Jürgen Tautz

Exploring the world of the honeybee

New data – new insights

HOBOS
HONEYBEE ONLINE STUDIES

Audi
Stiftung für Umwelt

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New data - new insights

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Die Erforschung der Bienenwelt
Neue Daten – neues Wissen

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Introduction

One of the most challenging and oldest puzzles for behavioural biologists studying social insects is to understand how the many individuals in a colony work together and to a certain extent coalesce to form a new complex being, a “superorganism”, that is more than the simple sum of its parts.

Attempts to solve this problem have led to the proposal that superorganisms are a highly complex outcome of evolution, a concept that has raised even more questions. Research in this area is vital and exciting, not the least through the many different points of view leading to different interpretations. As in all natural sciences, advances can only come from reliable observation and clear, repeatable experiments. Progress is dependent on the ideas of researchers and the methods available to them. This book provides an insight into current approaches in bee research and their outcomes.

The earliest known attempts to describe and understand colony-building insects are several thousand years old. Aristotle explained the collective lives of bees in the form of an insect colony as follows: “Their apparently perfectly functioning society is based on clearly distributed and accepted roles and submission to a single leadership”. The bees, in his view, represented an ideal social state. While expressions such as “queen bee” and “society forming insects” appear to suggest close comparisons between animals and humans, these terms in themselves have no explanatory value. Observation and experiments provide the only basis on which hypotheses can be proposed that are directed at understanding Nature. This also applies to research on honeybees which addresses many different levels ranging from the characteristics and abilities of individual bees through to the unique accomplishments of the bee colony superorganism.

Results of research into the world of bees are presented in this book. It begins with the founding of a new colony. Selected aspects of this process are introduced and new ideas and discoveries are presented here for the first time.

The beginning of a new bee colony is reported under Propagation of bee colonies – swarming in which half of the old colony leaves the hive with the old queen, searches for, finds and then occupies a new home. Furnishing the new home with combs is a prerequisite enabling the various sections of the colony to carry out their many different tasks. The nest hollow with its combs is a world in which the bees spend the greater part of their lives. Living comfortably is possible in the hive because bees continuously control the prevailing climatic conditions within it. Collaboration among the Bees during the organisation of swarming, the construction of combs, nest climate control and many other social accomplishments, is based on harmonizing the contributions of each individual bee. On the other hand the behaviour of each bee is determined by internal and external factors such as environmental stimuli and communication signals. Different individual bees, however, may react very differently from one another to the same signal. The consequence of interactive collaboration between individuals is that bees in a colony fuse to form a superorganism, an integrated living being, capable of achievements over and above the abilities of the individuals that constitute it.

New points of view, new research methods and increasingly powerful computing tools that can cope with large amounts of data, have gradually allowed an image of truth of the honey bee to emerge. Contrary to expectation and not in the least diminished by high-tech applications, honeybees continue to be viewed with awe and admiration.

Chapter 1

Propagation of bee colonies – swarming

Reproduction without sex

The oldest and simplest form of reproduction in living organisms is division. This leads to offspring with identical genetic constitutions. A critical prerequisite, though, for further evolutionary development is that propagation does not lead to identical offspring but instead to individuals that are genetically different, allowing adaptive flexibility and the possibility of natural selection. Variability in offspring from division can sometimes occur through gene mutations however these are random, unpredictable and relatively rare. The invention of sexuality where the production of offspring is, in every case, associated with a novel combination of hereditary characters was therefore a stroke of natural genius. The union of egg and sperm leads to an entirely novel individual and, through the genetic variability of the germ cells, to a potential for an infinite variety of types on which natural selection can operate.

Amongst the higher forms of life, honeybees have taken a unique path in which propagation by division and sexuality are both retained but temporally separated as in the very early forms of life and still found today in bacteria and unicellular organisms. The honeybee sexual phase occurs between virgin queens and male drones during their mating flights. Propagation of the honeybee superorganism, the hive, is achieved through division in the form of swarming.

Leaving the hive after division

A bee colony prepares itself well for division of the hive. The peak time for swarming in central Europe is, as a rule, in May by which time preparations within the colony are already completed. A primary consideration for division is that there must be enough available worker bees to form two fully functional colonies after the event. To this end the number of bees increases significantly in spring to the point where the hive becomes crowded. This is the first clear preparatory signal for swarming. A new queen is reared (sometimes several) during the period of rapid population growth who will, together with the workers that remain after swarming, take over the old hive and everything that belongs to it.

When swarming finally occurs, the old queen leaves the hive with part of the colony. Thousands of bees leave the hive within a few minutes and form a dense cluster around the queen who has often settled not very far away from the old hive.

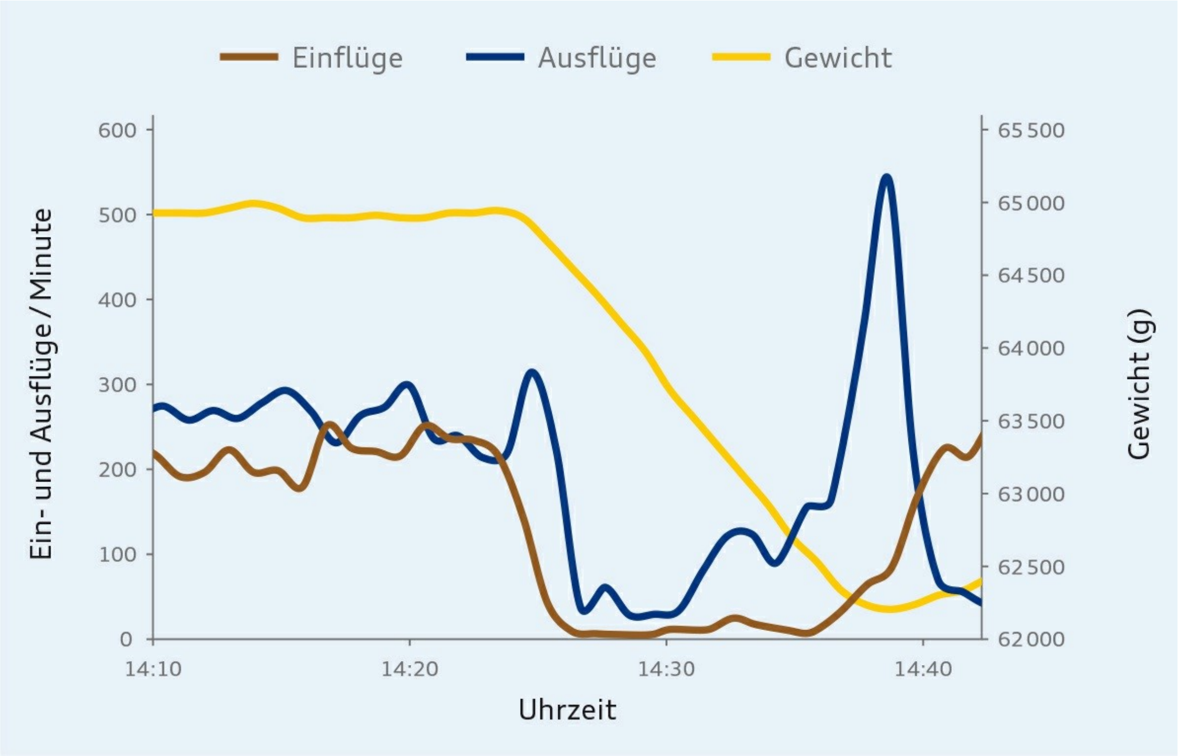
Observation of activity in the hive that directly precedes swarming has been difficult for many reasons: One could never guess the precise timing of the exodus from the hive and so needed considerable good fortune to be present for this event which occurs only once a year. Opening the hive to observe the swarming can be expected to significantly disrupt the process although the extent of this is difficult to estimate unless one can make a comparison between a disturbed and undisturbed hive. Precise data associated with the complex behaviour preceding swarming can only come from extensive measurements taken from within the hive and with as little disturbance of the natural procedure as possible.

A more recent and thorough study of the swarming behaviour in a beehive with minimal disruption was first made possible during the project HOBOS (www.hobos.de). Preliminary views of the recordings immediately provided new insights. A deeper analysis of the data that has been collected over years and is available to all, will certainly reveal much more. All HOBOS recordings can be accessed from stored data and the problem of missing a live view of swarming no longer exists. Further study of stored data can be continued at any time.

What new insights have the HOBOS observations brought to light?

Sensitive microphones installed within the HOBOS colony record “beeps” that cannot be detected without these devices. Temperature probes in the hive also reveal interesting data: the temperature over a period of about 30 minutes increases significantly, beginning at the normal brood comb temperature of about 35 degrees C and reaching a peak of nearly 39 degrees C which is well above the normal brood comb temperature and which never otherwise arises in a healthy hive. Endoscope cameras in the hive, using light sources with wavelengths invisible to bees, show them running back and forth across the combs – a clearly exaggerated state of excitement prevails. About five minutes later the swarm exits the hive at a rate of about 500 individuals per minute. About 2000 bees take part in a swarm from the relatively small HOBOS hive; in larger hives of beekeepers this can total up to 10,000 individuals.

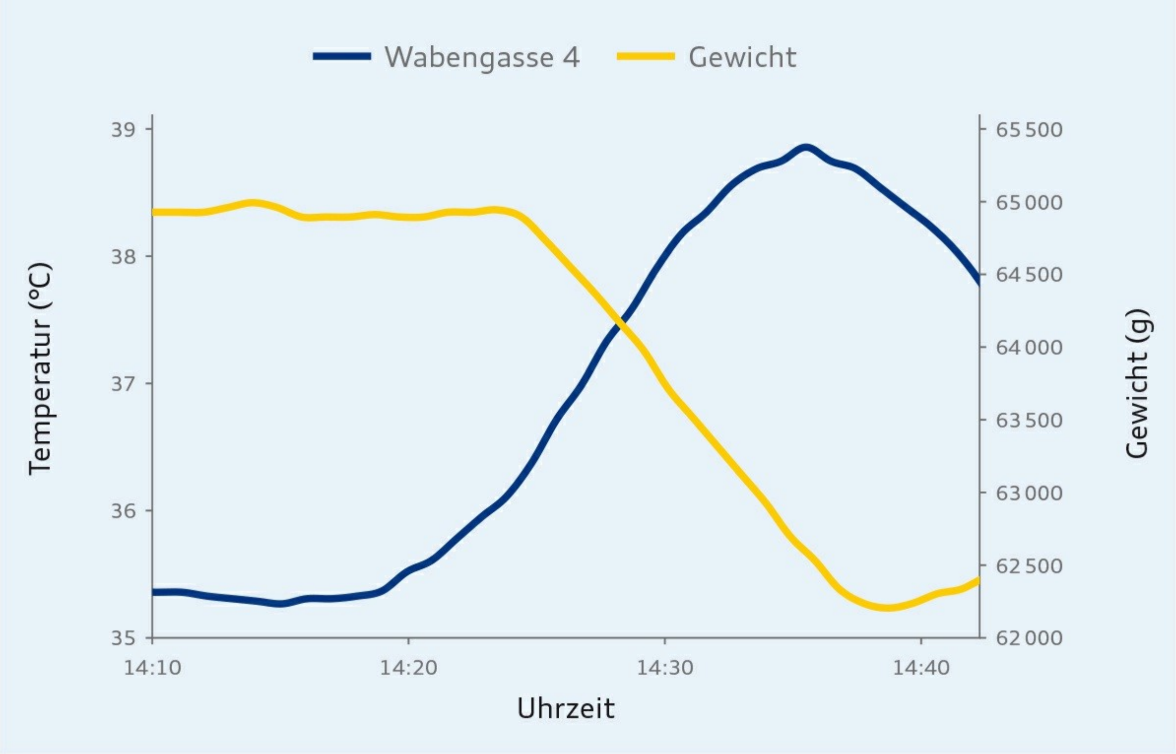
Surveillance and recordings of the weight of the hive and flight activity within the HOBOS colony reveal the entire sequence of events of a swarm exodus, beginning with a dramatic decrease in flight activity about 10 minutes before the swarm leaves the hive. The foraging behaviour which up to this point in time was normal, virtually ceases. Towards the end of the swarm exodus, a proportion of the bees does not remain with the swarm and return to the hive. The weight of the hive which had decreased significantly (see below) then increases to some extent.



HOBOS data for the swarm of 17 May 2012. The number of bees departing from and returning to the hive per minute is plotted together with the total weight of the HOBOS colony over a thirty minute period.

Data from 17.05.2012 show a large decrease in foraging activity: departure and return flights were significantly reduced and about 15 minutes before the swarm left, the hive exhibited a weight loss of about 2.5 kilograms. The overall weight of the hive began to sink as foraging activity decreased. That this significant weight loss occurs before the swarm leaves is surprising and so cannot be attributed to the departure of the large number of bees in the swarm alone. What is responsible for this? HOBOS data reveals the same phenomena in all swarming events that have so far been recorded: loss of weight is accompanied, on the same time scale, as the rise in temperature of the hive. Future studies may uncover physico-chemical and biological processes in bees which raise their temperatures in preparation for flight and may provide an explanation for the measured weight loss.

A thermocamera (one which colours the images of objects according to their temperature: blue – cold, red – warm, yellow and white – hot) focused on the hive entrance records an impressive firework display as the heated bees leave the hive with the old queen.

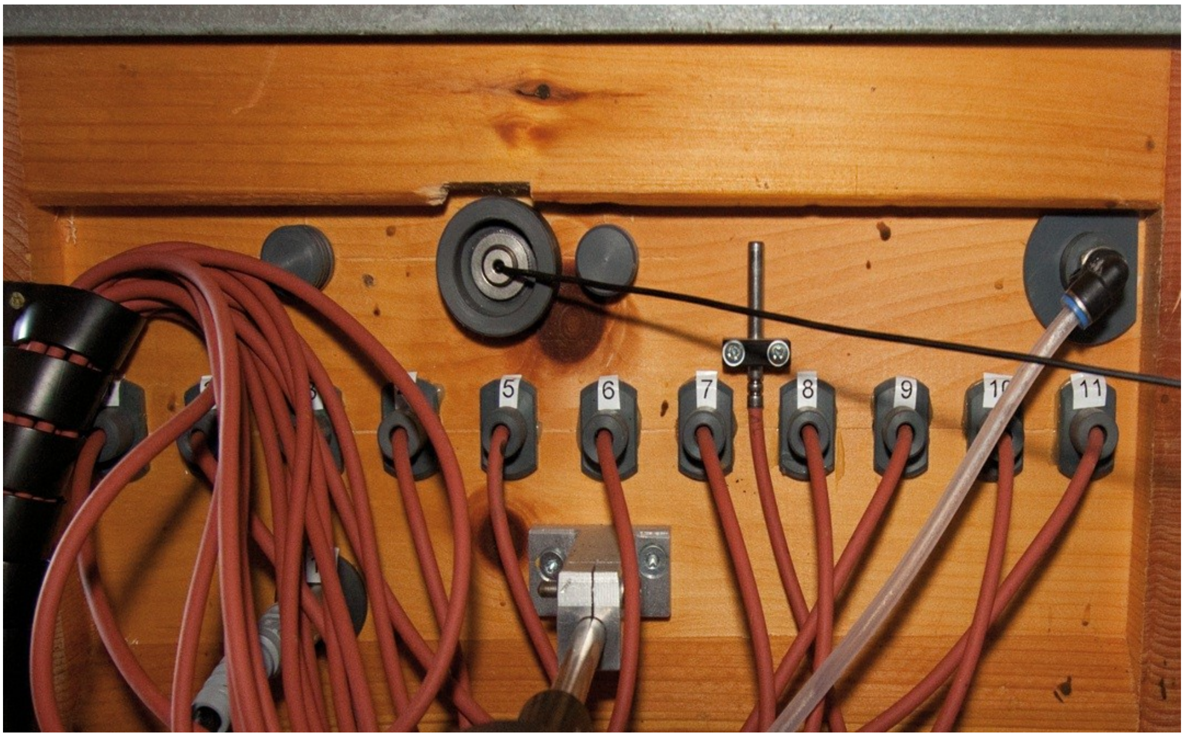


HOBOS data for the swarm of 17 May 2012. The total weight of the HOBOS colony and the temperature measured in comb passage 4, plotted over the same thirty minute period as in the preceeding Figure.

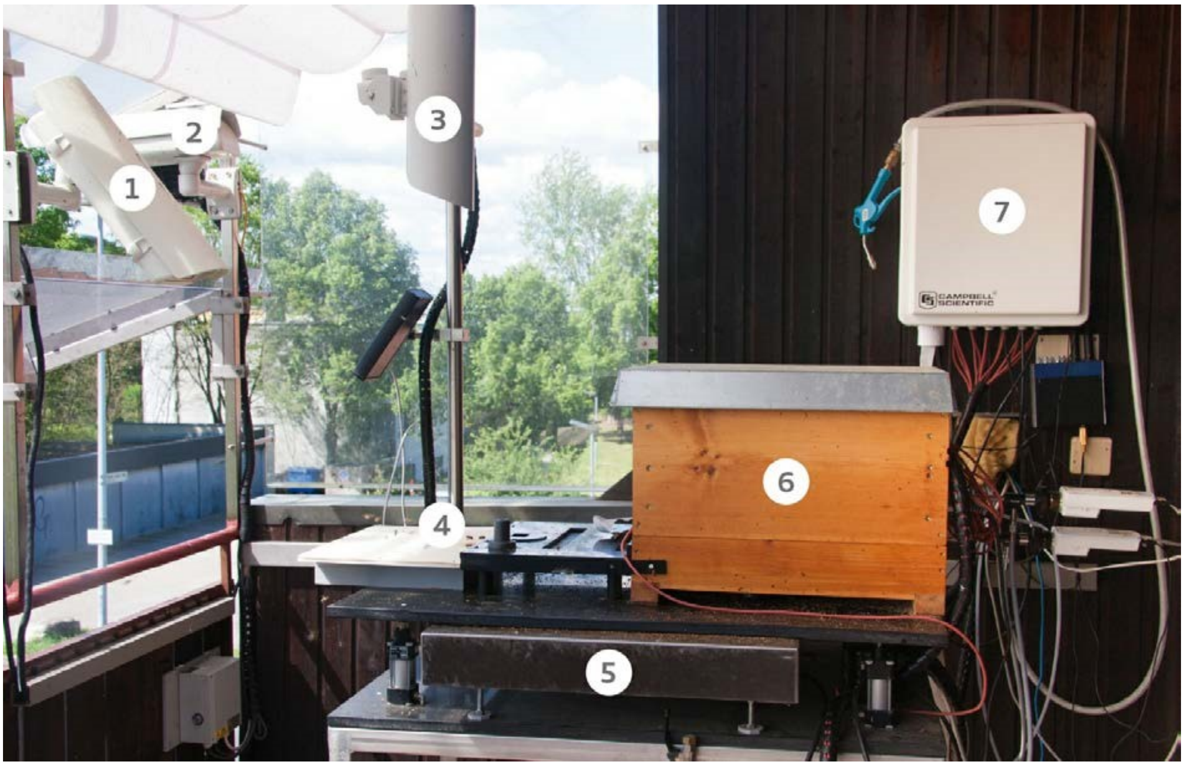
HOBOS

HOBOS (www.hobos.de) is an Internet platform with a living bee colony as its centerpiece which is monitored continuously in a variety of ways using modern technical and digital techniques. HOBOS, an acronym for HoneyBee Online Studies, provides extensive access to a living bee colony and its environment with cameras and sensors located inside and outside the HOBOS hive.

HOBOS delivers an endless stream of data about a bee colony, the weather to which it is subjected and the vegetation that surrounds it. Data collected from the bee colony includes the weight of the hive, the relative humidity, air temperature, including that between the eleven combs and at the front and back of the hive. The number of bees that fly out of the hive and that return to the hive are registered. HOBOS also delivers measured values from the environment surrounding the hive, namely the atmospheric pressure, air temperature and relative humidity, atmospheric electrical fields, precipitation, wind velocity and direction, solar radiation and the moisture content of the ground and leaves. HOBOS provides live videos with a camera focused on the entrance to the hive. This is also equipped with an infra-red light source in order to record night activity with an illumination invisible to bees. A temperature sensitive camera (thermovision) and two endoscopes with microphones record the activity in one of the passages between the combs and on the floor of the hive, again using infra-red illumination which does not disturb the bees. Finally, an extra camera with an infra-red light source records the environment and weather conditions in the area around the hive.



A bee colony delivers a permanent stream of data from a variety of sensors. (Photo: H.R.Heilmann, HOBOS-Team)



1. Hive entrance camera with IR illumination. 2. Garden camera with IR illumination.

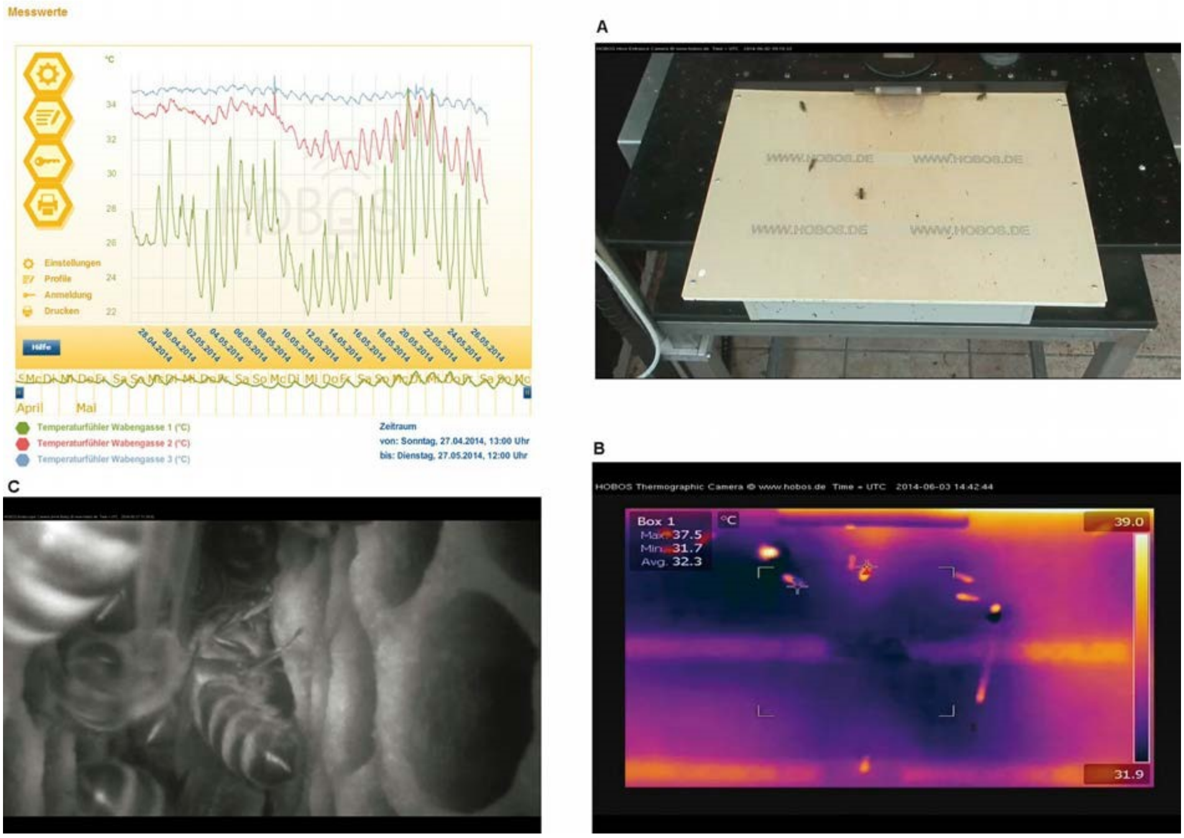
3. Hive entrance thermocamera. 4. Bidirectional optical gates across the hive entrance. 5. Scale to measure the total weight of the hive. 6. Hive box, containing the HOBOS colony and sensors. 7. Data logger for the HOBOS colony. (Photo: H.R.Heilmann, HOBOS-Team)

Live view videos can be viewed online or called up from video archives. Data tracks from the bee colony and its environment are also online and offline and available to all. Many questions can be answered by this data, for example:

- what is the weight of the hive when food for the winter has been stored?
- what do honeybees do in winter?
- how do honeybees sleep?
- how are workers fed that are busy in the brood combs?
- what sound does a young queen make before she emerges from her cell?
- does the number of bees flying out of the hive depend on the outside temperature?
- how quickly do honeybees return to the hive when a storm threatens?
- how warm is it in the center of the beehive or in the outermost passage between the combs?

The list can be expanded at will.

Storing the data gathered from the hive over many years provides not only high resolution temporal recordings but may also lead to the discovery of long term trends in the complex interactions between the bee colony superorganism and the environment. Every imaginable analysis and correlation of the recorded activities can be explored.



Life in the hive can be followed live through calling up current videos. A, activity of bees at the hive entrance with a normal camera; B, with a thermocamera, and C, with a camera and infra-red illumination focused on combs inside the hive.

Departure of the swarm to the new home

To witness the dispersal of a bee swarm and its departure to its new home belongs to one of the experiences that one never forgets. Approximately 10,000 bees leave the nest and immediately form a closely packed cluster around the old queen who usually settles quite close to the old hive and often on a tree branch. After a while at this temporary station they take off into the air, buzzing loudly and circle in cloud around the initial resting place. The cloud gradually takes on a cigar-like shape and moves first slowly and then with increasing speed toward the new nesting site. Swarms can move at speeds of up to ten kilometers per hour. Although individual bees can fly three times this fast, ten kilometers per hour for the entire swarm is remarkable when it is considered that most bees in the swarm do not know the location of the new nest site.

Were one able to be at the swarm's goal one could watch its arrival and occupation of the new home. Closer examination of the events above that seem so simple reveals a highly complex procedure, representing one of the most critical phases in the life of a bee colony.

Complex, because an enormous number of individual bees have to act in perfect spatial and temporal harmony; critical, because a new home has to be rapidly found and occupied. Honey reserves in worker bee stomachs are quickly exhausted and the swarm cluster hanging under the open sky is exposed to many threats from which the bees were safe in the protection of their nest. Heavy rain and a sudden decrease in temperature can result in the death of the entire swarm and so result in the miscarriage of the efforts of the original colony to propagate.

Researchers have long attempted to unveil the secrets of swarming through extensive and thorough behavioural observations. The German zoologist Martin Lindauer was a pioneer in the investigation of swarming behaviour.

His greatest contribution was the description of the bee dances that take place on the surface of the clustered swarm and his subsequent conclusions relating to the guidance of the colony to the new home. The work of Thomas D. Seeley, an American bee researcher, is of equal importance. We have him to thank for a detailed understanding of the decisions bees finally make about the new nest site, the criteria used, and how the location of the new site can be found by all the individuals in the swarm (Seeley 2013).

Thomas D. Seeley, a master of clearly structured bee experiments, with an experimentally produced swarm cluster. (Photo: Alexander S. Mikheyev, Cornell University)

The following is a list of currently known steps that bring a bee swarm to its goal, the new nest site.

1. New nest site search bees which are mostly older experienced foragers, fly off from the swarm cluster at its temporary station outside the old hive, and, if successful, return to dance on the surface of the bees in the cluster. In a large swarm of about 10,000 bees, only a few hundred individuals take place in the search for a new nest site.

2. Successful searchers initially dance and indicate the location of the site

they themselves have found. Hence at first, dances of different bees indicate many different sites but this is gradually reduced as dancers either stop or join the dances of others. Finally, all dancers are united in indicating only the best of all possibilities.

3. The dancers now fly back and forth between the swarm cluster and the new site. At the new site these bees circle around it in wide loops, buzzing noisily and marking the site with a pheromone (geraniol) which they release from Nasanov glands on their abdomens.

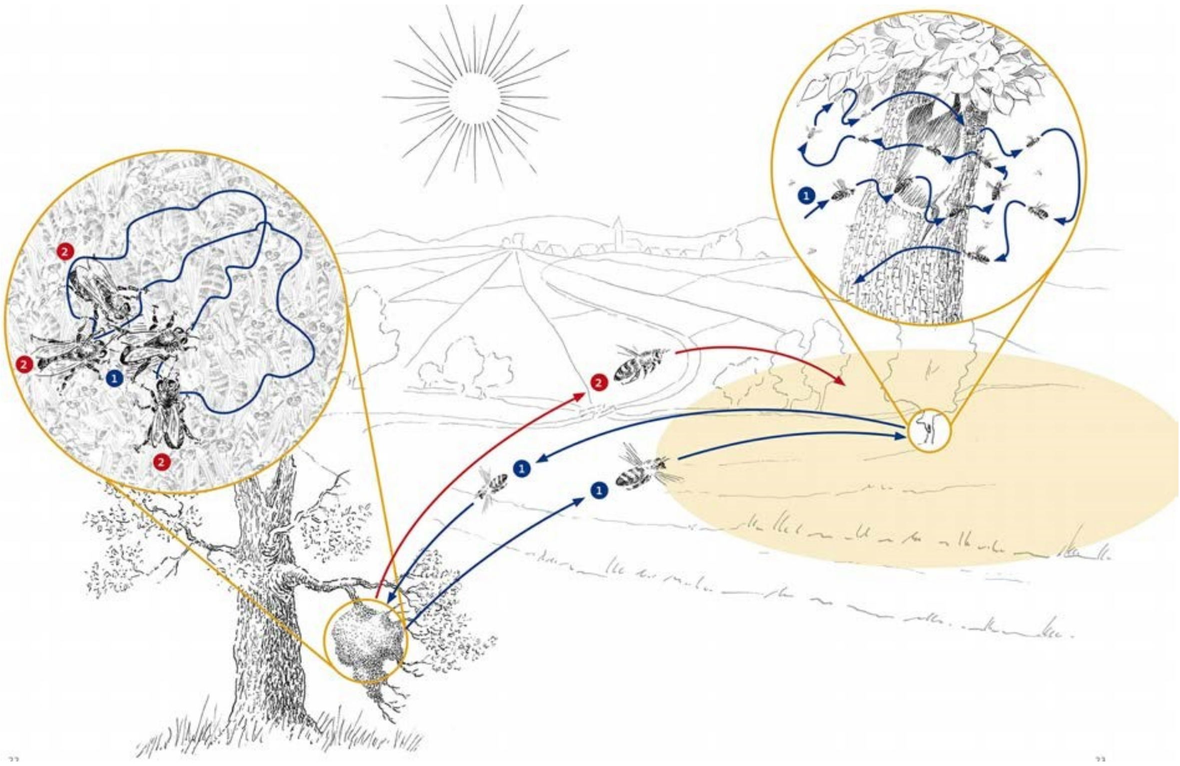
4. The scenting bees return to the swarm cluster, dance there again, return to the goal, mark it and then fly back again to the cluster. New individuals join in, guided by dances of those flying back and forth and by scent around the goal. Gradually a small group of informed bees accumulates which visit the new home site and fly back and forth between it and the swarm cluster.

5. Eventually the entire swarm cluster disperses into the air and flies off toward the goal. The swarm is guided over the entire distance by individuals who were engaged in both dancing and scent marking the new home site. These individuals now rapidly fly back and forth through the swarm cloud, their flight paths directed towards the goal.

6. On reaching the goal the bees and their queen land around the entrance to their new home and quickly occupy it.

That every single bee reaches the goal over a distance of often several kilometers, although only a small fraction of bees in the cluster are exposed to the dances and which anyway contain only inaccurate information (see Chapter 4), is indeed astonishing. The feat can be understood however when it is appreciated that bees which have learned the location of the new site, guide the swarm from their temporary station to the goal in a continuous, multistep process.

Not less astonishing is the almost explosive dispersal of the cluster which brings all the bees so suddenly into the air. Modern research methods have provided a deeper insight into this phenomenon. Thomas D. Seeley, Juergen Tautz and their collaborators investigated swarm clusters using special microphones, hair fine temperature-sensitive wires, video cameras and heat-sensitive thermocameras. Temperature measurements showed that over a period of about 30 minutes before dispersal, all bees in the cluster bring their body temperatures up to 37 degrees C. Once the cluster has reached this temperature, all the bees take off at virtually the same moment. But what induces swarm bees to heat themselves up in preparation for this? How do so many bees co-ordinate and initiate a joint action and in such a narrow time window? How do bees buried in the center of the cluster know what to do?



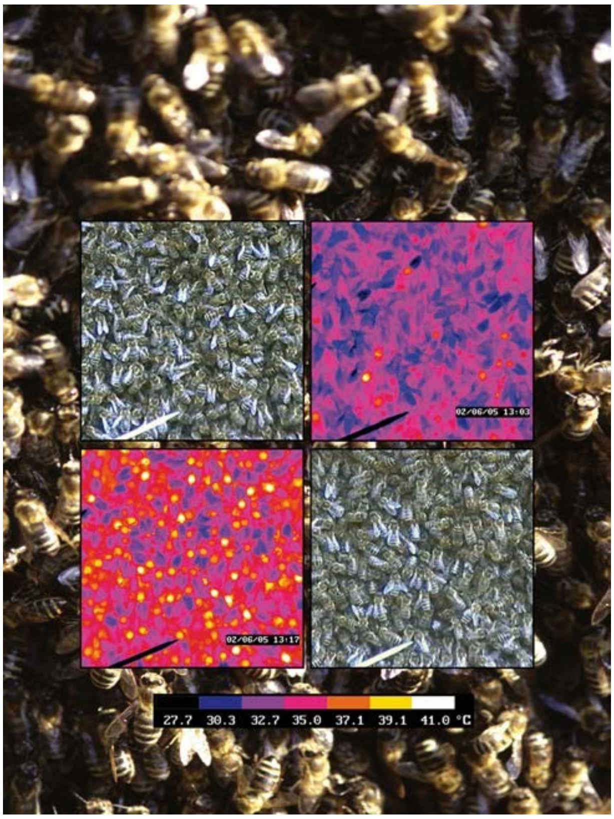
Guiding a swarm to its goal involves a sequential chain of behaviour including dances on the surface of the cluster, flights between the swarm and its goal, buzzing flights and scenting around the goal. The same few individual bees carry out all these steps to bring approximately 10,000 nest mates to the new nest site. The majority of the bees in the swarm have no information at the start about where they will go. The swarm allows itself to be guided to the new site by a few individuals which know its location.

Bees which have found possible new home sites for the swarm during their search flights begin their attempts to bring the swarm to the site by dancing on the surface of the swarm over the bodies of the clustered bees. Few of the clustered bees are able to follow the dances. Once the relatively few search bees have agreed upon a site, such as the hollow tree trunk shown here, a gradually increasing number of bees fly to the site where they undertake buzzing and scenting flights, flying back and forth and releasing scent from glands on their abdomens. In this way the swarm is eventually guided precisely to the new site. (Figure: D. Nikolaus)

The secret was revealed by the combined application of video and acoustic recordings. Bees which know the location of the site, have marked it during their buzzing flights, fly back and forth and dance on the cluster, also initiate heating of the cluster.

More than an hour before dispersal of the swarm cluster, dancing bees emit “beeping” sounds of a particular frequency during breaks between their dances. These sounds are of such a low intensity that they can seldom be perceived by human ears. Highly sensitive microphones allow these signals to be detected and recorded for subsequent analysis. The guide bees dance and run “beeping” first over the surface of the swarm and then, beeping continuously, force themselves down into the cluster. With two microphones it is possible to exploit a stereo effect and acoustically reconstruct the complex paths signaling bees trace through the interior of the swarm cluster. The bees themselves cannot hear acoustic signals but detect the associated vibration with their bodies. Bees are highly sensitive to vibrations of the substrate which they normally detect with their legs. The tightly packed individuals in a swarm cluster transmit the vibrations through close body contact. Thermovision cameras show that each bee which receives a vibratory signal immediately begins to raise its body temperature. Thermovision camera recordings first show a few traces of raised temperatures lying in the wake of a signaling bee. These traces soon spread and finally fuse into a glowing cluster which explodes into the air as the bees take off.

The armoury of behavioural patterns that bees have at their disposal to guide inexperienced nest mates precisely to a single location in the landscape is astounding. This goal-oriented behaviour will be seen again in relation to the mediation of feeding sites.



The swarm cluster heats up to flight temperature. Top, about 30 minutes before the explosive eruption of the cluster. Only a single hot worker can be seen in the thermoimage bottom, about 3 minutes before all the bees take off – virtually all the bees are now hot.

Chapter 2
Furnishing the new home

Building the combs

Honey reserves in the stomachs of swarming bees let them immediately begin with wax production and comb building after occupying the new nest. Wax, the self-produced building material for combs is extruded as small scales from special glands on the underside of the worker bee's abdomens.

The bees knead these small wax scales together into small lumps with their mouthparts and build them into small pyramids along the foundation of the future comb. The pyramids are pressed together into small bowls lying closely packed together which are then drawn up into hollow cylinders that slowly grow in height. It is difficult to see exactly what is happening at building sites because comb-building bees crowd together and shield the comb surface from view. The presence of “building chains” is an indication of the activity taking place beneath the bodies of the bees. Building chains are formed when several dozen bees hook themselves together with their legs to create a large-meshed living “net” which hangs vertically from the comb foundation, anchored by clinging bees.

These “nets” have only been described in relation to comb building and a functional link has been sought between them and the building process, but so far not convincingly demonstrated. A popular view has been that the net provides a template to determine the direction a developing comb should take. While this is an interesting proposal it is not really plausible because to act as a template or plumb line for the newly constructed comb, the net has to be viewed from afar. Such a view is not available to bees embedded in the net and building it in the darkness of the hive. Furthermore, every bee possesses sense organs which let them determine the direction of gravity. A plumb line is redundant.

Finally, building chains do not only occur at comb building sites. Endoscopes employing light with wavelengths invisible to bees and recording undisturbed behaviour of bees in passages between combs, sometimes reveal nets hanging down at night from the lower edges of combs, exactly as at building sites. These nets disappear during the day.

Net-forming bees often hang completely motionless for hours. Hooked together with their neighbours they have body temperatures which are the same as their surroundings. This is characteristic for inactive or even sleeping bees. Have these bees established a temporary dormitory? But why then favour comb building sites?

The function of bee nets remains a mystery. The slightest external disturbance leads to their break up, but approaches such as those employed by the HOBOS project, with continuous long term observation of undisturbed bees, could eventually provide an explanation for this curious behaviour.

Bee master builder techniques

Precise, regular patterns and structures in the living world are so rare that they quickly attract attention and arouse interest and fascination. Six cornered structures (hexagons) belong to the more common naturally occurring patterns. These can often be found along boundaries or surfaces where forces are in equilibrium. Hexagonal patterns form as ridges in sand on the bottom of standing water ponds, or when male fighting fish subject their territorial boundaries to waves. Hexagons are also produced during the construction of paper nests of social wasps. However, these and nearly all other examples of naturally occurring hexagons do not, in fact, meet very high standards of structural precision. Hexagons in pond sand are often crooked with sides of unequal length. Cells in wasp nests include open unused spaces at the corners, the angles between the cell walls are variable and the walls themselves are uneven and not all of the same thickness.

The cells of bee combs are notably different. Hundreds of years ago their structural precision led the astronomer and mathematician Johannes Kepler (1571-1630) to credit bees with an understanding of mathematics. The French natural historian Rene-Antoine Ferchault de Reaumur (1638-1757), known mainly for his development of a temperature scale, suggested that bees have access to a universal standard of length. So impressed by the precision of the bee comb, he proposed that the dimensions of their cells be used as a standard unit for the measurement of length. This proposal was forgotten subsequent to the introduction of the original meter on 1st of August 1793. In fact de Reaumur's proposal would not have been very satisfactory because while the hexagonal form of comb cells does not vary in precision, they do vary in their dimensions between different species and also between small brood cells of workers and larger cells of drones.

Modern research methods reveal that bees manage to construct their combs without mathematical insights. Instead the physico-chemical properties of the building material (wax) and the ability of bees to produce heat are responsible for the precision of the end product.

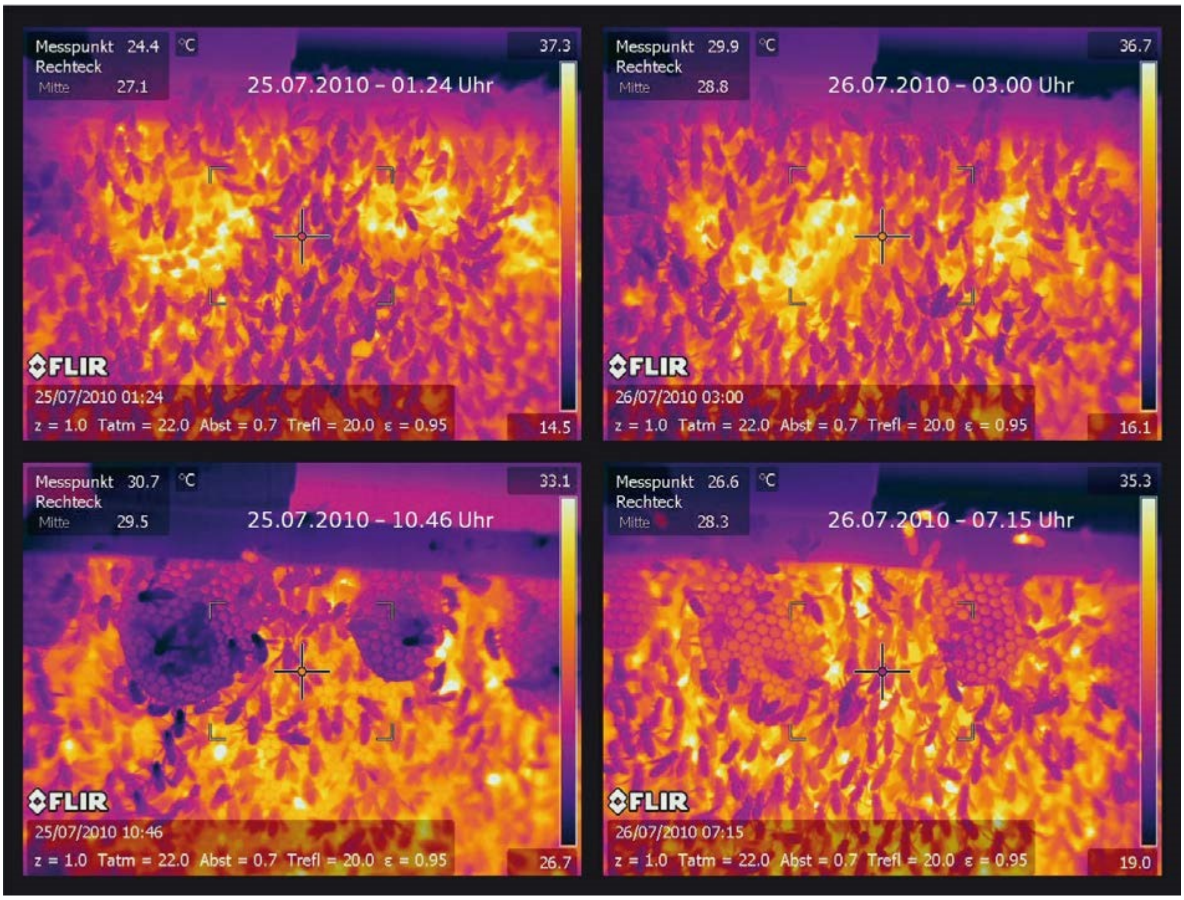
Hair-fine, temperature-sensitive wires set into the wax at a comb building site record it to be up to 38ºC while shielded by the builder bees. Wax, like glass, is a super cooled fluid that does not have a melting point but instead becomes softer and more pliable as it warms. Physicists refer to a transformation region where the viscosity of the wax changes from being structurally more “firm” to “fluid” with increased temperature. The temperature at which deformation of a wax structure occurs depends on the physical forces acting on it. Freshly built comb cell walls, consisting of paper-thin wax scales that are chewed and stuck together, are the most pliable structures of the comb and deform at the lowest temperatures. Bees at building sites produce such temperatures and it is the mechanical tensions within the circular comb cells that lead to smooth thin walls with uniform thickness and precise angles to one another, not the skill of the bees. Johannes Kepler would have immediately recognized the self-organizational principle of the comb formation, had our methods of measurement been available to him. The same self-organizational formation of a precise structure can be seen in soap bubbles lying close together on a surface. If one has the skill to maneuver six bubbles of the same size into a circle, a precisely hexagonal comb cell-like bubble suddenly appears in the centre.

Thermographic recordings of comb building activity confirm the temperature measurements made with the fine wires embedded in the wax. For this purpose the temperature sensitive camera was installed within a naturally built nest as a variant of the HOBOS hive. One can recognize glowing wax at a building site warmed by heater bees in thermographic images and particularly that of the walls around the edge of the site as they are gradually drawn upwards.

This is a representative example of a project of the HOBOS Team, founded about 15 years ago by the BEEgroup 2006, and emphasizes that HOBOS is not only to be seen as an interactive educational platform but one in which education and research are united.

Time-lapse thermographic recordings are highly enlightening in relation to the process of comb building. Only some newly discovered details are given here: The building phase is continuous and spans up to 10 hours; the resting phase can last up to 20 hours. Construction of large combs often begins simultaneously at several spatially separate sites along the same foundation. These are developed toward one another and finally joined to form a single comb. Small irregularities occur at the seams between the two separately constructed combs.

Deployment of a time-lapse thermovision camera in a modified HOBOS hive led to another new discovery: The alternating building and rest phases occur at the same time at neighbouring building sites. The basis for the co-ordination of building activity is totally unknown. Both an external signal for all the builders or an internal communication between them is possible.



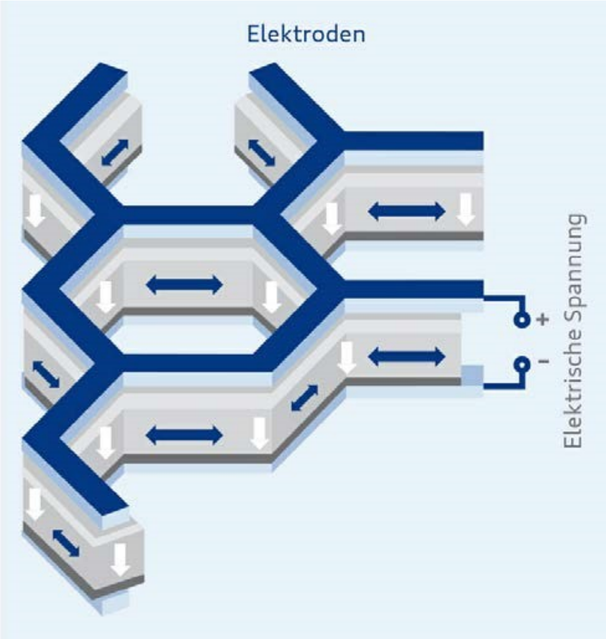
Thermoimage selections from the development of a comb over a three day period. A and B, active building phases; B and C, building pauses. Progress of comb construction and coordination of activity at the three building sites are clear to see.

This and other puzzles maintain the excitement in the research on comb building. How is the slightly angled long axis of the cells, which helps to prevent the nectar spilling out, brought about?

How, for example, do builder bees construct significantly larger brood cells for drones?

Learning from bees – the bionic bee comb

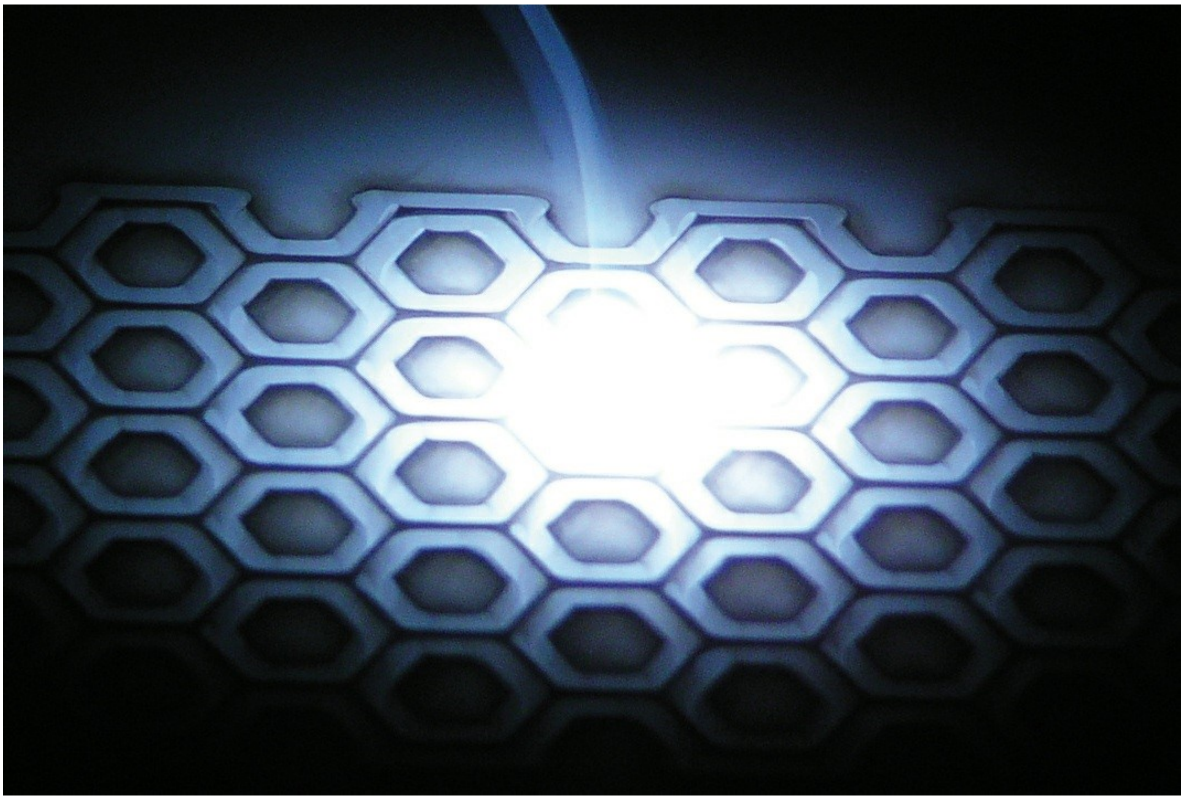
Combs with hexagonal cells have excellent static qualities allowing a mere 40gms of wax to contain and support 2kgms of honey. Not surprisingly we find copies of this structure adapted to many technical applications where weight saving is a critical factor, for example in the construction of automobiles, air and space craft. Such structures can also be built using triangular or square cells but these lack a highly useful characteristic found only in hexagons, namely that forces in hexagonal cells are optimally and evenly distributed across their 120 degree corners. This distribution is critical in the design of “actuators”, devices that can be electrically driven to produce movement useful in communication technology (vibration alarms in cell phones) or to suppress mechanical oscillation and noise in robotics, space travel and vehicle technology). The basis of this technique is known as impedance matching: maximal mechanical control can be transmitted to a structure to which the impedance of an actuator is perfectly matched. The impedance is minimal with dynamic matching and only small forces are required to produce large displacements. This is also the case with bees. The impedance of the comb is perfectly dynamically matched to that of the bee body. Optimal tuning of the mechanical characteristics of the comb with forces along the rims of the cells enables bees moving along these rims to transmit vibratory signals across the combs.



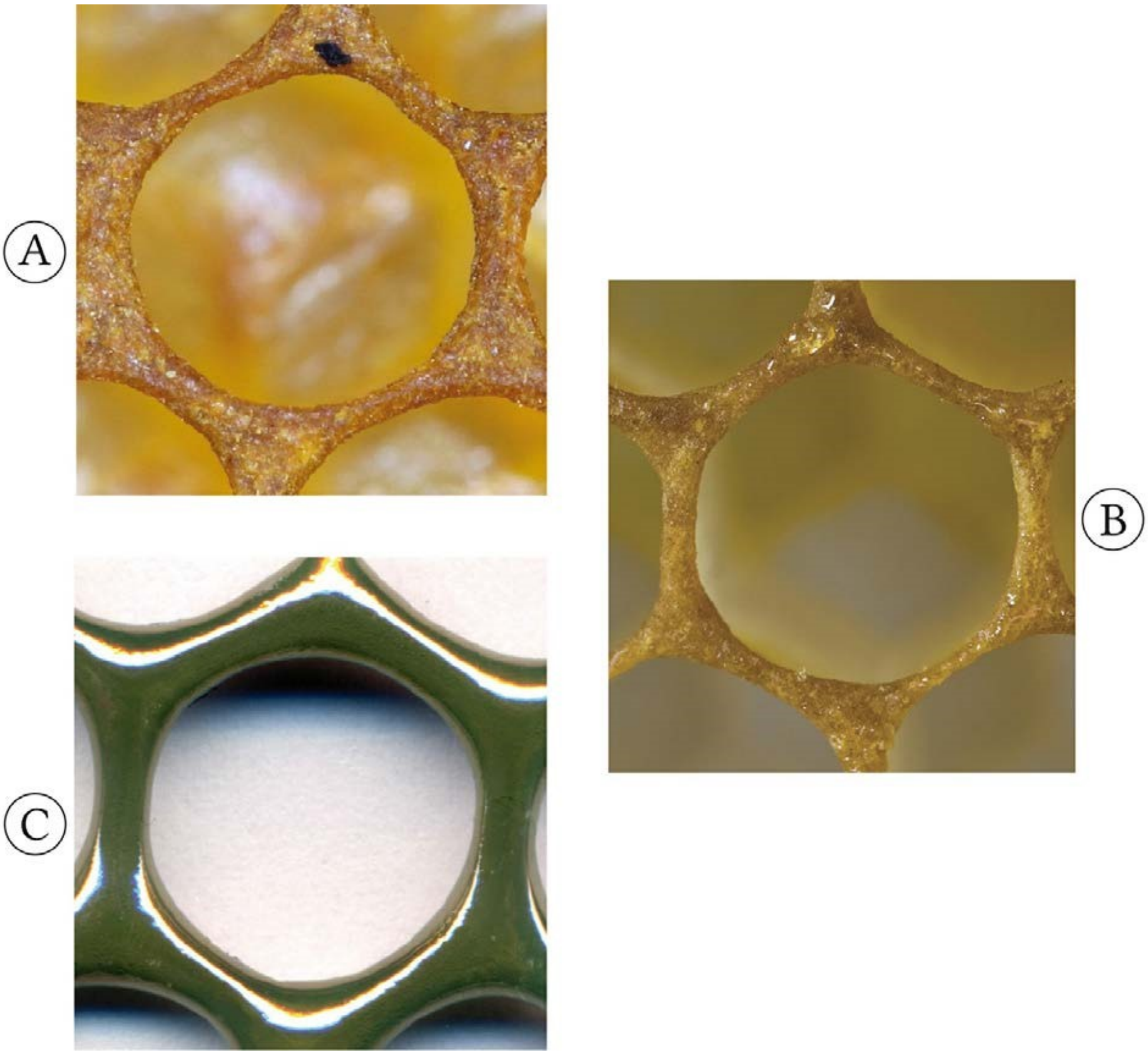
Applying an electrical potential to a honeycomb-like structure made from an appropriate material results in displacements in the directions of the arrows shown on the diagram. (Figure: Prof. Dr. Jörg Melcher, DLR Braunschweig)

Bee combs are also of interest to technologists for another reason: Under the direction of Joerg Melcher from the German centre for air and space travel in Braunschweig, engineers of the TU Clausthal-Zillerfeld and biologists of the HOBOS Team at the University of Wuerzburg, asked whether the high precision achieved through the self-organizational process of bee combs could be adopted in technical applications. If so, it could be an ideal basis for the mass production of comb-like actuators. The choice of material is critical for the adaptation of the bee's method. Bees are able to use the easily deformable wax for their constructions because a large number of them are continuously occupied with subsequent maintenance. This is impractical for technical applications which require virtually maintenance-free structures that are significantly more robust than bee combs formed from wax. Ceramics fulfill these criteria and there has already been progress on a small scale using a sintering process to mimic the bee comb self-organizational process.

Complex calculations with models of bee comb carried out by Joerg Melcher have confirmed that the deformation radii and exact shape of the hyperbolic geometry of bee comb cell rims precisely fit the predictions of the model. This could also be optimally transposed to artificially constructed combs



Sintering ceramic material with a hot laser beam enables the self-organizing manufacture of a honeycomb-like piezo device. (Figure: Prof. Dr. Jörg Melcher, DLR Braunschweig and Prof. Dr. Jens Günster, TU Clausthal)



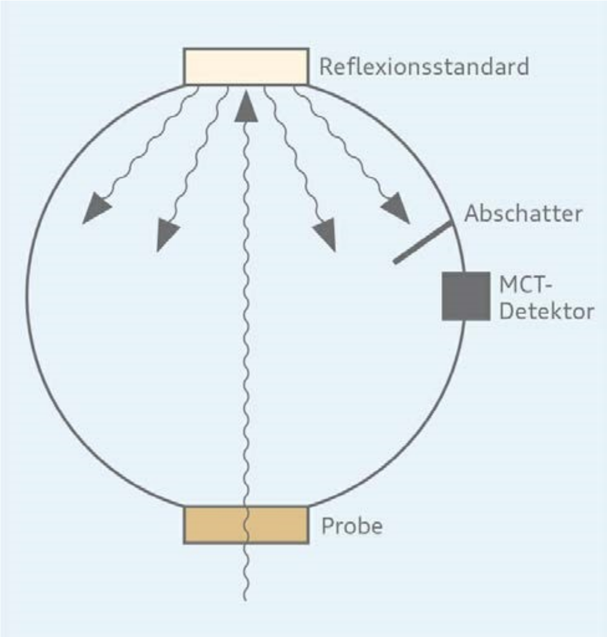
Precise deformation lines determined by a mathematical function occur in a comb in which the forces are optimally distributed. The result of such an optimization is identical in honeybee combs (A and B) and comb-like structures constructed from ceramic elements (C). (Photo A and B: H.R.Heilmann, HOBOS-Team)

The brood nest as a hothouse

Brood nest heater bees lie in empty cells between closed pupal cells and provide warmth to cells surrounding them, including those on the opposite side of the comb. Heater bee body temperatures reach values up to 44ºC. Pupae in their heated cells are warmed to 35ºC. The pupae themselves are then a source of heat should heater bees leave the empty cells next to them. This raises two questions: What physical pathways do bees employ for heat transfer? How can rapid cooling of pupal cells be prevented? Heat transfer from heater bees to pupae can occur in two ways: through conduction across the cell walls or by radiation. The magnitude of both modalities was measured with the support of the Bavarian Center for Energy Research (ZAE) in Wuerzburg by Marco Kleinhenz as part of his doctoral study (Kleinhenz 2008) . Kleinhenz found the heat conduction capacity of wax to be 0.15watt/mK, a value that is comparable with that of solid wood (the value for wood fiber insulating boards is 0.05 W/mK; for steel 50WmK). Wax is therefore a good insulator and not suited for the conduction of heat across the comb. The transmission of radiated heat across the comb walls is much higher which opens interesting possibilities for the development of a hothouse effect in the brood nest.

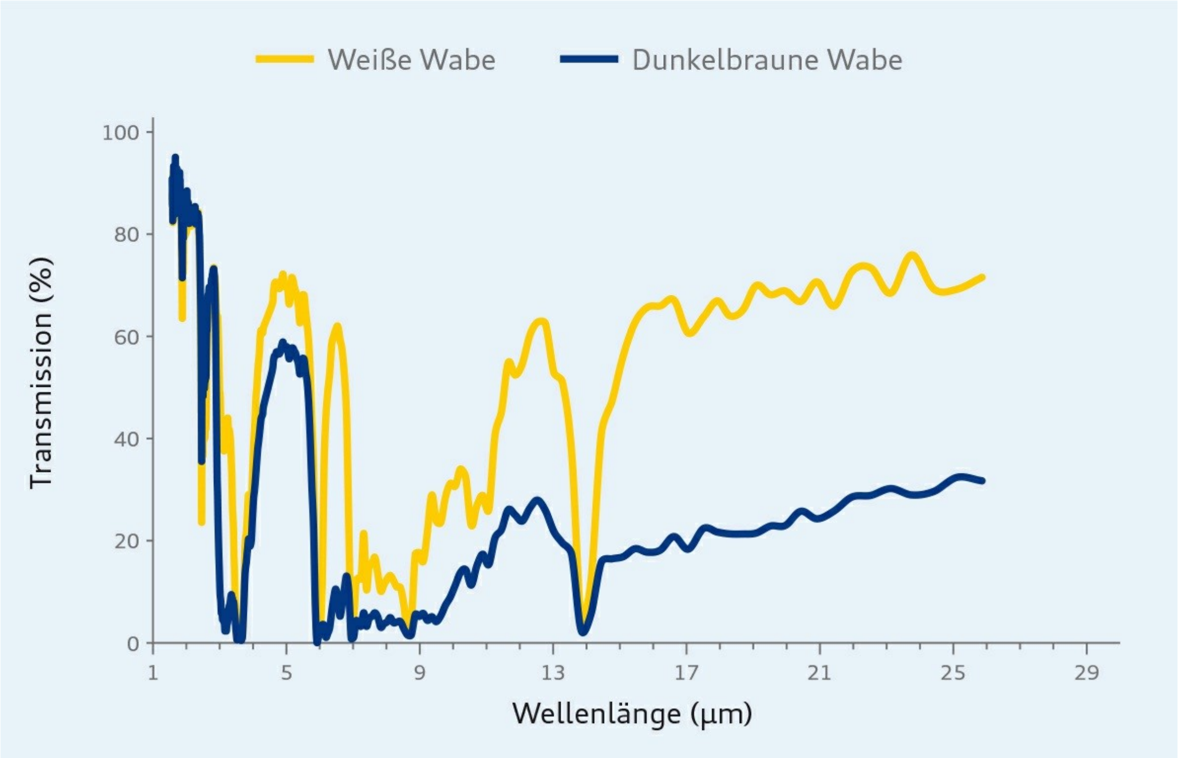
A hothouse effect arises when the transmission of heat through materials and gases is different for different wavelengths. In the long wave length region, radiation is equivalent to warming so that through the hothouse effect a space can become a trap in which objects are heated by the entering radiation but from which little or no heat can emerge. The maximum radiation that normally occurs on Earth lies in the infrared region of the electromagnetic spectrum and is not visible to us or to the bees.

Transmission of heat radiation through materials is measured with a device of which the essential element is an Ulbrich sphere. This allows one to determine which radiated wavelengths penetrate a particular material, in our case the wax wall of a comb cell, and which do not.



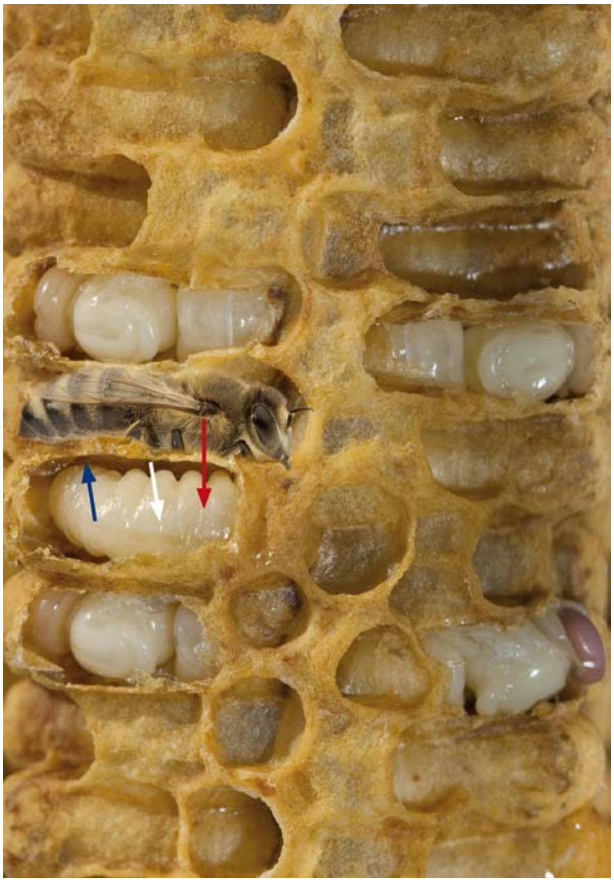
A diagram of an Ulbrich sphere used to measure the transmission of heat radiation through the walls of comb cells (sample). MCT=Mercury-Cadmium-Telurid.

For infrared radiation and temperatures relevant for bees of between 30 and 45 degrees C, we obtain a very interesting result.



The transmission of radiation of different wavelengths and temperatures through the sidewalls of brood combs. The difference between white freshly built cells and older dark brown cells is minimal for the relevant wavelengths. The transmission of longer wavelengths through fresh wax is significantly greater than through the older wax.

All components for the generation of a hothouse effect are present in the brood nest: Heater bees are warmer than the pupae and the transmission curve of the wax shows that at the relevant wavelengths (and so the temperatures in the brood nest) extreme differences in transmission (i. e. between 0% and 90%) lie adjacent to one another. Radiant heat enters the brood cells and warms the pupae but due to the isolating properties of the wax walls, little can escape..



The hothouse effect in brood combs of honeybees. A pupa is warmed by a neighbouring, radiating heater bee (red arrow). Some of the heat from the pupa passes to the space around it in its cell (blue arrow). The insulating properties of the wax cell walls however, keep the heat within the cell (white arrow demonstrates the hothouse effect). (Photo: H. R. Heilmann)

Chapter 3
Living comfortably

The beehive as an organized unit

The bees which swarmed out of the old hive have chosen a new nesting site and prepared this for comb building. The walls of the hollow in a tree trunk have been smoothed and freed from splinters. Unnecessary splits and grooves inside the hollow are sealed with resin (propolis) collected mainly from plant buds by forager bees.

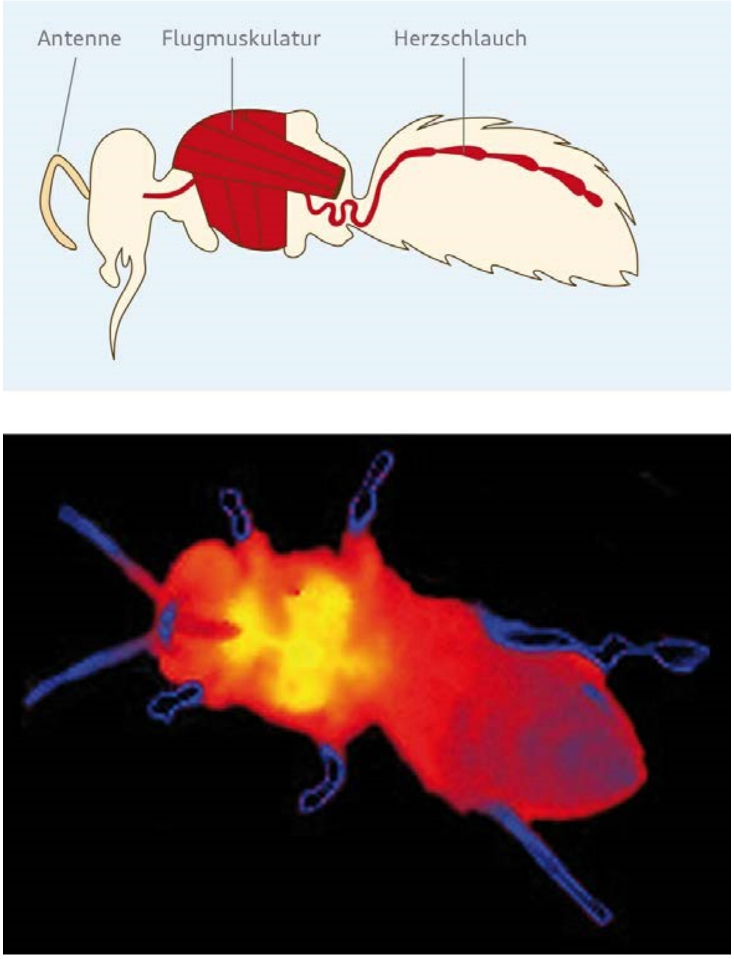
The first combs are constructed when these initial tasks have been completed. The nest in the tree trunk, combs and populating bees form an organic unit in which many local and global control loops ensure that important relationships and values in the colony are kept in a state of equilibrium. The maintenance of this equilibrium, a homeostasis, can have both temporal and spatial aims and preferred values depend on a variable higher dynamic. This dynamic concerns not only space and time but also the tolerance for acceptable variations of the values. For example, a bee colony regulates the temperature conditions in the hive differently in winter than in summer and tolerates smaller variations in brood nest temperature than in parts of the nest where honey is stored. Such a system is virtually independent of the outside world. Nevertheless a bee colony in its nest could only survive for a short time if it were to be completely isolated because it requires energy and material for its maintenance. Bees have organized themselves somewhat along the same lines that humans would have to if they were to establish extra-terrestrial colonies on neighbouring planets. Beneath their dome enclosed worlds such colonists would have to set up storage areas and depend on excursions beyond their shelter for provisions to replenish the energy and materials necessary for their continued existence. Honeybees are faced with precisely this situation.

With the exclusion of mating flights and the propagation of the hive by swarming there is no reason for bees to leave the interior of their small world unless their reserves are exhausted. Bees do not play happily around on flowers in the sun as human observers may suppose – they are there out of pure need.

The sun is the energy source for most living organisms which they take up as light and warmth. Plants are at the beginning of the energy chain and metabolize the energy of the sun into chemical energy which they store. Animals that eat the plants release the “fixed energy as warmth. Warmth however is an undesirable by-product for many organisms because it corresponds to an energy loss. The situation is very different for animals that actively generate warmth and these enjoy a significant advantage over those that cannot. Homoeothermic animals like mammals and birds are independent of variations in environmental temperature. They are able to remain active over a wide range of temperatures in their surroundings including cold days and seasons. They can also inhabit colder regions of the globe.

Centrally heating the hive

By activating their thoracic flight muscles – the most powerful they possess – bees can generate body temperatures up to 44ºC and adapt to a wide range of environmental conditions. An anatomical refinement in their anatomy limits the generated warmth to the muscular “hot spot” so that little or no heat spreads to the abdomen. The tubular heart of the bee, lying along the dorsal surface of the abdomen pumps cool blood forwards against the warm blood that flows from the thorax back toward to abdomen. The result is a functional “constriction” between the thorax and abdomen, and the formation of a stable temperature block or heat exchanger. The thorax stays warm and the abdomen remains cool.



Above: A, a diagram of the bee flight muscles and blood system used for generating and distributing heat in their bodies. B, a thermoimage shows the effect of the heat exchanger between the abdomen and thorax, and the resulting concentration of heat in the thorax. (Figure: Meiko Tautz)

The heat source focused in their thoraces is used by bees to maintain the hive temperature, thicken the honey, build combs and kill wasps that force their way into the hive. Warming pupae in the brood combs is of overriding importance. The temperature of brood comb with its closed pupal cells is maintained at 35ºC (close to that of the human body) by heater bees which have two strategies for warming pupae: Heater bees may press the ventral surface of their thoraces down onto the cell lid beneath them and thus warm a single pupa. A more efficient strategy is to slip into one of the empty cells in the brood comb from where the radiated warmth from a single heater bee extends up to three cell widths away from her on both sides of the comb, and including up to 70 pupae. Heater bees lie head first in the cells and their cool abdomens creates a seal between them and the comb surface, reducing heat loss to the surrounding air.

Empty cell distribution amongst the pupae in brood combs is often close to the theoretical optimum in terms of energy transfer. Workers do not appear to purposely include empty cells in the brood combs. A variety of factors could lead to the empty cell frequency of about 3% to 10% in colonies that are healthy and well nourished and is considered normal for “good” brood combs. Computer simulations reveal that even this relatively low proportion of empty cells is very effective in the distribution of warmth to brood. Combs with seasonally fewer empty cells are rare, while that with larger proportions of empty cells indicates a colony in poor condition and with heat distribution problems.

There are many possible reasons for the occurrence of empty cells: Errors of the queen in the sequence of egg laying in the brood comb in which she “misses” individual brood cells; the temporary use of brood cells for storage after the emergence of young bees which are emptied after a short period and again accessible to heater bees. Culling and removal of larvae whose development stops through genetic defects, or termination by the workers, is another cause for the appearance of empty cells.

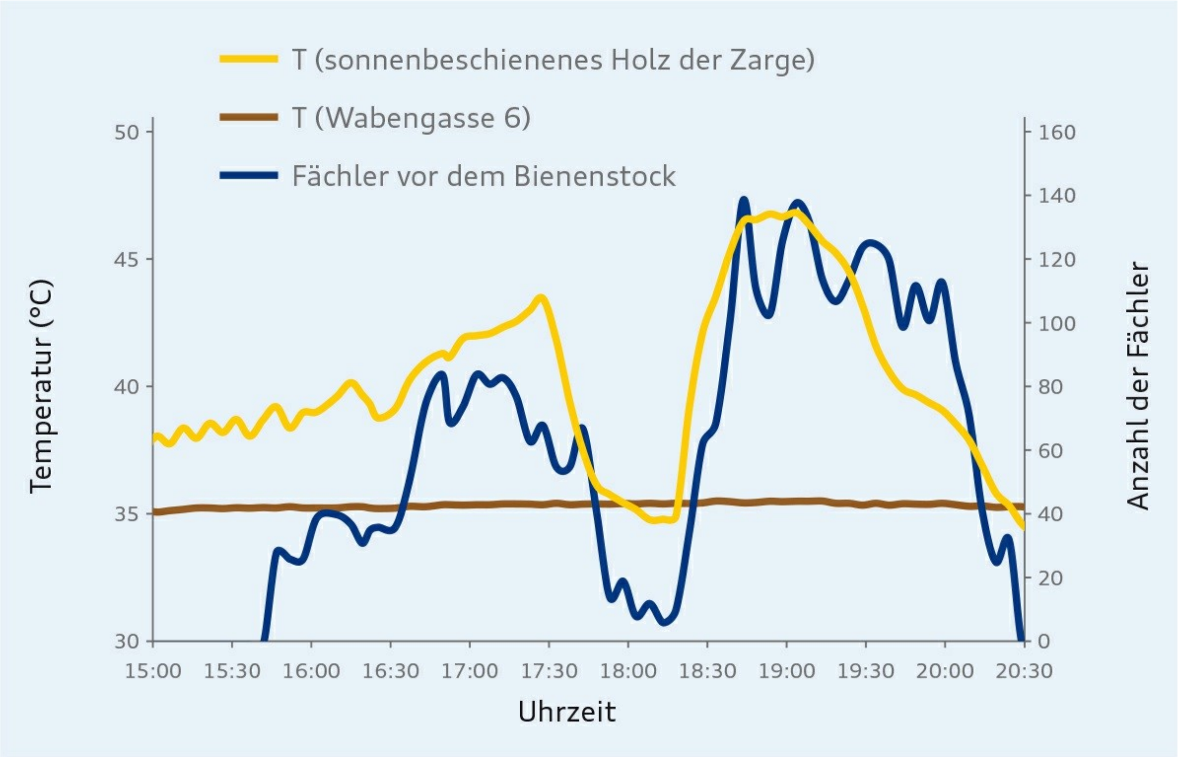
Diploid drone larvae constitute the most common genetic defect. These occur if identical sex gene alleles randomly come together after the fusion of egg and sperm. Workers can discriminate between defective diploid and normal haploid drone larvae arising from unfertilized eggs, and remove the diploid larvae from the cells.

Air conditioning the beehive

Nest temperature control requires not only heating but also cooling to maintain the desired temperature range. Individual bees use elementary methods to cool areas of the hive and comb but also join in a more complex procedure to cool the entire hive that demands the co-coordinated effort from many individuals. Should a localized region of the comb become too warm, workers act as living heat pumps. They take up heat from warm combs with their bodies, move to cooler areas of the hive, cool down and lose this heat. An opposite strategy is employed by ants: ant workers warm themselves passively in the sun, carry the heat in their bodies into the cool depths of their nest where they give up their heat to the surroundings. A more sophisticated cooling technique employed by individual bees was described decades ago by Martin Lindauer: “Water gatherers pump themselves full with water from water sources outside the hive, return to the hive and combs, regurgitate a drop of water and spread this over the surface of the comb” (Lindauer 1954).

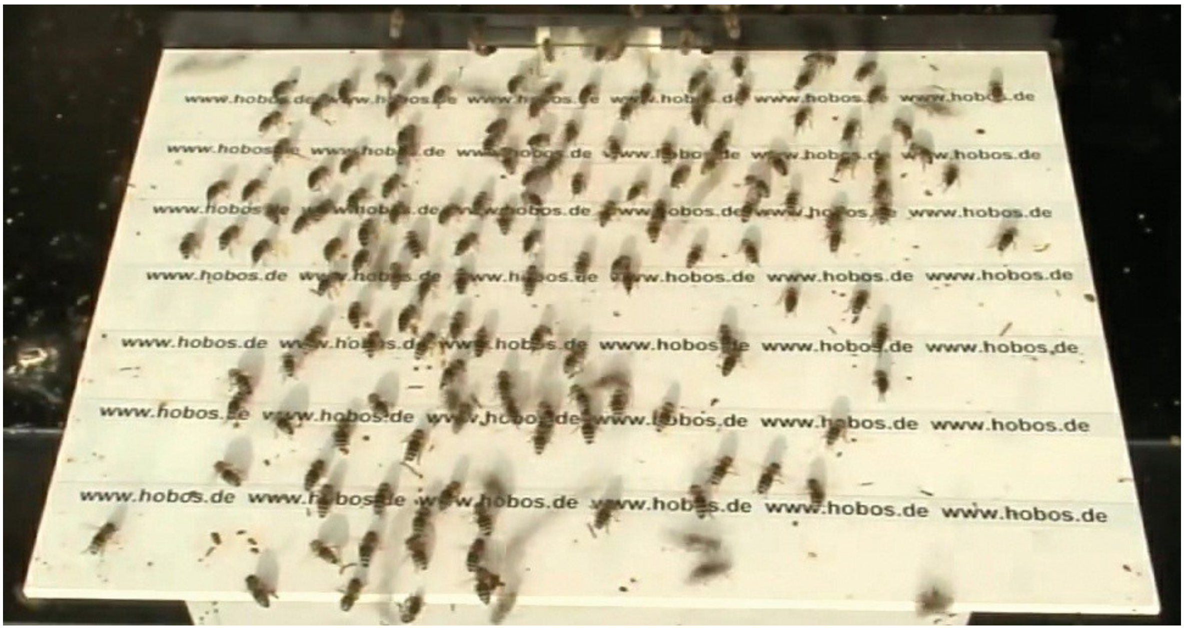
The water film on the surface of the comb evaporates and cools the warm comb. Lindauer also described a particular movement of the proboscis that is associated with this behaviour. Bees move their moistened mouthparts vigorously to accelerate both the evaporation and consequently the cooling effect. These cooling methods are locally applied and by single individuals.

In contrast to individual and local cooling efforts, global cooling of the hive requires many bees to work together in a finely tuned harmony. Should a hive become too warm, bees collect outside the entrance to the hive and draw hot air out of the hive causing cooler outside air to flow in. This will only occur if the appropriate number of bees assembles in a geometric plane and the sum of the small air currents evoked by their wing movements produces an effective airflow.



Despite constant outside temperature, temperature within the hive rises when the wooden walls of the hive are heated by direct sunshine. The number of active ventilator bees increases to counteract this. (HOBOS data of 30 June 2012).

During global cooling of the hive, bees line up outside the hive entrance with their heads facing towards it. To create airflow they fan their wings as though flying. Focusing a HOBOS thermocamera on a formation of fanning bees on the landing platform of the experimental hive reveals the cooling effect on the surrounding air. The camera records blue regions (blue = cool) surrounding each bee. With increasing numbers of ventilator bees the blue patches around them merge to become a large cooled area.



Ventilator bees on the landing platform outside the entrance to the HOBOS bee colony during a peak hive temperature. (Photo: S.Kennedy, HOBOS-Team)

But how does the cool air surrounding the fanning bees get into the hive which is completely closed apart from the one small entrance? The following model has been proposed: The fanning bees do not work without pause; instead they carry out co-coordinated cycles of activity alternating with rest periods. This leads to a sort of “breathing” of the entire hive. Hot air in the hive rises; the ventilator bees work against the air current in the hive draw air out of the hive. When they all stop fanning, warm air in the hive rises again drawing the fresh cooled air in from the outside and up between the combs. According to this hypothesis the bee colony – like our lungs – empties and fills, exhaling during fanning and inhaling during breaks. Measurements of air currents within the passages between the combs will show if the hypothesis holds.

Data from HOBOS, available to all at anytime, permit a study of the pattern formation of ventilator bees on the landing platform and their behaviour. How long will a bee continue to fan? Does she change her location or always stay in the same place? When does she begin and end her activity?

The number of active bees changes appropriately: the warmer it is the more there are that ventilate. How is the response to the particular need controlled? The secret lies in the different sensitivities of individual bees. Stimuli to which bees respond must be perceived differently by different individuals to release action at different intensities. There are extremely sensitive and insensitive individuals and all grades between. The bee colony has the mating strategy of the queen to thank for this broad range of sensitivities. During her mating flight the queen may pair with more than a dozen drones. The result is the gathered progeny of these many fathers in a single nest. The genetic diversity in a bee colony is correspondingly high.

Many fathers, one climate

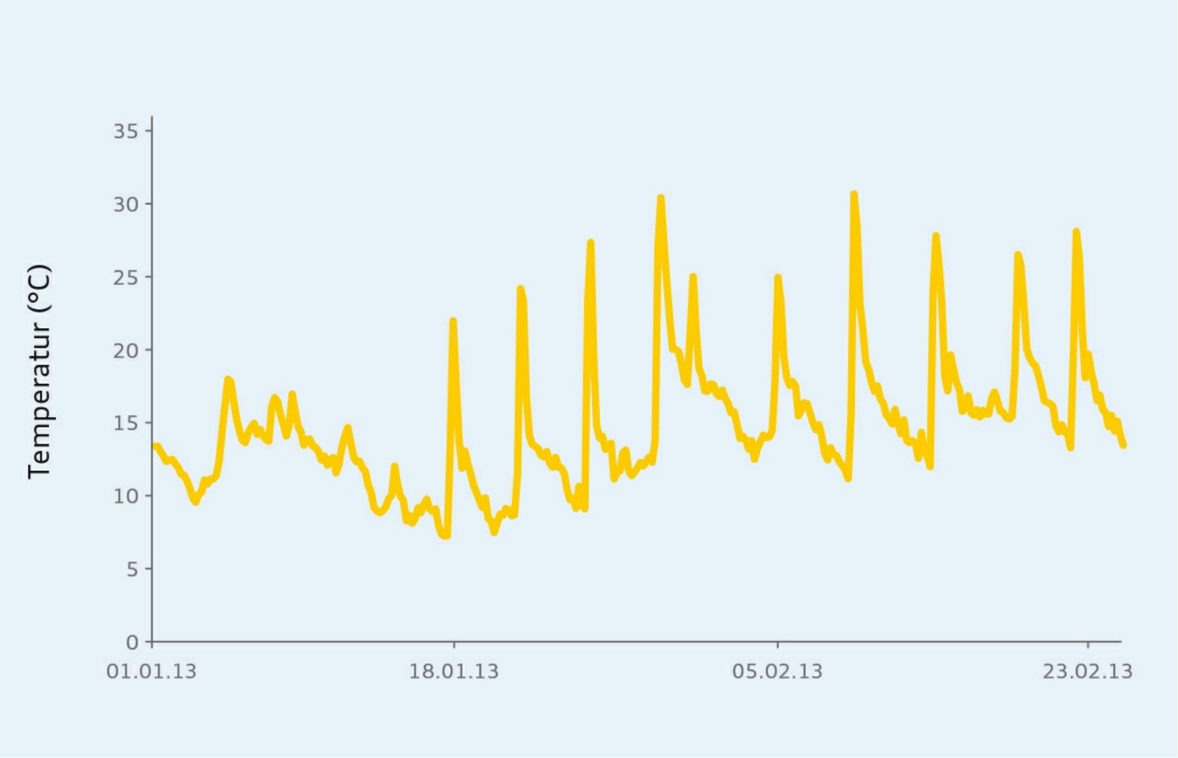
Combining behavioural biology and modern molecular biology has confirmed that multiple fathers bestow a considerable advantage on bee colonies. To begin fanning behaviour when the hive heats up, and to end it, has different thresholds for the daughters of different fathers. The overall result is an appropriate number of actively fanning bees necessary to prevent overheating of the hive at that particular time. How do we know this? Modern molecular biology allows a fatherhood test for honeybees. In a joint German-Chinese project with Songkun Su, a technique has been developed to determine the father of a worker bee without having to touch her. The larvae have the same genetic makeup as the adults. Small amounts of this genetic material are present in the larval skin that is shed during growth and which is left behind in the cell when the bee emerges as a young adult. She is immediately labeled with a dab of paint or an RFID chip on emergence so that her subsequent behaviour can be observed and recorded. The chip carries the individual identification number of the bee which can be detected by an electronic reader.

A group of worker bees at an artificial feeder. All are equipped with an RFID chip and their activity can be individually monitored. (Photo: Dr. Christoff Schneider)

The paternal line of the marked bee can be determined from the larval skin and hence the behavioural tendencies correlated with the hereditary line.

Honey bees in winter

Through their ability to produce heat, bees can survive winters in temperate zones and even begin early with brood at fairly low external temperatures. In deepest winter bees gather into a tight cluster and remain motionless for most of the time. Long term measurements from the spaces between the combs of the HOBOS hive have brought new insights into the overwintering biology of honeybees. The temperature in passages between the combs is maintained for most of the time at a level just above that at which the bees stiffen and below which they would eventually die. The winter cluster heats the nest over cycles of several days, holding the temperature raised over one day and then letting it sink back to the previous level. The warming may serve to soften the stored honey which at the lower temperatures is too firm to be taken up by the bee's proboscis. Once through the winter the colony can begin its work with the first spring flowers outside the hive.



A new HOBOS discovery: During winter an undisturbed bee colony heats the hive in cycles lasting several days in which the temperature is raised and then allowed to sink to a value just above the level at which bees would become stiff and motionless. (HOBOS data of January and February 2013).

Chapter 4

Collaboration among the bees

Division of labour in the nest

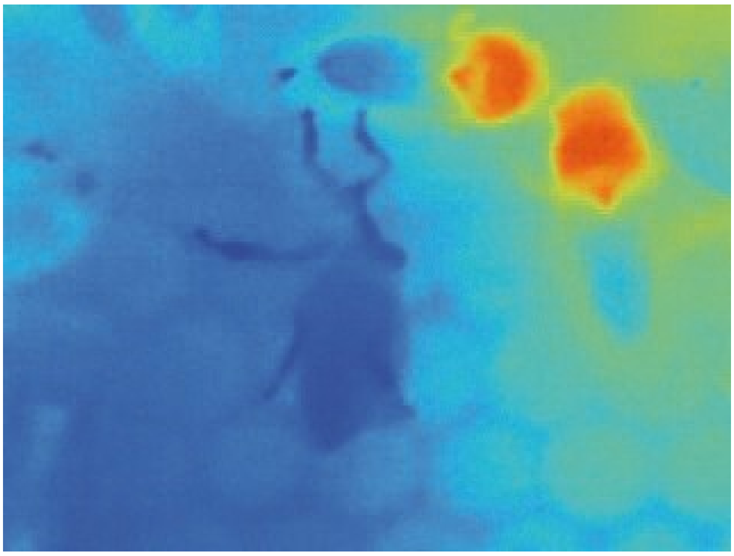
The remarkable achievements of a bee colony superorganism emerge from the integrated and coordinated activity of all the individual bees. Each bee must decide at each point in time, and for each location, to be active or to join the "silent reserve". If she does become active it has to be clear which task is to be performed, with what intensity and for how long.

If all the workers of a colony were to communicate signals or to respond to stimuli from their surroundings with the same willingness and intensity, the entire colony would be operating on an "all-or-nothing" principle. Appropriately graded responses and actions would not occur. The foundation for the highly effective integrated behaviour within the colony is its differentiated social structure. To begin with, the various tasks, or vocations are mostly carried out by bees of particular ages according to an age-dependent sequence. Secondly, bees of each particular vocational group show differences in their readiness to act. This aspect is examined in detail in this chapter.

The different vocation with which each bee is occupied at a particular period in its life allows a bee colony containing bees of all ages to undertake all possible tasks in parallel. Builder bees, nurse bees, heater bees and sentry bees are several examples of the vocations that are performed for periods in the life of a worker bee.

Careful micro-behavioural research that includes all perceptible details of behaviour of a particular individual bee, and the application of modern technology continue to lead to the discovery of previously unknown vocations such as the heater bees described in Chapters 2 and 3, and filling station bees. Heater bees warm pupae in the brood cells, heat nectar to remove water during its conversion to honey, heat wax during the formation of comb cells or kill wasps that enter the nest by overheating them. Barrett Klein of the HOBOS Team has produced a small movie which impressively documents the many different applications of honeybee heating (see details in the Appendix). Filling station bees search across the comb for exhausted heater bees whose energy reserves, after 30 minutes of heating, are depleted. They then provide the heater bees with honey so that they can immediately resume their tasks.

Bees are not always busy. They also sleep. The German bee researcher, Walter Kaiser and the American Barrett Klein are pioneers in the study of sleep behaviour in bees. Kaiser was the first to describe sleeping behaviour in bees and studied its physiology. The observation of sleep in bees was the first time that such behaviour had ever been reported for insects. Barrett Klein followed in Kaiser's footsteps and researched many detailed questions relating to sleep in bees, some of which he has already answered: Which bees sleep? Where do they sleep in the hive? For how long do they sleep? What, if any, advantages accrue from sleeping? The researchers, themselves without sleep, could have well been envious of the sleeping bees they observed around the clock for several days.



Thermoimages make it clear to see: The sleeping bee hanging motionless on the comb (left) has adopted the same temperature as her surroundings. (Photo: B. Klein)

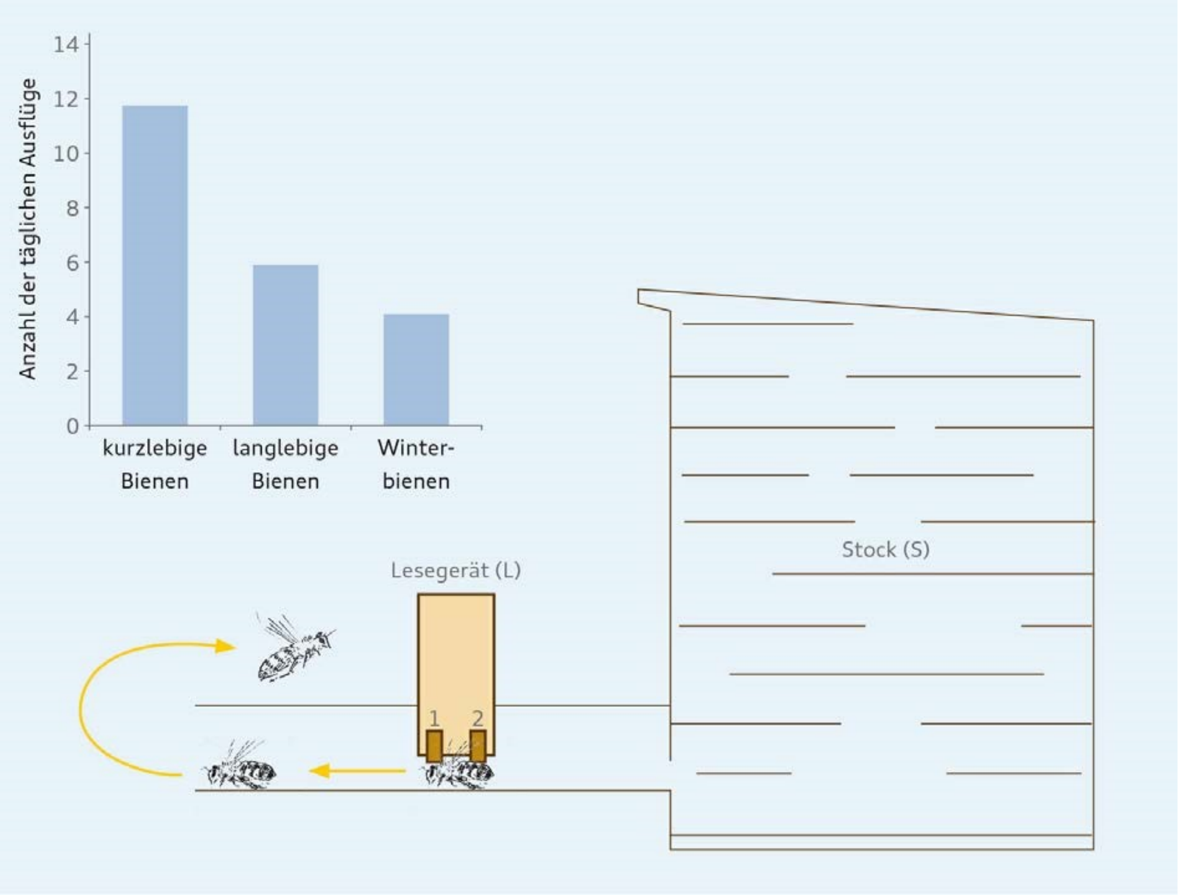
Walter Kaiser (left) and Barrett Klein with an observation hive they are using with a thermocamera to study sleeping bees. (Photo: M. Stiegler)

For most activities in the hive it is important that the expended effort precisely matches the need. If there is a shortage of pollen in the hive this must be met by harvesting as much pollen needed to balance the deficit, neither more nor less. An appropriate effort could be achieved by a fixed number of bees who are more or less active depending on the need. The expended effort could also be regulated by altering the total number of bees that are all working with the same intensity. In fact in turns out that it is the number of bees busy with a specific task that changes with need. The most famous example here is the recruitment of forager bees to a specific feeding site through the “dance language”.

Single forager bees are individually not so very hard working; it is the colony as a whole that represents industriousness.

The foraging diligence of each individual bee can be detected by equipping each with a small RFID microchip which contains its own personal identification number. An electronic reader at the entrance to the hive records the departure and the return times of each individual and so the number of foraging flights can be documented.

A worker bee equipped with an RFID chip on which her individual identity number is recorded. (Photo: H.R. Heilmann)



Forager bees equipped with RFID chips are automatically registered by two sensors (1 and 2) attached to a reader (L) when they leave or return to the hive.

Foragers that have found an attractive feeding site do not collect more intensively, nor do they fly more often so as to increase the harvest. Instead they recruit more workers from the hive. The bee dances serve this purpose.

The bee dance – still a challenge for bee research

The ingenious bee researcher, Karl von Frisch was honoured in 1973 with the Nobel Prize for his work on honeybees. Von Frisch measured and described the dances of bees in an observation hive with a stop watch and a protractor. The stop watch was set going for 15 seconds and the number of dance cycles was counted over this interval. Von Frisch noticed that during the dance, which approximates a figure 8, the central track along which the bees “waggle” their abdomens, was consistently aligned in a particular direction. He placed a protractor over the glass window in the observation hive and measured the angular direction of the waggle phase in relation to the vertical.

He also noticed that the recorded number of cycles of the dance changed with the distance to the feeding site. This was the first indication that the dance could have something to do with the recruitment of new foragers. Nevertheless, even with these simple methods and early measurements it was evident that significant differences in the details of the dance occurred although distances to the feeding sites were identical.

Significant differences in the angular direction of the waggle phase of the dance were also measured for the same feeding sites. These were not related to systematic changes in the angle that accompanied the time of day and position of the sun. Instead these aberrations in angular direction occurred between dances that immediately followed one another. Despite these variations experienced by recruits within the dark hive, von Frisch and his collaborators found that not only experienced bees but also the newly recruited followers all turned up at the correct location.

Von Frisch, justifiably amazed wrote in a publication in 1957: “The bees dispatched from the hive fly to the goal with a greater accuracy than would be expected from the variability of the single dance times (von Frisch and Jander 1957 p263) [one must add: and from the variability of the direction indicated by the single waggle dance runs – auth]. Von Frisch was not only the first to measure the angular direction of the bee dances within the technical possibilities of his time, but also the first to realize that his data presented a problem: How can an imprecise input (the dances) lead to a precise output (the arrival of the recruits at the feeding site.)?

Von Frisch formulated a possible solution to this puzzle. In the same publication (Von Frisch and Jander 1957 p263) he wrote “One can deduce that the dance followers are averaging many individual values”. From a purely statistical point of view this is highly plausible. Sector statistics, a special area that concerns the distribution of directions proposes the following: If a marksman fires five times and misses the target more or less to the right and the same number of times to the left, sector statistics provides an average of a direct hit (that in fact never happens). The directional information in the dance could therefore, purely statistically, indicate the correct direction of the goal.

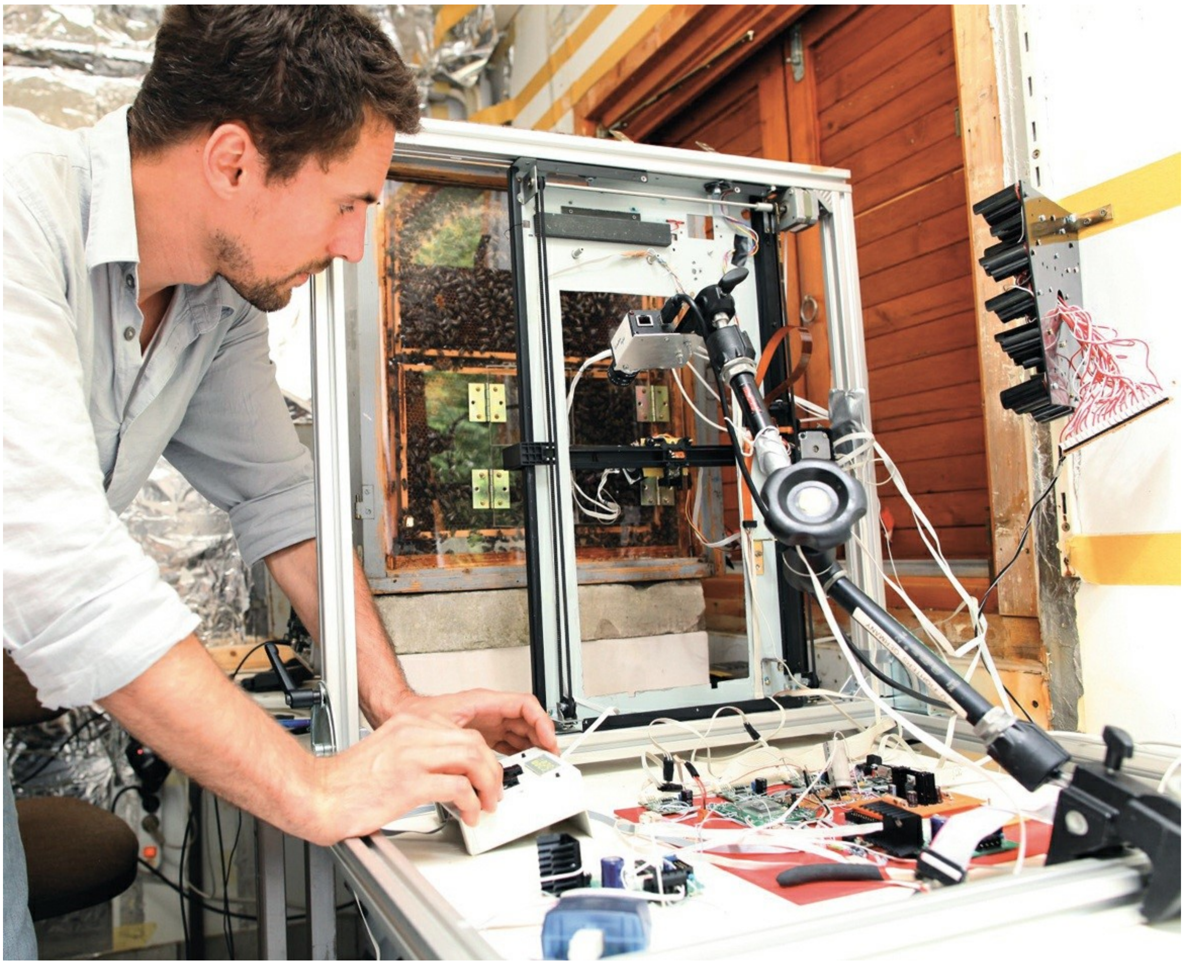
The suggestion that the dances are averaged provides to this day the basis for the thinking and arguments of many bee researchers although until now this has not been supported by experimental evidence. On the contrary, measurements of many dances show that such averaging does not lead to the satisfactory precision.

With infinite patience, the Argentinean biologist Rodrigo de Marco, a student of the renowned bee researcher Josue Nunez and working in Randolf Menzel's group in Berlin, analyzed over 1300 dance paths of more than 20 dancers that all danced on a comb after a flight of 215 meters to the same goal. He determined the average angle of the dance in relation to the vertical, and the duration of the waggle phase. He then calculated a vector that indicated the location of a point in the field.

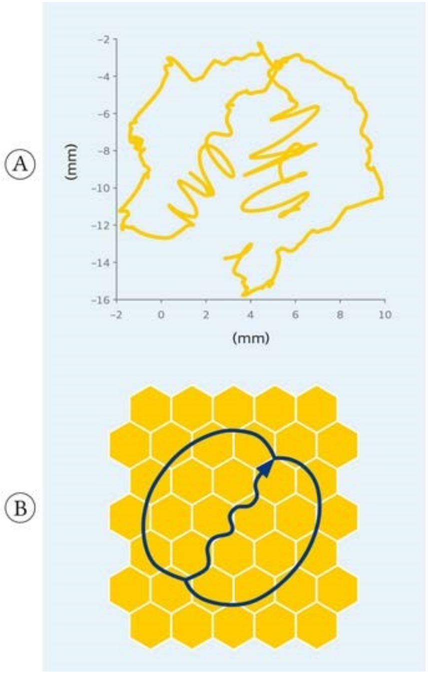
Rodrigo de Marco (right) discussing a bee experiment with his mentor Josue Nunez. (Photo: A. Schumann)

Merely 15% of all dances provided a goal that lay within a radius of 50 meters of the feeding site. 90% of the dances indicated a location within a radius of 150 meters around the goal. The area of 90% certainty had a diameter of 300 meters which was considerably larger than the 215 meter flight path between the hive and the feeder.

The line encloses the area indicated by 90% of all dances of bees trained to the feeding site at F and who danced in the hive at H. (After de Marco et al., 2008).



Tim Landgraf with a highly complex experimental set-up used to precisely record bee dance movements. (Photo: S. Pramme)



A, an electronically recorded image of dance movements of two sequential waggle phases of a bee advertising a feeding site 215 meters away. B, a graphic representation of the dance frequently found in zoology texts and school books and in which the waggle phase is abstracted as a series of sine waves.

While Von Frisch would have again been puzzled by the accuracy of the recruits had he known about de Marco's analysis, he would have been even more intrigued by the results of the Berlin mathematician and computer expert, Tim Landgraf who analyzed precise video recordings of the exact paths of dancers with a special computer program. Landgraf found that the actual movement pattern of dancing bees differs significantly from the idealized sine wave seen in the usual graphic descriptions. It was immediately clear that human observers have subjectively interpreted the motions of the bee. Where is the directional information (the angle in relation to the vertical) in the figures recorded by Landgraf, and where the information about distance (the duration of the dance)? Where does the waggle phase begin? Where, exactly, does it end? Which value can be taken as the indicated angle, that from the first round or the last round; from the average of all?

A variety of problems can be added to these questions. The length of the waggle phase increases less and less for a greater separation between the hive and the feeding site and so becomes ever more inaccurate as an indicator of distance. This would seem to be fatal, because it is precisely those feeding sites far from the hive, for which accurate information is essential in order to find them. Furthermore, the length of the waggle phase is also dependent on the nature of the landscape over which the bee flies. The odometer of bees is based on optical flow, which is the movement of images over the surface of the eye created by the passing landscape. This is dependent on the structure of the surroundings through which the bees fly and so is relative in the true sense of the word and only helpful as a rough indication of the distance travelled. At least for human observers but apparently not for successful follower bees!

Decisive breakthroughs to new concepts in the research of the dance communication were achieved through both low- and high-tech approaches. The low-tech approach required virtually no research funding but nevertheless resulted in front page articles in the exclusive journals, Science and Nature.

The low-tech approach: a look into the bee brain and misleading bees

The following story about the development of tunnel experiments in researching distance measurements by honeybees is presented here because it exemplifies how chance can often play an important role in breakthroughs in Science.
From an earlier research visit to the Australian National University in

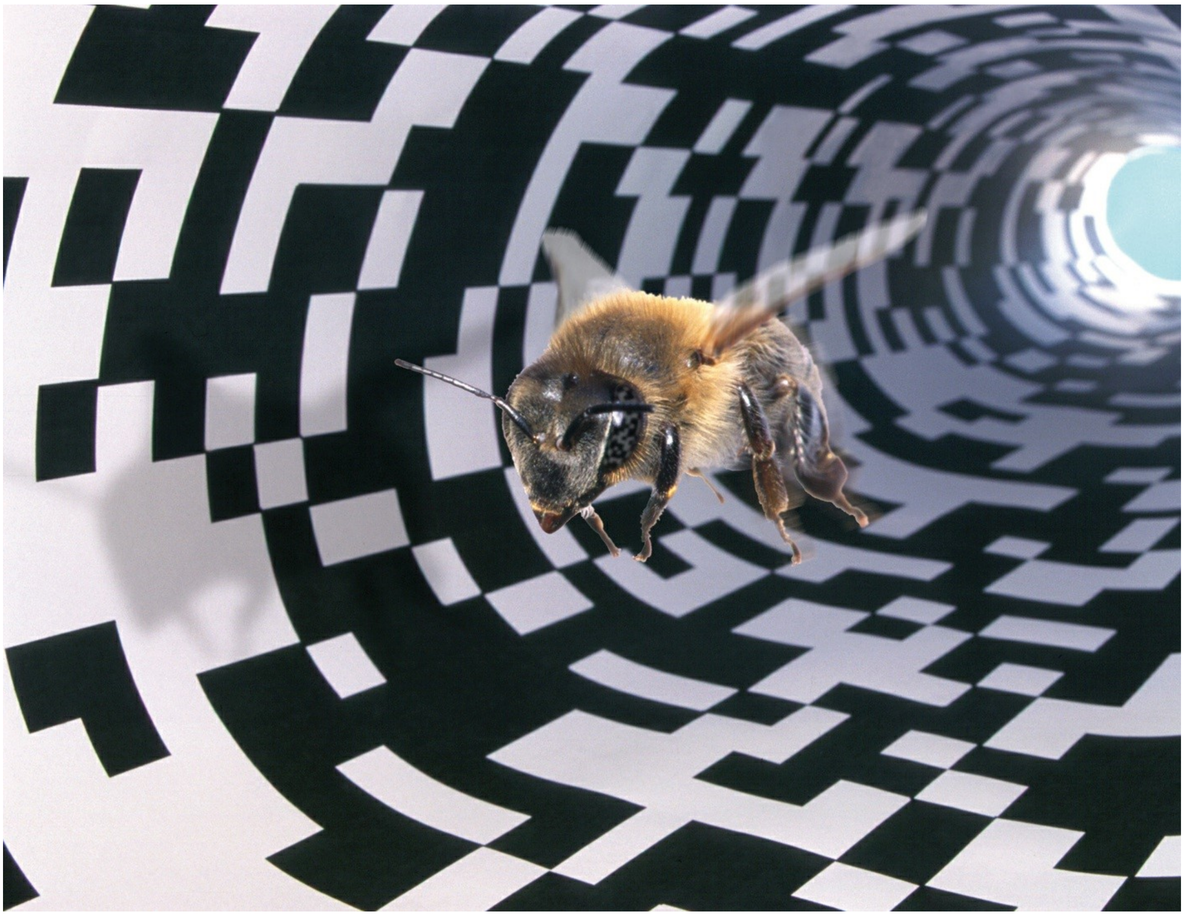
Canberra as a guest of Professors Mandayam Srinivasan and Shaowu Zhang, I was aware of their experiments in which bees were made to fly through tunnels with optically patterned walls. They wanted to establish how precisely bees in the tunnels could recognize locations where they had been rewarded with food. I was also aware of the older work of the German zoologist Harald Esch. Esch and his collaborators provided the first evidence that bees do not measure distance as first supposed, through the consumption of energy, but instead from optical flow. Esch compared the waggle path of dancing bees which flew between the roofs of two tall buildings, with that of bees which covered the same distance close to the ground. He found that the higher the flight paths were above the ground, the shorter were the waggle paths of the dances. The way it is with ideas, a question suddenly occurred to me: Do tunnel flying bees dance, and if they do, could my Australian colleagues measure these dance? If optical flow provides free flying bees with information about the distance they have flown and the dances mirror the subjective impressions of the bee, what are these in the extreme optical flow conditions of the tunnels? In the first telephone conversations with Canberra the questions arose: Is such an observation possible? How does one measure the waggle phase of the dance? What does one need to do this? I had learned years before from Martin Lindauer how to employ observation hives and so I was able to pass this information on to the Canberra colleagues. To accelerate progress I commissioned our own beekeeper and cabinet maker, Heinrich Demel, to build a new observation hive from descriptions of the original model used by Karl von Frisch. This was constructed, packed and shipped from Wuerzburg to Canberra. Monika Altwein was persuaded to undertake the task of initiating the Canberra colleagues in the use of the observation hive and the measurement of the dance parameters in the tradition of von Frisch and Lindauer. She duly followed the observation hive to Canberra in the spring of 1999. The German-Australian collaboration eventuated in an unequivocal confirmation of the ideas of Harald Esch and provided the first quantitative data relating to the optical flow odometry of bees. The ability of forager bees to measure distance was calibrated in this study. A strong dependence between the distance indicated in the dance and the optical structure of the

environment through which the bees flew was firmly established.
Experimentally obtained distance curves from the analysis of the dances were true only for those locations and particular optical structure for which the measurements were made.

These results were published in Science. I proposed a front page illustration that would present the basic concept of the experiment and entrusted this to a member of the BEEgroup who then produced the famous tunnel montage picture. This won the first prize in the competition “Visual Science” in the year 2000.

These experiments led me to suppose that it should be possible to employ tunnel bees as “misleading” bees. Such bees would indicate a long flight path in their dances although they had in fact only flown a very short distance in the tunnel. One could now test if bees which followed the dances of the tunnel bees would search for the feeding site at a distance equivalent to the actual length of the tunnel at the end of which the dancer found the food, (the recruits did not fly through the tunnel), or instead would be caught at a more distant location from the hive as indicated by the dance. To honour Harald Esch, the discoverer of optical flow odometry of bees, I suggested to my colleagues Srinivasan and Zhang that we invite Harald Esch to Wuerzburg for the experiments. The joint study showed that the “misleading” bees were taken seriously. Searching foragers and their recruits were caught in sweep nets at the location indicated by the dance. No bees were caught short of this location or beyond it.

The explanation of the tunnel experiments is as follows: A bee flying through an area with an optical structure induces images which move backwards across her eyes. These moving images, in other words optical flow, are used by the bee to determine the length of the travelled path. The system can be easily misled, however, by making the bee fly along a narrow tunnel in which she experiences high contrast visual patterns which are closer to her eyes than she would normally experience in the natural world. The bees interpret this as a flight distance which is much greater than that she has actually flown.



A montage illustrating the principle of tunnel experiments in which a bee is made to fly close to optically high contrast patterns. (Figure: M. Kleinhenz)

This experiment also shows that the dance can indeed cause recruited bees to fly with a high probability to a particular location where they fly around, although without further guidance or reward they finally leave.

The high-tech approach: radar tracking flying bees

The English physicist, Joe Riley, provided a significant boost to bee research by mounting a very light-weight radar reflecting antenna (transponder) on the backs of bees. Under good conditions it is possible to track the flight paths of these individuals. The disadvantages of this method, namely the not insignificant size and weight of the radar antennae, the minimal range (a few hundred meters) and the screening of the bees by bushes and trees, has not dampened the enthusiastic employment of this technique.

Juliet Osborne, a pioneer in the application of modern radar-technology to behavioural research on honeybees, and the associated apparatus (lower disc – transmitter; upper disc receiver). (Photo: A. Martin)

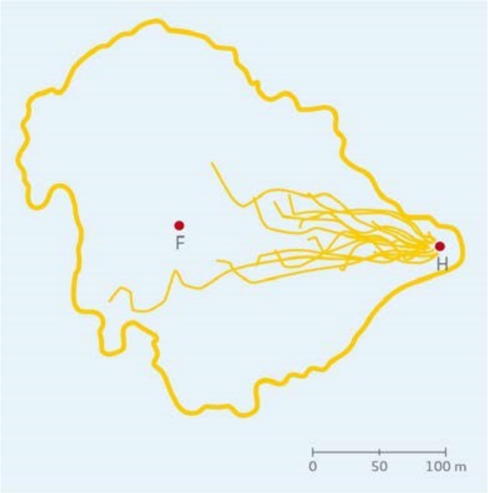
J. R.Riley, Randolf Menzel and their collaborators have used the radar method to record flight paths of dance followers who were captured, transported to, and then released at a different location (i. e. not their hive). As in the tunnel experiments all the clues that are normally present in the natural situation outside the hive are absent (see below). Instead the direction of the recruit's flight path is determined purely by the information it has received from the dance. The radar traces clearly show how the individual bees leave the hive and spread out in a broad fan along a “corridor of uncertainty” as Rodrigo de Marco deduced from his analysis of the dance patterns.

A honeybee in the research program of English biologist Juliet Osborne. The transponder fastened to the back of the bee makes it possible to locate and track the bee's flight with harmonic radar. (Reynolds et al., 2008, Osborne et al., 2013)

Not surprisingly the recruits do not take more accurate paths than the dances indicate. On the other hand it is very clear that the dances do influence the general direction of the recruit's flight path.

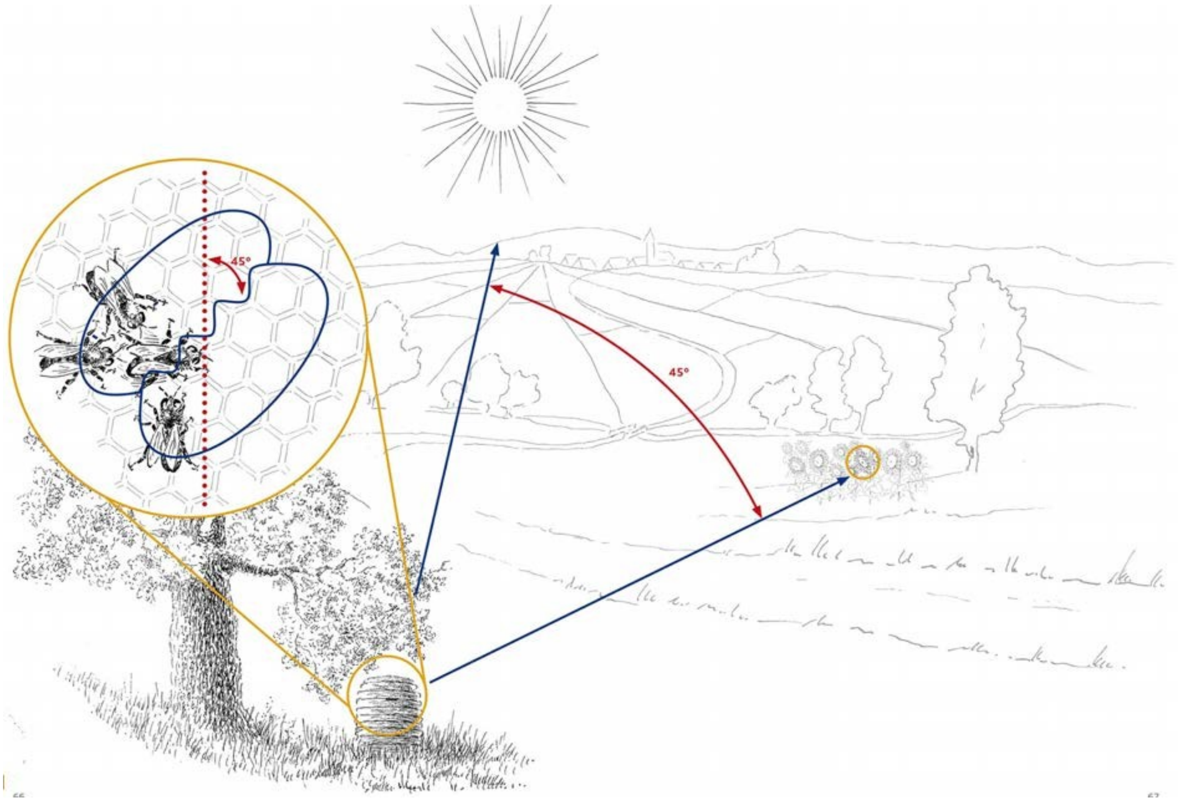
The initial notion that follower bees obtain precise information about the location of a single point in the landscape from movement patterns in the bee dance has, considering the many limiting factors, become much less persuasive. More than half a century and mountains of publications on the bee dances later, an alternative is formulated here which is the synthesis of many different experiments. The consequence is the beginning of a new chapter in bee communication studies providing opportunities for a great deal of new and exciting research.

Two models are contrasted here representing the older and more recently developed proposals of how experienced forager bees recruit novices to feeding sites. The differences between the models are not only in the details but in fundamentally different perceptions relating to the “dance language” and a basic understanding of the mechanisms that enable the recruits to reach the goal.



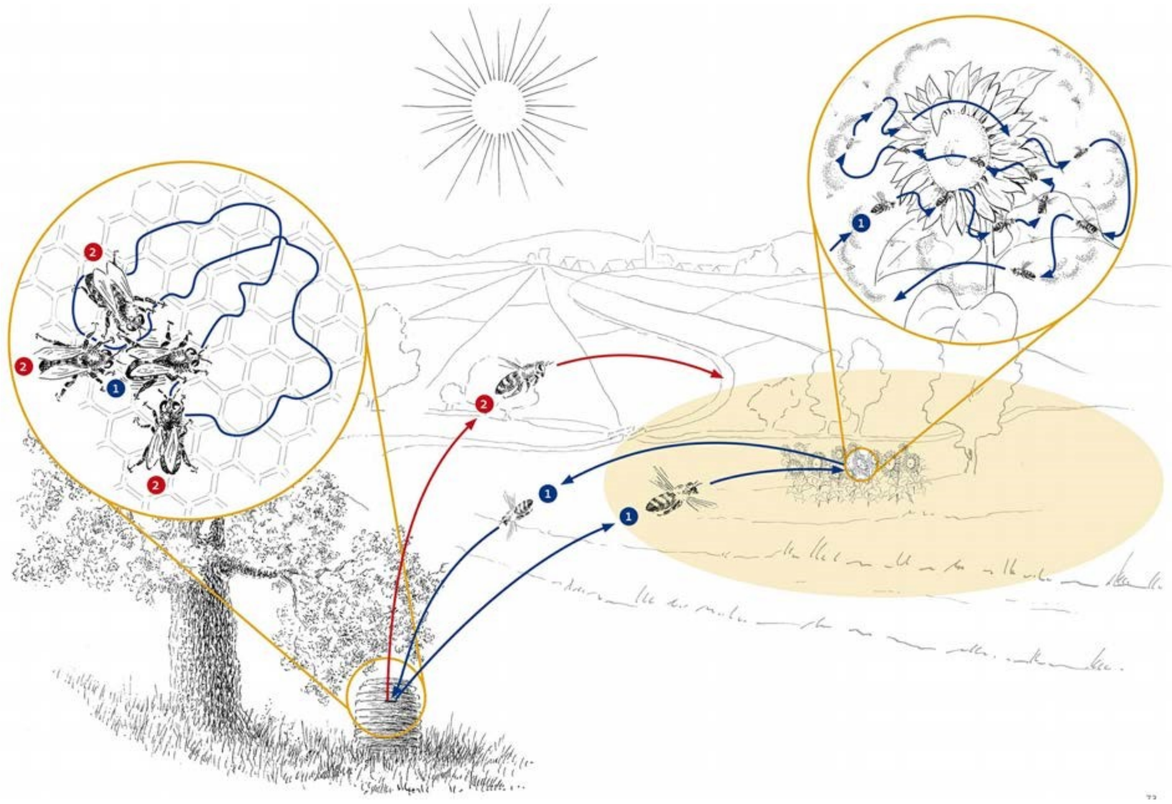
The line in the figure encloses an area indicated in 90% of the dances of bees that were trained from the hive H where they danced, to the feeding site at F. Superimposed on this figure are the initial, radar tracked flight paths of recruits that followed the dances in the hive but which were then taken to a completely different area and released there. These recruits were without the assistance of the scent of the flowers or the presence of experienced bees. The traces of the flight paths show that although the general direction taken by the bees is correct, not a single bee would have flown directly to the feeder using only the information that it had received from the dances. (combined from de Marco et al., 2008 and Riley et al., 2005).

The classic view, established in the minds of many (Model 1), is widely spread, found in zoology texts, school books, encyclopedias and the internet, and is the following: The dance provides information about the direction of the food source and its distance from the hive. The waggle phase of the dance contains all the instructions necessary to guide a recruit which has followed the dance on the surface of the comb, directly to the goal. The angle the waggle phase run makes with the vertical can be detected by the dance follower in the darkness of the hive and is equivalent to the elevation of the sun outside the hive. From this she can deduce the direction of the correct flight path. The length of the flight path is given by the time taken for the dancer to complete the waggle phase. A geometrical vector can be reconstructed from these two factors. The origin of the vector lies in the hive, the termination lies at the food source for which a dancer is attempting to recruit helpers. Equipped with this information the followers can fly to the food source. This is the usual story. The role of additional help outside the hive is often vaguely mentioned or not at all. The scent of flowers, in this view, merely initiates landing at the site. Experienced bees in the field or underway between the hive and the food source and which attract notice with their buzzing flights and scenting at the site are not included in this model. Instead, it is proposed that the bees need only the vector based information to know where they have to land.



Model 1: The classical model of recruitment of honeybees to a feeding site. The waggle dance pattern traced out in the dark hive by the returning forager contains the information from which the recruits can find the food source. The angular direction of the waggle dance on the surface of the hanging combs in relation to the vertical is equivalent to the angle outside the hive between the sun's azimuth and the goal, and hence the direction of the flight path. The distance to the goal is provided by the length of the waggle phase of the dance.
Recruits that have followed the dances in the darkness of the hive fly to the goal on the basis of the information in the dance. Once they have arrived the scent of blossoms that the followers have previously detected on the dancer, release landing. (Figure: D. Nikolaus)

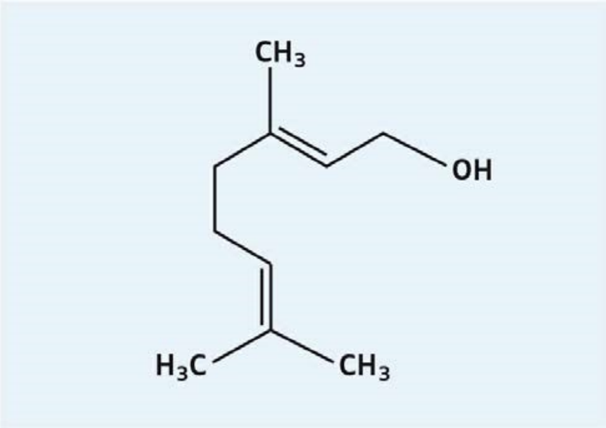
In contrast to this the new view (Model 2) stems from a synthesis of decades of work by many research groups and a re-examination of older observations that are, with a few exceptions, seldom carefully and thoroughly considered. In this view the dance is only the beginning of a chain of events that help recruits discover orientation signals and stimuli in the field to guide them far more rapidly to the food source than random searches in various directions and distances from the hive.



Model 2: The new recruits begin their flight along a “corridor of uncertainty” (orange coloured area). In the field recruits are assisted by bees that fly back and forth, the buzzing flights around the goal, the scent of the blossoms and experienced bees at the goal. Blue: Experienced foragers (1) which have danced in the hive, flown back and forth between the goal and the hive and scented the feeding site. Red: Novices (2) which find the goal from information in the dance and further assistance in the field.
Above right: The search flights of recruits in the field (2) are unsuccessful without help from the experienced bees (1). They either return to the hive or visit other flowers they find by chance. If the goal is very strongly scented, novices will find it, but then they don't need the information in the dance. (Figure: D. Nikolaus)

The synthesis offered here comes from information available in the literature. The existence of this knowledge, some of it for a very long time, has nevertheless not led to an overall research effort that focuses on the combination of factors that lead the recruits finally to their goal, instead of concentrating on just one aspect of this process.

The dance then is the first link in a chain of behavioural patterns performed by forager bees. The same bees which dance in the hive carry out remarkable buzzing flights around the goal. These are acoustically and visually so pronounced that humans have no difficulty in hearing and seeing them. The experienced bees also mark the goal with a scent specific to bees (geraniol) extruded from Nasanov glands on their abdomens and spread around the goal like vapor trails streaming behind jet aircraft.



Bees use geraniol among other scents to mark the feeding site. Geraniol is also used in perfumes because it has a pleasant odor.

Reference to both phenomena (buzzing flights and scenting) can be found in the oldest review on the bee dances (von Frisch 1923). On buzzing flights he writes: “Spitzner in 1810 had already described bees which discovered a store of honey, attracted other bees from their own and neighbouring hives with a high pitched tone” (von Frisch 1923, p150). Von Frisch described his own observations in the same publication on page 151 as follows: “Because the foragers arriving at the feeder usually fly around it for a while before landing, searching bees which have left the hive in response to dances and are in the area can be led to the site. At rich sites, when the number of foragers exceeds about a dozen, a continuous high frequency tone can be heard”. Von Frisch could show that it was not the tone which led the bees in to the feeder. That bees are deaf could only be conclusively demonstrated in later studies. They are able to perceive airborne sound only when it is intense enough to displace their antennae or the substrate on which they stand.

Von Frisch had already laid the trail towards solving the problem he himself had set, namely the precise navigation to the site after following inaccurate dances. In the study cited above he writes on page 161: “Foragers which fly from the hive and arrive at filled food dishes often swarm around the site in irregular loops for a noticeably long time before landing. (…). Only now have I noticed that most of the bees circling the site have their scent organs extended and impregnate the area around a rich feeding site with a special scent. (…). The longer a bee has danced on the comb, and so advertised more intensively for recruits, the more actively she scents the feeding site on her return to it”. Dancing foragers in most cases perform buzzing flights at the goal; foragers which do not dance because the food source is not attractive enough do not make buzzing flights (see videos of the HOBOS Team for more detailed information in the appendix).

Simple behavioural experiments after the tradition of Karl von Frisch and Martin Lindauer can deliver important insights, confirm old ideas or also dispel them. More than a hundred years ago the Belgian writer, Nobel Prize winner for literature and bee researcher, Maurice Maeterlinck, showed that recruited bees only arrived at feeding sites if experienced bees were also allowed to fly to these sites. Maeterlinck wrote: “I once marked the body of a particularly small Italian bee with a spot of colour. On her second visit [to the feeder – auth] she arrived with two sisters. I captured these without disturbing her [the marked bee – auth]. On her next visit she came with three of her partners…” (Maeterlinck 1919, p96). Maeterlinck continued: “I repeated this experiment twenty times [i. e. trained individual bees to a feeding site and marked them there – auth] with different bees and each time removed the recruits so that others could not follow their tracks (…). If the marked bee came alone [from the hive – auth] I simply caught and removed her and waited in my room [where the feeding site, a dish of honey, was placed as for the other experiments – auth] for the arrival of her friends to whom she had passed the message (…). I have to confess that only one arrived at the feeding site (ibid p98ff).

These early experiments carried out decades before the idea of a dance language are truly wonderful but unfortunately virtually unknown. In more recent literature about the bee dance there is only a single mention of the work of Maurice Maeterlinck in the doctoral thesis of James L.Gould (Gould 1975) and there, sadly, misrepresented. Gould wrote on page four of his dissertation: “Maeterlinck (1901) tested this explanation [the matter concerned the view of Aristotle that recruits from the hive simply fly after the experienced foragers – auth] by letting a forager find the food and return to the hive [it was not one, it was twenty different bees, and all employed as marked foragers – auth]. He then caught the forager on its way back out of the hive. Even though recruited bees had no forager to follow, some of them [only one of them in twenty experiments – auth] nevertheless found the food”. It may seem petty to lay such importance on numbers, but precise information about measurements or counts are the soul of quantitative behavioural biology to which the study of bees belongs. The incorrect statement “…even though recruited bees had no foragers to follow some of them nevertheless found the food…” leads along a different trail and to very different conclusions about the mechanisms and efficiency of recruitment than what Maeterlinck actually reported, i. e. that twenty forager bees led to the visit of only a single recruit when they were not present.

If we put together what we know we get the following picture: Experienced bees begin the business of getting recruits to the feeding site by dancing on the combs in the dark hive and continue their active role at the food site by buzzing around it and scenting. The flowers themselves attract over a short distance with their colour and shape and over a greater distance with their scent. This aspect was studied in many experiments by the American bee researcher, Adrian Wenner. However we know virtually nothing about what happens between the hive and the feeding site, apart from the existence of one further goal-finding clue. Over a period of time a flight path corridor forms between the hive and the feeder along which bees that know the location of the site fly back and forth, with more and more recruits “in tow”.

Together, all of these components bring the novices to the goal. The strongly idealized scheme of Model 1 that relies solely on the role of the dance movements does not encompass the complexity of the recruitment procedure. It is of significant interest that these very same components ensure the success of one of the most important phases in the life of a bee colony, i. e. that a swarm of several thousand bees find a new nest, the location of which is known to only very few in the swarm. Recruitment of nest mates to feeding sites exhibit all the building blocks of the swarm behaviour and one could describe the foraging process almost as the initiation of a miniswarm.

A short list of critical questions is listed here to stimulate the imagination and provoke new experiments:

1. Are there other clues apart from the five named here (the dance, presence of experienced bees flying to and from site, buzzing flights around the site, geraniol scenting, scent of the flowers) that could provide additional assistance for recruits in finding the feeding sites?
2. How do the known elements of communication and environmental stimuli work together?
3. Do these elements change their relative importance, or weighting, on the flight between the hive and the feeder, and if so, how?
4. How does the interaction between the five goal finding aids depend on the conditions inside and outside the hive?

For recruited novice leaving the hive for the first time, the sky is open and all directions are possible. The information in the dance provides the initial clue to limit the area in which the recruits can expect to find subsequent necessary guides to the goal. For the recruits this is a significant advantage for without further assistance in the field the dance alone leads nowhere.

Outlook

Like all other organisms, the lives of honeybees are dependent on the flow of material and energy both of which they obtain in a usable form from flowering plants. In exchange for nectar and pollen, bees are messengers of love for plants. They transport pollen from flower to flower and ensure fertilization, seed production and hence the propagation of the flowering plants.

Over millions of years these two partners have, through natural selection, achieved such a perfect fit that an inseparable union has resulted – honeybees and flowering plants are bound together in a close mutual interdependence.

Beginning with man's first agriculture, a new partnership with mutual interdependence and joint advantages arose – that between honeybees and humans. Agriculture is the basis for a world population that has risen from about five to ten million in the Stone Age to about seven billion today. The major component of human nutrition is fruit and vegetables and originates from the world of flowering plants. Many of these depend on animals for pollination, the majority of which are insects. These include non-social wild bees, wasps, beetles, bugs and others. Honeybees are the number one global pollinators. It takes about five hundred bumble bee colonies to match the pollinating ability of a single bee colony. Honeybees through their pollination of all fruit and most vegetables provide more than a third of the nutritional needs of humans. Indirectly the proportion is even larger when it is considered that food for meat production consists, for the most part, of flowering plants pollinated by bees.

This importance of the honeybee makes people dependent on them; humans need honeybees as pollinators. Honeybees need people as guardians in an environment that is today not the same world in which the bees evolved and for which they were originally adapted. After many generations under human protection and interbreeding the bees themselves are not the same wild forms that coped perfectly in an undisturbed natural world.

There are many other good reasons for taking good care of honeybees. Pollination of natural plants is essential for the maintenance of species diversity. This leads not only to a colourful and balanced appearance of the landscape itself but also one that offers a habitat to all animals such as birds, butterflies and many others that depend on plants for their necessary living conditions. Here too the bees make an overwhelming contribution.

And there is more. Humans have the pollinating insects to thank not only for the larger part of our food and drink. We enjoy flowers, their forms, colours and perfume. We cultivate flowers in gardens, parks and window boxes and give them to our companions. We should be conscious of the fact that we are the beneficiaries of the sensory world of the pollinators. Flowering plants exist in a highly competitive world in which they contest for the attention and visits of insects, and in particular from honeybees. The variety of flowers stems from their attempts to outbid one another and be maximally noticeable for insects and appealing especially to their visual and olfactory senses.

Alone through their presence bees offer us a certain quality of life. The humming of bees in a flowering fruit tree implies the awakening of spring after winter. A bee-silent spring is a dreadful prospect. There are enough reasons to care responsibly for honeybees.

Enduring care for bees, however, must be based on an exact knowledge of their needs and also of their problems and threats to their livelihood. New data and knowledge is essential in order to sensibly and sustainably support bees in an ever rapidly changing world. This can come from basic research spread across a broad front. Here the established research methods of behavioural biology, molecular biology and biophysics have their applications. Most important is the further development of radar tracking of flying bees, extended to enable the simultaneous tracking of several bees. This would make it possible to determine where the interactions occur between the experienced and inexperienced bees that reach the goal together. New methods need to be developed to cope with the overwhelming complexity of the bee colony and which simultaneously include a large number of individuals in the collected data. This would allow an even deeper penetration into the intricate details of the biology of a hive. So far the technical possibilities to record events in a bee colony both spatially and temporally with modern imaging methods such as positron-emission tomography (PET) have not been explored but based on the HOBOS project, such developments are conceivable.

Whatever methods we develop and however we generate new data, bee research is an exciting and important field. Every new insight helps us to learn more about this amazing organism on which we are so dependent – the honeybee.

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Video-links:

HOBOS-Team videos of experienced forager bee landing approaches:
– Buzzing flights of a dancer: http://www.hobos.de/de/Film1
– Quiet and quick landing of a non-dancer: http://www.hobos.de/de/Film2

“Thermal Society” a series of sequences (ca 6 minutes) about the use of heat in bee hives. A film from Barrett Klein produced by the BEEgroup and HOBOS-Team: http://www.youtube.com/watch?v=iYr158rwLBI