There are several different types of dances within a colonies life:

Round Dance

The round dance indicates that there is forage within near to the hive, the bees recruited are left to discover the direction of the forage. To assist in the “discovery” of the forage the dancer will exchange nectar with awaiting workers before and after the dance so that they can employ the odour of the forage to orientate. A worker will only be inclined to do a round dance if the sugar content is high in the forage, plus higher sugar content is also demonstrated by more vigorous dances (more pronounced abdominal vibrations.)
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Wagtail

The figure of eight waggle dance recruits foragers to nectar and pollen sources, the dancer will dance in a straight line whilst shaking the body vigorously from side to side and buzzing, at the end of the straight section the worker will loop in one direction back to the start of the line, repeat the waggle and loop the other direction.

During the dance the dancer will stop and exchange nectar with nearby workers, sometimes this is initiated by the dancer other times by the dance followers “begging” by means of a squeaking sound.

Direction of the of the forage is indicated by the angle of the straight part of the dance to the vertical plane of the comb, this deviation is the angle in relation to the sun. The dance is normally in the vertical plane however if the dance is on the horizontal plane the direction of the straight line is the direction of the forage.

The distance to the forage is indicated by the length of the straight line, the time of waggle and buzz, and the total duration of the dance, forage further away means a slower dance and slower the waggles. Distance is not a measure of physical length rather energy required so that workers know how much food is required in their crop to complete the forage.

Transition Dance

Different races of bees relate different distances to dances and the transition from a round dance to a waggle dance. So the round dance may mean less than 15m to forage for one race of bees. Usually there is a transitional dance (open figure of eight with waggle) for distances between 15 and over 100m some races have slower transition, other more direct. This could cause distance misinterpretation between hybrid bees.

DVAV (dorsoventral abdominal vibrating dance)

The DVAV dance is where a worker will clasp or mount another bee and vibrate it by oscillating her abdomen in the vertical plane. The dance is important in foraging and swarming management:
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Foraging
- it is used to recruit more foragers during a nectar flow or when the colony is in need of food.

Swarming
- once queen rearing has started the retinue vibrate the queen until just before the swarm exits the nest
- vibration will be performed on cells containing maturing queens, this is assumed to control the timing of the emergence of the new virgin queen

Virgin Queen Mating Flight
- It is suggested the DVAV dance prepares queens for mating flights

Piping

Occurs on two occasions, before the queen emerges from her cell and just after emergence. Prior to emergence is thought to be an indication to the colony that they have a viable queen. After emergence piping is seen as a call to fight other virgin queens, generally following an afterswarm. Sometimes a mature queen will pipe prior to swarming.

Other dances include:

Trembling - to attract more forage receivers

Jostling run - Returning foragers agitate other workers by running at them and pushing them aside, this is a sign that there is information about forage in the dance area.

Spasmodic dances - Occurs during food distribution where short tail wagging movements interrupts the transfer of food. It is thought that it might imply good forage flow, similar to jostling.

Buzzing runs - In this dance the worker runs through the colony buzzing their wings. This is used as a signal for a swarm to exit the hive or alight, it basically causes increased activity in the colony.

Shaking dance - The worker shakes her body from side to side inducing others to groom her.
6.7 the behaviour of the foraging bee and its work methods in the field including orientation;

General behavioural facts:

- Bees forage from 3 – 6 weeks of age and die away from the hive
- Bees will change from pollen to nectar foraging but not vice versa
- Generally pollen and nectar loads are single varietal
- Collection split
  - 58% nectar only
  - 25% pollen only
  - 17% nectar and pollen
- Generally foragers will return to same crop as long as good flow
  - Same time each day
  - For up to 20 days
  - One time of day crops e.g. chestnut (morning nectar) bees will be idle in hive for rest of day
- Will enter and leave crop at same place each visit
- Start foraging closer to hive, move further away with age
- Average distance from hive of forage 2.2km, maximum 3 km
- Best crops will always be worked irrespective of distance
- Will travel further for pollen (lighter load)
- Forage location learnt initially from dances
  - Location, shape of dance
  - Time of day for forage, time of dance
  - Quantity, number of workers dancing
  - Quality, vigour of dance and sample
  - Hazards, alarm dances

Loads collected:

- Nectar 30-50mg
- Water 25mg average
- Pollen 16mg (8mg x2)
- Propolis unknown
- Nectar collection is more energy efficient
  - 8:1 gain pollen
  - 10:1 gain nectar (40% nectar load)

Pollen flower types (Parker 1926):

- Open flowers, bee bites the anthers with mandibles and uses forelegs to pull them towards her body
- Tubular flowers, workers insert proboscis into corolla searching for nectar and pollen is collected incidentally adhering to mouthparts and legs
- Closed flowers, bee forces petals apart with forelegs and gathers pollen on the mouthparts and legs
- Spike or catkin flowers, bees run along the spikes or catkins shaking off pollen onto her body hairs
- Presentation flowers, pressing abdomen against inflorescence, causing a pollen mass to be pushed out of the flowers
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Orientation and Navigation

Worker bees orientate and navigate themselves based upon a combination of well integrated systems:

- Visual
  - Direction of sun
  - Polarisation of sunlight (sun not visible)
  - Landmarks
- Earth’s magnetic fields
- Smell

Young bees will initially go on orientation flights to orientate themselves in relation to hive location.

Young bees will navigate to forage by sun orientation, older bees rely more upon landmarks (bees learning ability).

Young bees are informed about the location of the forage by the wagtail dances which are based upon orientation to the sun. Older bees will remember the location of good forage.

The bee is able to calculate the variation of sun location by time of day.

On cloudy days the worker can detect UV light and when the sun is not visible detect the polarised light patterns of the sun.

The worker has cells with iron containing granules in front of abdomen and around the abdominal segment, these are thought to enable it to work out magnetic orientation.

Water is odourless so sites are marked with Nasonov and foot odours, it is thought that local odours will attract workers. Colony odours definitely direct bees on return flight.

Visual location locally of flowers and landmarks are key for a successful forage.
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6.8 the behaviour of the worker bee towards intruders and the theories advanced to describe the means by which colonies recognise intruders;

A colony is defended at its entrance by guard bees, but bees are constantly patrolling within the colony ensuring awareness to threats.

Intruders include:
- Wasps/hornets
- Moths
- Ants
- Drifters
- Robbers
- Beekeeper

Each colony has a distinct odour, this comes from the mix of nectar and in the shared colony crop. A guard bee (worker transitioning from house to foraging bee) will check the scent of each bee entering the colony. If the scent is OK the bee will be allowed to enter.

If a bee from another colony enters with a load of nectar/pollen enters the hive confidently i.e. has made a location mistake the guard is likely to let the drifter pass, although she may follow the incomer to check nothing untoward happens.

If a young worker drifts into another hive they are likely to hesitate and will become submissive when inspected by the guard, curling up with legs and abdomen tucked in, she make release some nectar for the guard to sample and continually pull the proboscis through her front feet. The guard will evict the drifter without harming her. If the drifter has good load of nectar she may be allowed to enter.

If the bee trying enter a colony is intent on robbing she will zig zag across the entrance of the hive before trying to enter. The guard bee recognises this movement and raise itself into guard posture (mandibles opening and closing, front legs raised and standing on rear two) whilst releasing the alarm pheromone 2-heptanone.

If the alarm pheromone does not scare the robber away as soon as it lands the guard will fight it and try and sting it releasing the stronger alarm pheromone. Robbers never adopt the submissive position, they run or fly away.

The alarm pheromones recruit additional bees to the cause with subsequent bees stinging in the same location as the original sting which has the pheromone Isopentyl acetate released by the previous stinger.

Wasps, hornets and moths will be attacked within the hive in this manner. It is key that the wasps and particularly the hornets do not escape as they will bring back reinforcements and in the case of hornets that can be the end of the colony.

Bees are aware of vibration, scent and movement, if the guard bees sense vibration and/or movement close to the hive they will raise the alarm and investigate the source. Beekeeper perfume, perspiration and CO₂ can illicit the defensive nature of bees, bees sense CO₂ for locating the most advantageous place to sting.
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External factors that affect defensive mechanisms:

- Time of year, generally accommodating in spring and more defensive in autumn
- Colony conditions, need to defend is clear a times of change such as superceding or swarming
- Genetics, some bees are more aggressive/defensive than others and this is not always a bad thing when it comes to defending itself.
6.9 The collection of nectar and water and their use by the colony:

The colony requires water to:
- dilute stores ready for feeding
- dissolve granulated sugar
- for manufacture of brood food which comprises 70% water
- cooling the interior of the nest

The colony requires nectar to:
- as only source of energy through metabolism
- to create stores
- to feed older larvae

Key diagram from Hooper and other sources:

The average honey content of the bee is 50:50 Nectar:Water and this needs to be maintained. The honey is continually transferred between bees. 50:50 is the right mixture for digestion and hence energy.

Rate of flow of nectar into colony will be a determining factor in the growth rate of the colony.

The foraging bee has a short life, basically it dies after 80km of flight, it requires a reservoir of glycogen in the flight muscles in order to survive, older bees cannot create more so after approximately 800km flight the forager dies. This can be after a few days or 3 weeks in the summer.

2% of colony population act as scouts for the foragers, passing on source info through wagtail dances.

Water foraging and nectar foraging bees for different groups, water group much smaller than nectar group.

The liquids are sucked into the bee via the proboscis (tongue). Briefly the inner part is the glossa down which saliva can flow, surrounding this tube is the food canal which opens at the top into the
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cibarium. It is the expansion of the cibarium muscles which cause the liquid to be drawn up into the mouthparts. If the bee encounters solid food e.g. solid honey, saliva flows down the glossa and is "rubbed" into the food by the hairy underside of labellium at the end of the proboscis prior to being sucked up.

From the cibarium the liquid heads on to the pharynx for mixing with enzymes and on to the crop, via the oesophagus.

Foraging patterns are different for water and nectar:

**Water**

- 100 flights per day
- 90% of trips take less than 10 minutes
- water source close to colony
- prefer stagnant water with organic matter
- mark site with Nasanov pheromone and tarsal (foot) pheromone
- load up with water for up to 1 minute
- average load 25mg (maximum 50mg)
- 2 – 3 minutes spent in colony off loading water
- water is not stored in colony

During winter to cold to forage for water, bees expel water through trachea this condenses on hive surfaces and is recycled. Some stores are always left uncapped the hygroscopic nature of honey absorbs surface water increasing water content and hence the usability of stores for consumption.

**Nectar**

- 10 flights per day, 30 – 60 minutes per flight
- prefer forage with higher nectar content, can vary between 20 and 14%
- average nectar load 40mg (can take up to 100mg, bee weight 90mg)
- visits 100 – 1,000 nectar sources per forage trip
- off loading time 4 minutes
6.10 the inter-relationship of nectar, honey and water in the honeybee colony;
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6.11 the conversion of nectar to honey including the hydrolysis of sucrose, the evaporation of water and the role of the honeybee in accomplishing these changes;

Hydrolysis

Hydrolysis breaks the glycosidic bond, converting sucrose into glucose and fructose. Hydrolysis is, however, so slow that solutions of sucrose can sit for years with negligible change. If the enzyme sucrase is added the reaction will proceed rapidly. Hydrolysis can also be accelerated with acids, such as cream of tartar or lemon juice, both weak acids. Similarly gastric acidity converts sucrose to glucose and fructose during digestion.

Raw nectar will contain 20-70% water and various sugars, mainly sucrose, glucose and fructose, in differing proportions depending upon the source of the nectar. If stored in this form the high concentration of water and the presence of natural yeasts and bacteria would cause the nectar to ferment and grow moulds.

There are two principle changes that take place to convert nectar into honey:

- Evaporation of water to reduce the content to 17 – 18%
- Chemical changes due to addition of enzymes

Water is evaporated by the action of the house bees. A bee takes a drop of nectar onto its partly folded proboscis, so exposing it to the air then swallowing it again. This process reduces the water content by 15%, when complete the bee will paste the nectar in the top inside edge of empty cell or in an unsealed cell already containing nectar. Other bees create a current of air throughout the nest and evaporation of water from the exposed drops and the surface of nectar in open cells.

The chemical changes are due principally to two enzymes, Sucrease and Glucose Oxidase. The enzymes are generated by the hypopharyngeal glands in older bees:

- Sucrease is added by the bee which collects the nectar in the crop as it transports the nectar back to the hive. It splits each molecule of sucrose into two smaller molecules glucose and fructose (hydrolysis). More Suscrase is added by the house bees as part of the regurgitation process of evaporation.

\[
C_{12}H_{22}O_{11} + H_2O = C_6H_{12}O_6 + C_6H_{12}O_6
\]

- Glucose Oxidase acts on glucose, breaking it down to give Gluconic Acid and Hydrogen Peroxide. The hydrogen peroxide is important as it destroys bacteria.

When the water content has been reduced sufficiently, the bees seal over the honey with wax cappings and it will then keep for a very long time. Bacteria and yeasts are unable to grow because of the high concentration of sugar, the antibacterial activity of the hydrogen peroxide and the exclusion of water and air.
6.12 the collection, storage and use of pollen by the honeybee colony;

The honeybee will visit approximately 100 flowers in order to collect a full load of Pollen. By various methods (dependent upon the flower type) such as brushing against the pollen or cutting the anthers with its mandibles pollen becomes attached to the bees hairs.

Whilst flying the bee will groom itself with its legs and directing the pollen with a bit of nectar to the surface of the basitarsi of the hind legs. The opposite hind leg will rake the pollen paste onto the flat surface of the auricle from there it is pushed onto the corbicula.

On returning to the hive the bee will unload the pollen itself into a cell near the brood. All other types of collection are removed by receivers. Pollen is removed by hanging one leg into the cell and releasing it with the other hind leg.

Workers will pack the pollen within the cell and mixing in more nectar to pickle the pollen to become “bees bread”. Un-pickled pollen goes mouldy.

Pollen contains in various mixtures:

- Water
- Protein
- Fat
- Starch
- Sugar
- Ash

Pollen is the only source of protein for the colony and has various roles throughout the bees life:

- Consumed by nurse bees to produce brood food and royal jelly
- Fed to worker larvae
- Mixing with wax to make brood cell cappings porous
- Consumption by workers to re-activate their hypopharyngeal glands in order to feed larvae
- Consumed by workers in autumn to build up fat bodies and hypopharyngeal glands to extend life in order to over winter
- Consumed by workers for the orderly development of their glands, particularly the wax glands
6.13 the collection and use of propolis by the honeybee colony;

Collection

- 100g required by normal colony per annum, different strains have propensity to collect differing amounts
- found in various plants trees
  - Horse chestnut, alder, popular, prunus, conifer
- Collected in summer/autumn when warm, hardens at 5°C
- Worker uses mandibles to scrape/pull resin from plants
- Passes to forelegs then transferred to basitarus of middle leg
- Pressed into pollen basket of hind leg on same side (different from pollen to save use of pollen brushes)

Return to hive

- Used in location and not stored
- Workers nibble propolis off forager
- Takes up to 1 hour turn around

Use

- Filling cracks and crevices in hive
- Reducing entrances
- Smooth out surfaces
- Mixed with wax to strengthen where comb joins wall
- Varnish cells before use (antineptic)
- Embalm large intruders that cannot be evicted from hive e.g. mice
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6.14 the conditions leading to swarming

Colony size
- 40 litre and 23,000 cm$^2$ of comb
- Queen rearing starts when 12,000 workers within nest
- Swarm initiated when 20,000 workers

Brood nest congestion
- Congestion of brood
  - 90-95% cells in brood contain some stage of brood
- Crowding of adult bees

Worker age distribution
- Low mean worker age
  - E.g. 50% workers < 8 days old queen rearing starts
- Need sufficient number of workers, so low population queen rearing will not occur

Reduced transmission of queen substance
- Distribution of queen substance
  - Overcrowding prevents movement of queen
  - Strength diminishes as transferred amongst more bees
- Queen pheromone production diminishes
  - Age

Resource abundance
- Strong pollen and nectar flow
  - Induce colony growth
  - Facilitate preparations for swarming

Strain of bee
- Apis mellifera carnica has tendency to swarm
6.15 the conditions leading to supersedure:

Ageing Queen

- Reduced queen substance production
- Reduced rate of lay
- High drone population
- Presence of Nosema??? (Yates)

Injured queen

Large hive space

- Colonies with large hive space more likely to supersede than swarm
  - E.g hive capacity 80 L 50% supersede, 21-41 L 80% swarm

Supersedure cells

- Less than swarm cells 1-10 compared with 5 – 20
- Look like emergency cells, drawn from worker
- Position, swarm cells on edge
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6.16 the behaviour of swarms and the method of selection by the swarm of a site for a new home;

Leaving the hive

- Preparation
  - Fill crop to 50%
  - Wax glands start to become active (protein diet)
  - Foragers become scouting bees prior to swarm initiation
  - Bees will start to cluster outside the hive
  - Queen is slimmed down so she can fly
  - Lay rate drops off due to lack of food
  - 3 days before swarm scouts start looking for new home

- Scout bees will call to action
  - Good weather
  - Queen cells capped and known to be good
  - Worker piping and buzzing runs, as well as shaking workers into action
    - Piping involves worker pressing thorax to another bee and vibrating wing muscles with wings clasped tight, frequency is 200 – 250 hz with harmonies 400 – 2000 hz, resembles F1 car sound
    - Middle C is 261 hz
  - Retinue will push queen out and whoosh swarm has launched

Forming a cluster

- Swarming bees form a cloud 10 – 20 m across
- Swarm forms a cluster on a short distance from the original hive
  - Some workers settle on a branch or such object
  - Queen joins them and then rest of swarm
  - Drawn by the queen substance 9-ODA and Nasonov pheromone, but cluster stabilises on 9-HDA

- cluster structure
  - the cluster behaves just as one would within a hive
  - bees at centre hot 35° C and outer bees static at 17° C
  - temperature is managed by cluster closing or loosening

- scouting bees commence search for new home

Scouting for new home

- Ideal location
  - Entrance less than 15 cm² (30-40mm diameter)
  - Cavity capacity of 40 litres, approx 20 x 30 x 100 cm
  - high above ground 2-5m
  - South facing entrance
  - Previous colony comb
  - Entrance at bottom of cavity

- Site inspection
  - Will investigate inside, measure capacity by walking and short flights
  - Will spend just as long inspecting outside as inside
  - 1st visit duration average 37 minutes
  - Single scout will return to site up to 6 times, subsequent visits shorter (13 min average)
  - Scouts will scent mark the site with arnhart and nasonov pheromones
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- Communication with swarm
  - Scouts will return to colony and perform waggle dance on surface indicating location of site, the better the site the more agitated the dance
  - Dance recruits investigate the site and return to dance their impression
  - Initially can be several potential sites and hence disparate dances, weaker dances will cease through lack of recruits
  - After several cycles of visits and dances scouts will retire

Travel to new home

- Start of travel conditions
  - Quorum of agreement on perfect home measured by number of scouts at preferred site
  - Waggle dances 100% for preferred site
  - Scouts do buzzing runs interspersed with piping, waggle dances and shaking of workers
  - Bees on outer surface heat thorax to 35 degrees, ready to burst into flight
  - Swarm cluster loosens to enable simultaneous lift off

- Method of travel
  - Rise up to form swarm approx. 10 x 8 x 3 m within 60 seconds
  - Wait for about 30 seconds before moving off
  - Only scout bees know where new home is (3-4% of population)
  - Lead by scouts, travelling faster through swarm in direction of new home
  - Throughout checking the queen is present by sensing her 9-ODA pheromone
  - If lose her retrace, all way back to start
  - Move off slowly accelerating to between 5 and 8 km/hr
  - Direct to new home site
  - Pause at site

- Entering new home
  - Foragers go to entrance and mark with Nasonov pheromone
  - Bees enter hive within 10 minutes, queen in midst of entrants
6.17 the initiation of comb building and the construction of comb;

Colonies do not build all their comb at once, but rather add to it in pulses coinciding with periods of nectar intake (Hepburn 1986). The initiation of these building pulses depends on two conditions being satisfied:

(1) the colony is currently collecting nectar and

(2) the colony has filled its available comb beyond a threshold level with brood and food.

Once building has started, it will continue as long as nectar intake persists, regardless of comb fullness.

With a swarm, once a new home has been located comb building is immediately initiated for the brood and storage of stores.

The colony employs a population of what appear to be generally inactive young worker bees in the comb construction.

The colony will initially create a thick base of wax which will be drawn out into comb. Construction begins on the roof or side of the nest cavity, with possibly 2 or 3 construction sites being started at the same time. Construction continues in a random manner with several cells being drawn out at the same time and several bees contributing to each cell.

The foundation provided by the beekeeper emulates the starting base from which the comb is drawn out.

When construction begins the workers hang together in tight chains, forming a cluster to maintain the temperature at 35°C (the ideal temperature for wax manipulation). The worker removes the wax from the gland on the underside of the abdomen with its hind legs and passes it forward for the worker to mix it with saliva and manipulate using its mandibles and forelegs.

Thick layers of wax are first placed at the base of what will become each comb, these are drawn out into cells by elongating and thinning the wax out to form the cell walls. A single worker will apparently in a random manner move from cell to cell and site to site smoothing out or adding wax as necessary. The worker is aware of what needs to be done at each cell. Each site will eventually join forming a contiguous comb.

Some Stats:

- Each cell takes 4 min to remove and manipulate each wax scale from the wax gland
- 66,000 bee hours to produce 77,000 cells from 1 kg wax
- 1 kg wax capable of supporting 22 kg weight
- Each cell is a hexagon, offset from the cell on the reverse side
- Worker cells are 5.2-5.4 mm in diameter, Drone cells 6.2-6.4 mm
- Bees build cells horizontally at an angle of 13° and each cell is at 120° to its adjacent cell
- Wax thickness of the cell wall is 0.073 mm
- Distance between comb is 0.95 cm
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6.18 the colony in winter and summer with special reference to ventilation, humidity and temperature control (homeostasis);

Winter

Bees begin to cluster at external temperatures of 18°C, the cluster contracts as the temperature drops below 14°C the cluster has a compact outer of relatively quiet outer bees and an inner core where bees have space to move around. Below 0°C the cluster no longer contracts and the bees begin to generate heat rather than conserve heat through compacting the cluster.

The bees in the shell continually exchange places with those within the core in order warm themselves prior to returning to the shell and conserving heat.

In the winter there is little or no brood production so the inner core temperature can drop to 20°C but not below 13°C, with the shell being a minimum of 8°C (below which the bees can no longer cling together).

The cluster will operate at the lower temperatures in order to conserve energy and stores required to create energy/heat.

Summer

During the spring, summer and autumn when the queen is laying and there is brood the core of the colony needs to be maintained at approximately 35°C independent of the outside temperature. So in cooler weather the brood must be warmed and in warmer weather cooled, strategies for each case comprise:

Cool weather – nest heating
- Bees can generate heat through flexing their wing muscles whilst leaving their wings motionless.
- Bees form a thin layer over the brood in order to maintain the incubation temperature
- If the temperature drops and there are not sufficient workers to cover the brood the outer brood is abandoned, resulting in chilled brood

Warm weather – nest cooling
- The colony will disperse allowing cooler air to flow through the colony
  - In extreme cases bees will cluster outside the colony
- As the colony disperses bees will fan, creating cooling air flows, bees will face the same direction on the frames and beat wings to create the flow, others will fan at the entrance causing air to be sucked into the nest and warm air to be expelled
- Bees use the evaporation of water to cool the nest. Water is spread throughout the nest in puddles on capped cells, thin covering on open cells or as hanging droplets on the frames. Fanning over the cells causes evaporation and hence cooling effect. Workers can also “tongue lash”, rapidly extending and rapidly contracting their proboscis causing water to evaporate.
- Encouraging the foraging of water

Bees are able to accurately sense small temperature changes through sensors on their antennae.
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6.19 laying workers and drone laying queens and the conditions leading to their development;

Laying Worker

Laying workers develop in the absence of open brood as produced by a proper queen. Pheromones from the brood prevent the developing of the workers' ovaries. The pheromones that prevent development of laying workers are brood recognition pheromones. In some cases, a failing queen is not superseded, and a laying worker can develop in the presence of a true queen. The process of developing a laying worker usually takes 3 weeks after the loss of the original queen.

All methods of identifying a laying worker bee involve inspection, in which the beekeeper examines the brood pattern and type to identify if a healthy queen is present, or a potential laying worker. The beekeeper looks for a number of symptoms, including:

- **Brood Pattern**: Laying workers lay eggs that lack the queen's egg recognition pheromone, meaning that other workers may remove the eggs. This results in a spotty brood pattern, in which empty cells are scattered heavily through capped brood.
- **Number of Eggs per Cell**: The beekeeper looks at the honeycomb cells to see how many eggs are laid in each one. Queen bees will usually lay only a single egg to a cell, but laying workers will lay multiple eggs per cell. Multiple eggs per cell are not an absolute sign of a laying worker because when a newly mated queen begins laying, she may lay more than one egg per cell.
- **Egg Position**: Egg position in the cell is a good indicator of a laying worker. A Queen bee's abdomen is noticeably longer than a worker, allowing a queen to lay an egg at the bottom of the cell. A Queen bee will usually lay an egg centered in the cell. Workers cannot reach the bottom of normal depth cells, and will lay eggs on the sides of the cell or off center.
- **Drone Brood in Worker Cells**: Another good indicator is drone brood in worker sized cells. Drones are raised in larger cells than workers. Drone cells are recognizable by their larger size, and when capped Drone cells are capped with blunt pointed cappings. Drones in worker cells are a sure sign of a failing queen or laying worker.

Drone Laying Queen

Upon examination of a hive with drone brood, one comes across a queen. This usually occurs when returning to check on a **newly introduced queen** with a package of bees. Queens like this are usually small as far as queens go. One may find several queen cells started but not always and the eggs in the queen cells are still unfertilized eggs. It is important that the queen in this case be killed, and replaced immediately with a new queen. **Older queens** may also be failing. Either they were poorly mated or have exhausted the supply of sperm to fertilize her eggs. They should be killed as well. We are assuming that there still is a sufficient population of bees to support a new queen. If not, if use can be made of the colony it should be united with another weak colony, bear in mind the workers may be old and past useful colony contribution.
6.20 the effects of pathogens and pests on bee behaviour;

Generally pathogens affect the life cycle of the colony in that it reduces the number, strength and longevity of the young honey bee. In some cases in highly infested colonies the sick bees are either ejected or leave the nest and it is believed that colonies may abscond as a result of varroa and Chalkbrood infestations. Lack of fit young bees eventually reduces the foraging population and hence the ability for the colony to increase and overcome the pathogen. With Nosema and varroa related diseases it is known that the foragers orientation is affected which further decreases the ability for the hive to feed itself.

Pests like acarine and varroa as well as shortening the life of the bee are vectors to viruses to which colonies have little resistance. Larger pests such as wasps and hornets cause the colony to become defensive fighting at the entrance and within the colony. Mammals external to the hive such as cattle again cause defensive reactions. Mice coexist within the hive with the bee cluster moving away from the intruder. Wax moths coexist with the colony however if the colony is weak it will be further weakened by a wax moth infestation. Colonies near a badger run apparently become aggressive.

Below is a table of specific effects.

<table>
<thead>
<tr>
<th>Pathogens</th>
<th>Effect</th>
</tr>
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<tbody>
<tr>
<td>Brood Disease</td>
<td></td>
</tr>
<tr>
<td>AFB</td>
<td>Workers uncap sealed brood and clean out cell, queen will not lay in infected cell (pepper pot pattern)</td>
</tr>
<tr>
<td>EFB Chalkbrood, stone brood and chilled brood</td>
<td>Workers clean out affected larvae</td>
</tr>
<tr>
<td>Sacbrood,</td>
<td>Workers uncap brood and clean out cells</td>
</tr>
<tr>
<td></td>
<td>Life shortened</td>
</tr>
<tr>
<td></td>
<td>Become foragers earlier</td>
</tr>
<tr>
<td></td>
<td>Stop feeding larvae</td>
</tr>
<tr>
<td></td>
<td>Rarely collect pollen</td>
</tr>
<tr>
<td>Adult Bee Disease</td>
<td></td>
</tr>
<tr>
<td>Nosema</td>
<td>Black queen virus and colony can go queenless</td>
</tr>
<tr>
<td></td>
<td>Queen can stop laying and is superseded</td>
</tr>
<tr>
<td></td>
<td>Foragers lose orientation</td>
</tr>
<tr>
<td></td>
<td>Stop feeding brood</td>
</tr>
<tr>
<td>Chronic Bee Paralysis Virus</td>
<td>Bees nibble hairs of affected bees and eject from hive</td>
</tr>
<tr>
<td>Pests</td>
<td></td>
</tr>
<tr>
<td>Varroa and Acarine</td>
<td>Shortens lives and can cause foragers to lose orientation (they get lost) With acarine bees walk from hive and climb up stalks of grass.</td>
</tr>
<tr>
<td>Wax moth</td>
<td>Infestation can destroy comb and cause bald brood reducing lifespan of bees</td>
</tr>
<tr>
<td>Wasps/hornets</td>
<td>Cause bees to become defensive and fight</td>
</tr>
<tr>
<td>Mice</td>
<td>Ignored by bees who move away abscond</td>
</tr>
</tbody>
</table>
Module 6 Honeybee Behaviour

6.21 the learning behaviour of honeybees;

In the context of foraging behaviour, bees perform two forms of learning, latent (or observatory) and associative learning. Latent learning plays an important role in spatial orientation and learning during dance communication.

- Worker will observe a dance and will eventually partake in the dance in order to learn the source of nectar/water/pollen or even new nest site
- The worker will memorise landmarks around the hive on orientation flights and en-route to learnt locations for future navigation
- The worker must re-memorise location markers after a swarm as the “home” location will have moved

In associative learning, stimuli experienced immediately before reward (usually nectar source) are memorised for the guidance of future behaviour.

- A forager will associate odour with nectar/pollen/water source within 1-2 trips enabling constancy in revisiting the same source on repeated forages
- The association of colour requires up to 5 visits to attain the same constancy

The ability to learn means that the colony can adapt to the changing environment within which it must survive. As forage changes with the seasons so the colony will find new sources of nectar and pollen through scout bees discovering new sources and “teaching” foragers through the dances. For the colony to reproduce through swarming it must move, find a new home and establish that location, this requires all the bees to learn the new environment.