

8 Cultivated Intelligence

The temperature of the brood nest is a controlling factor in the self-constructed environment with which bees influence the characteristics of their future sisters.

Organisms are exposed to the uncertain influence of their environment. Amphibians suffer from dryness, birds from lack of food, butterflies from the cold. The freedom to move provides most animals with the possibility of avoiding unfavorable situations, and searching for better conditions. Amphibians bury themselves in the earth; birds change their locality, and in extreme cases as for migratory birds, their continent; butterflies select sunny places. The environment provides possibilities from which animals choose the best solution. Selection ensures that species that have found an appropriate solution survive, whereas those that do not vanish completely.

The environment is not really only a palette from which organisms either choose well, or suffer unhappily. Environments can also be constructed. Earthworms form the substrate in which they live, through their feeding and burrowing habits. The leaves of trees shade, and thereby influence the leaves sprouting beneath them. Aquatic animals affect the acidity of small ponds by their excretions. Such influences on the environment, if not neutral, are followed by reactions that in turn impact on the animals involved. Such reactions are often negative: if the water in small ponds becomes too acid via the effects of animals living there, this kills the polluters.

But what if organisms could arrange their environment to their advantage, and include specifically manipulated positive effects? Would this not introduce an entirely new quality to the game of “environment, organism, and adaptation”?

And what if the environment shaped by the organisms could determine, or influence the characteristics of the organisms themselves? Would that not lead to a system in which cause and effect—and even the limits of the classical environment–organism model—become blurred?

In an evolutionary time span, an actively shaped environment that incorporated properties influenced by the organisms living within it would merge with the genes of the organisms that shaped it, resulting in a unity in which the elements would develop together.

Such organisms would have freed themselves from being slaves of an environment to which they had to adapt in order to survive and reproduce.

Steps toward independence from the environment have been taken by humans, but also by honeybees—comparatively, those taken by honeybees are perhaps more fundamental than those of humans. For us, the usual method of conditioning our environment is determined by constructional possibilities, and depends on the prevailing natural environment. It is possible that in conditioning our living and working areas, we merely achieve a feeling of comfort that satisfies an existing need, rather than truly changing ourselves over the short or long term.

In the 30 million years of their evolution, colony-building bees have achieved what is yet to be shown for humans—they can shape their environment to their own advantage.

We are gradually beginning to understand the highly complex and numerous feedbacks and interactions between bees and their self-controlled environment. One of the latest advances is the recognition that the temperature of the brood nest is of great importance for the entire biology of honeybees.

Hot Bees, and Warm Pupae

The brood nest of honeybees (Fig. 8.1) is an extremely important and sensitive part of their living world that they control with amazing precision, and the temperature of the area that contains the capped pupa cells is particularly exactly regulated.

Beekeepers have long known about the warmth that is developed in the brood nest of honeybees, and that can be detected



Fig. 8.1 The brood nest of honeybees is that part of the comb in which each new member of the colony is individually cared for by a brood nurse during its development from larva, through the pupa to the adult bee

even with the bare hand. For some time, it was believed that the brood itself produces the localized high temperature, and that bees went there to warm themselves. This opinion was shown to be incorrect, and was replaced by a much more exciting insight into the biological significance of the nest climate of honeybees. The employment of heat-sensitive cameras in particular, coupled with patient behavioral observation and careful manipulation of bees and bee colonies, have provided completely new perspectives, the consequences of which are far from being fully appreciated.

Animals are able to produce warmth by metabolizing energy-rich substances such as fat and carbohydrates, or through muscular contraction, as we do when shivering with cold. Honeybees warm themselves by shivering with their flight muscles, which not only are used for flying, but as we have seen in Chap. 4, also are responsible for the production of vibratory pulses in waggle dance communication. Warmth is produced by these muscles in a slightly different way. Bees uncouple these muscles from the wings by means of the ingenious action of tiny steering muscles, and by contracting and relaxing these, increase their metabolic rate. Antagonistic muscles work against one another, and muscle trembles ensue that result in vibrations. These are far weaker than those produced by the dancers. In terms of heat production,

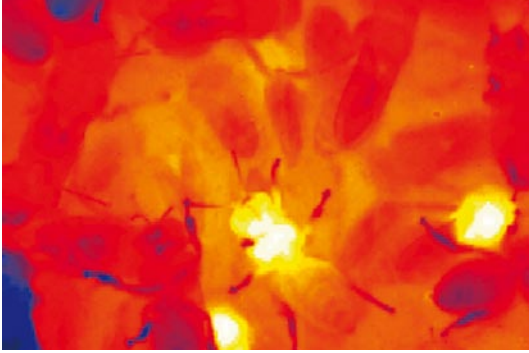


Fig. 8.2 The distribution of temperature in the bodies of heater bees becomes visible in thermographic images. The artificial coloring of the images indicates low (*blue*) and higher (*yellow*) temperatures. An ingenious employment of the counter stream principle prevents the passive dispersion of heat through the bee's abdomen, and warmth is confined to the thorax, where it is generated by strong flight muscle trembling

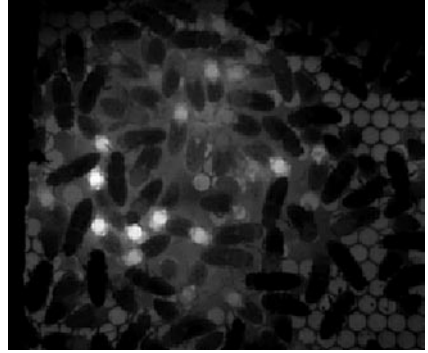


Fig. 8.3 Thermographic images show that “hot bees”, with thoraces that appear *white* here, collect in the capped areas of the brood nest. The surrounding uncapped area of the comb, recognizable by the dark rims of the cell walls, is free of heater bees

the result of this trembling can be appreciated in pictures from a thermo-sensitive camera (Fig. 8.2).

Many insects, including honeybees, have developed the ability to heat their flight muscles through such contractions, to prepare themselves for flight. The solitary evolutionary predecessors of honeybees, which do not form colonies, probably already possessed this ability, and a possible way to control the nest temperature. This inheritance was one of the most important physiological requirements for the development of colony-forming honeybees.

Thermocamera pictures have been taken of many insects preparing to fly, and show that moths, for example, heat their flight muscles before they take off into the cool night air. The same warm-up occurs in the flight muscles of honeybees that are preparing to fly, and this is the original function of an ability that honeybees have exploited to achieve a very different end.

A view of the brood comb through the lens of a thermocamera reveals “hot” heater bees with “glowing” thoraces clearly outlined on the capped cell region (Fig. 8.3).

These bees press their thoraces down onto the cell cap that lies beneath them, and transfer their warmth to the pupae enclosed beneath the cell cap. This heating posture, in which they sit at

least half a body height lower than other bees on the comb, is easily recognized (Fig. 8.4), and they will maintain this attitude, completely motionless, for up to 30 min. One could take these bees for dead. The antennae do not move, but are held in contact with the cap of the cell in front of the bee, presumably to measure the temperature of the wax caps of the pupa cells, because the tips of the antennae carry the greatest concentration of heat-sensitive receptors.

To believe that the bees are resting, sleeping, or even dead would be doing them a great injustice. They are as active as a honeybee can possibly be. Only strenuous flying can match the energetic activity of a heater bee.

After maximally 30 min in this posture, and a heating performance corresponding to a body temperature of over 43°C, the animals are exhausted and interrupt the activity. The lid of the warmed pupa cell will “glow” for some time after a heater bee has completed heating, and has moved away (Fig. 8.5).

A heater bee can warm up only one pupa cell lid at a time, because this has the same dimensions as her thorax.

A heating engineer would wonder about the efficiency of a system in which warmth is transferred from the bee thorax to the single cell. Hot bees radiate heat from all sides, not only down to the pupae that need warming. They lose more warmth to the surroundings than they transfer to the underlying cells on which they have focused. This method of heating looks more like that of a hotel room with defective windows in former times of socialism: the windows were not repaired—the heating was just turned up.

A closer look at all the bees in the area of capped brood cells shows the efforts they indeed make to keep the loss of warmth as small as possible (Figs. 8.6, 8.7). Non-heating bees, for example, are thickly packed on the comb, insulate it, and reduce heat loss through radiation.

In addition, bees have adopted a far more ingenious and effective way to warm their brood, which is described below.

The Colony's Incubator

Bees always begin the establishment of the brood area in the center of the comb. This spreads out on all sides as the queen continues to lay eggs, and cells are closed with a lid during the



Fig. 8.4 A heater bee in typical heating posture can be seen in the center of the picture. Pressed close down onto the lid of a cell, she holds her wings firmly closed, and the tips of the antennae in continual contact with the lid of the cell. Bees can remain immovable for up to 30 min in this position, while the bustle of life on the comb carries on around them

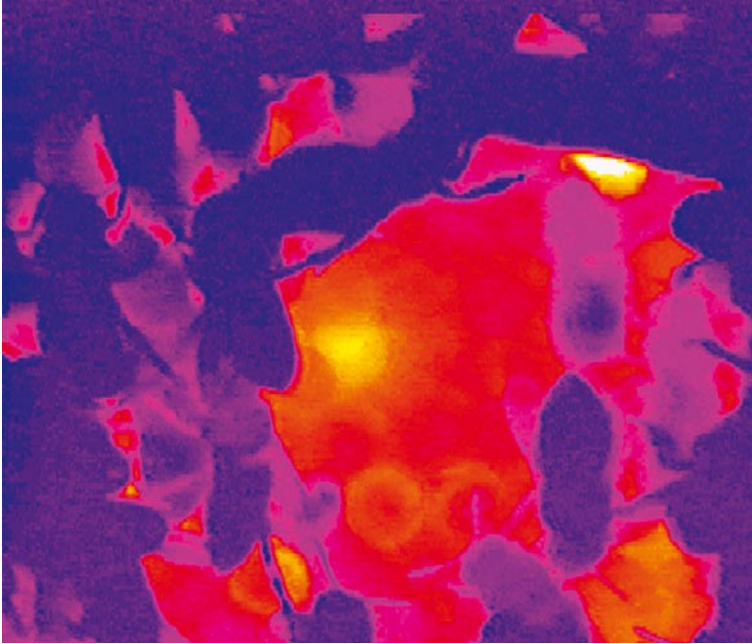


Fig. 8.5 If a bee that has been pressing herself down onto the lid of a cell for some time is moved aside, the thermo-camera will detect a hot spot, precisely at the point where the bee's thorax had been, and seen here as a yellow area in the center of the picture

final larval stage so that they can pupate undisturbed. The capped area of the brood comb in honey bee colonies is not completely closed; empty cells, constituting 5–10% of the total number, are distributed among the capped cells. This percentage varies, depending on the outside climate.

Unused cells can be found in all stages of development of the brood nest (Fig. 8.7). A percentage of empty cells in a brood comb exceeding 20% of the total can be the result of unusual situations in the colony, such as the unwanted appearance of a large number of diploid drone larvae that the workers then remove from the brood nest.

Cells in the brood nest that remain empty can be found even after a queen has newly established a brood nest area (Fig. 8.8), and consequently after the emergence of the larvae (Fig. 8.9). This becomes functionally interesting when it is realized that (Fig. 8.10) these apparently empty cells are, in reality, seldom empty at all. Instead, they are frequently occupied by bees, lying headfirst in them (Fig. 8.11).

This behavior was initially described as “cell cleaning”, or “resting”, because it was not possible to determine what the bees were doing in these cells.



Fig. 8.6 Most of the bees are located in the region of the capped brood cells. The heater bees, with their bodies pressed down on the comb (four heater bees are marked here, see also Fig. 8.7), are partly hidden by a majority of standing, non-heating bees. The bodies of the non-heating bees form an effective insulating layer, and help to keep the warmth in the brood



Fig. 8.7 An enlarged view of the marked region in Fig. 8.6, with four heater bees pressing their thoraxes down to transfer the warmth from their bodies onto the lids of the cells beneath them



Fig. 8.8 The queen does not lay an egg in every cell. Empty cells are scattered throughout an area in which a queen has deposited eggs



Fig. 8.9 Empty cells become conspicuous when the hatched larvae begin to develop

Fig. 8.10 About 5–10% of cells in the capped brood region are usually empty, a proportion that is ideal for warming the pupae

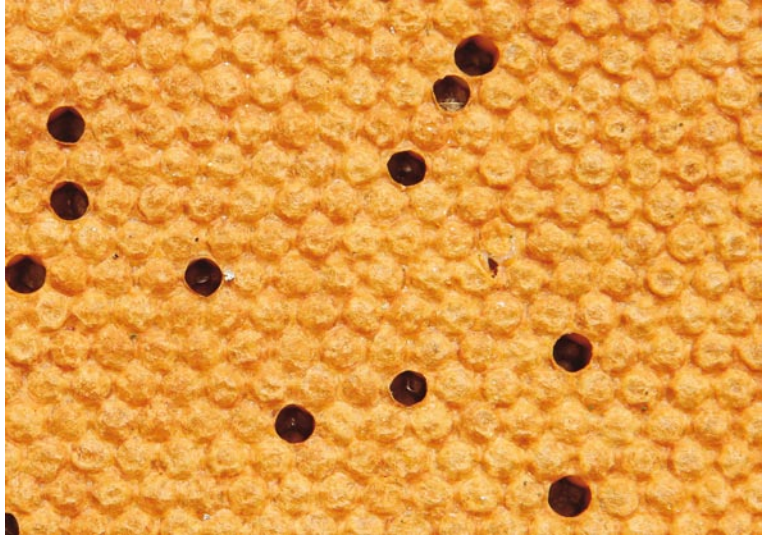


Fig. 8.11 Three workers, deep and headfirst in empty cells of a capped cell area of a brood nest



All that can be seen from the outside are the tips of the bees' abdomens, the ends of which are rapidly telescoping in and out, or show short periods of activity interspersed with long periods of rest. The rapidly telescoping activity is common across the brood area, the resting state, less so. Carefully opening the cells from the side exposes bees lying in the cells with their legs stretched out behind them. As pupae, they lie like this in cells with their heads

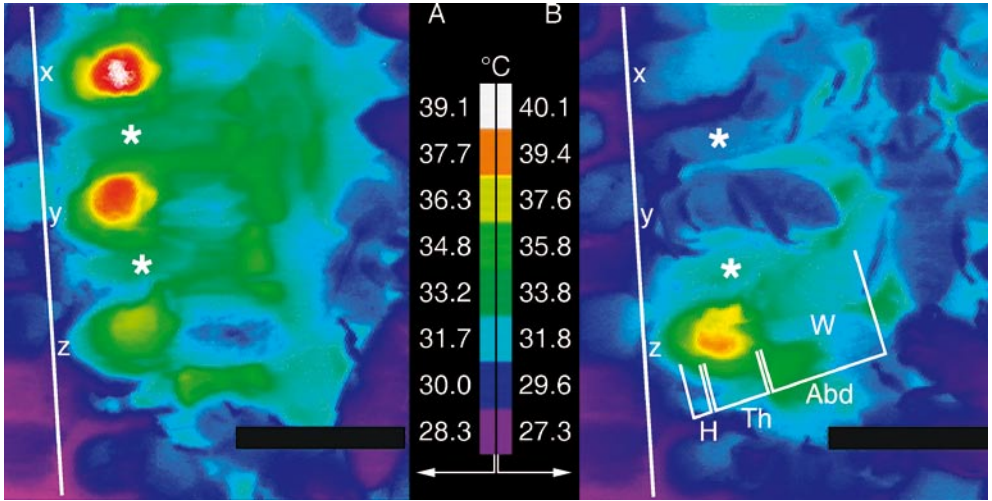


Fig. 8.12 A thermograph image of an area of a brood nest that has been cut open along the length of the cells. Four heater bees with different temperatures, and a resting bee at ambient temperature (*blue*, *y* in the group on the *right*) occupy cells close to one another. *x*, *y*, and *z* mark the bottoms of the six cells in which the bees are lying. The *asterisks* indicate the location of the pupae. *Abd* Abdomen, *W* wings, *H* head, *Th* thorax of the bees. The *scales* show the temperature calibration of the thermograph

facing out, but now the heads face in. The bees have an outward appearance of being completely at rest, apart from the pumping movements of the abdomen. A thermocamera directed at these bees shows a large difference in body temperature between individuals in the different cells (Fig. 8.12).

Strongly pumping bees have an average thorax temperature of up to 43°C, in contrast to bees in the resting state whose temperatures are the same as that of the ambient environment. The old interpretation that these bees are resting is true only for a small proportion of the cell inhabitants. All the others are actively heating. The behavior suggests a second heating strategy that is far more effective in transferring energy than is the case for pressing on the surface of cell caps. Measurements of body temperatures of the bees before they creep into the cells indicate that only those with high body temperatures slip into empty cells, and that they prepare themselves before entering the cells. Initially, they have the same temperature as the air in the hive, but before entering a cell, they run around rapidly over the comb, increasing the tem-

perature of their thoraces to an appropriate level. Bees that have cooled down, after a period of 3–30 min, leave the cells. The effort of continuously maintaining the body temperature at such high levels costs an enormous amount of energy, and explains the limited occupation of the cell. The bees' reserves are exhausted after 30 min at most. Heater bees do not maintain maximal heating performance for the entire period they spend in the cells. Phases of activity of up to 5 min are interspersed with pauses during which the bees allow their body temperatures to sink by up to 5°C, before increasing these again to regain maximal heating performance. Such temperature troughs are expected in a controlled system that has to be maintained at a specified level. The application of heat is turned down when the desired temperature is exceeded, and reapplication occurs when the temperature has fallen below this level. This heating behavior is bound closely to the sociophysiological control of the brood nest climate (► Chap. 10).

Bees that are occupied as heaters—unlike many other activities in the lives of bees—belong to no particular age class. The youngest bees that undertake the heating task are 3 days old, the oldest 27.

Sweet Kisses for Hot Bees

Bees obtain the energy for heating from honey. A strong colony can produce up to 300 kg of honey during a summer, although only a small proportion of this can be found at any one moment in the nest, because the turnover is high. Honey is not food in the usual sense, for the maintenance of body functions of the bees, but is used mostly to warm the brood nest in summer, and to keep the bees clustered in the hive from freezing during winter. The large reserves of honey of a bee colony are therefore not food, but fuel. A few relevant data:

- The energy content of a full crop of nectar amounts to 500 J (joule).
- The energy cost of a forager amounts to 6.5 J per kilometer flown. It follows that for an average flight, she will need about 10 J. She therefore brings 50 times as much energy back to the nest as the flight costs.
- During an average lifespan, a forager carries 50 kJ back to the nest.

- The foraging force of a colony, involving more than 100,000 individuals during a summer, undertakes several million foraging flights, and carries about 3–4 million kJ of energy back to the hive.
- A milligram of honey contains 12 J of chemical energy, bound to sugar. The combustion of a kilogram of honey produces 12,000 kJ.
- A bee uses 65 mJ per second to achieve the heating performance needed for her thorax temperature to be raised to, and maintained at a summer ambient level of 40°C.
- Such a heater bee will have burned 120 J that she has drawn mainly from the sugar in her hemolymph, after a maximum heating period of 30 min.
- During the entire brood period, heater bees will burn about 2 million kJ, which is more than two thirds of the total energy used in a summer.
- The heat energy for the control of the brood nest temperature is equivalent to a continuous power usage of 20 W (watt). If bees were able to channel this energy into a light bulb, they could brightly illuminate their dark world in the nest.
- Also, 2 million J are burned for warming the cluster of bees in the nest in winter. The remaining fifth of the energy stores gathered by the bees over the summer provides the energy for all their other activities.

Honey reserves in the hive are usually located at some distance from the heated brood comb. “Filling station” bees are continuously underway to spare the heater bees the long trip to the honey stores, and particularly during cold weather, to avoid any interruption of heating activities. This group of bees deliberately search for heater bees, and transfer the honey directly to their mouths in a “sweet kiss”. The direct transfer of nectar or honey from one bee mouth to another is called trophallaxis (Fig. 8.13).

Filling station bees must find the exhausted heater bees, with their small residual body warmth, in the darkness of the hive, and the highly temperature-sensitive receptors on their antennae guide them in this search. Highly concentrated honey of maximum energy content is transferred between the members of this team, and not immature honey, or simply nectar, of which a considerable amount is exchanged between other bees in the hive.

Fig. 8.13 A donor bee (*below*) provides an exhausted heater bee (*above*) with a trophallactic “energy shot” of high-quality honey



Filling station bees load up from open, or already capped honey cells, the lids of which they must first remove (Fig. 8.14), and then go off in search of bees that need energy. This behavior is promoted by the higher air temperature in the brood nest—this is biologically meaningful, because usually the high air temperature in the brood area results from the activity of many heater bees, which are correspondingly hungry after completing their task. A certain provision for self-catering is also present in the brood area. Empty cells in the capped brood region are often used as depots, and filled with nectar (Fig. 8.15), only to be



Fig. 8.14 Bees whose task it is to supply and recharge the energetically exhausted heater bees in the brood nest are shown here opening capped honey cells

emptied again after a short time. These cells serve as local stores for energy-hungry bees, but do not offer the high-quality “energy shots” provided by the mature honey that is transferred from mouth to mouth.

The correct combination of empty heating cells among the brood, filled depot cells, and filling station bees is a consequence of ambient temperature. Should this remain low for a long period, many more empty heating cells are introduced; should it become high for a while, the extra cells are not used for heating, but as temporary nectar depots (Fig. 8.16).

Fig. 8.15 Nectar-filled depots in the brood nest



Fig. 8.16 Heater bees will serve themselves from depots in the brood nest when these are available to them. Such cells remain filled for short periods, and contain merely “thin” nectar, not honey



Bees that are not actively heating form a living layer over the comb, and do their share of temperature regulation through passive insulation. Such insulation can contribute both to reducing loss of warmth from within, and also to guarding against overheating from without.

Bees not only have to heat, but also cool, in order to keep the pupae at their optimal temperature. In central Europe, the latter is required significantly less than heating, but even a short heat wave can damage the sensitive brood.



Fig. 8.17 Bees search for water that they will then distribute in small drops and in a thin film on surfaces within the hive, if the hive becomes too warm



Fig. 8.18 Once the water collectors have spread a thin film of moisture, nest mates go into action as living ventilators. The streams of air they produce with their wings evaporate the moisture, and cool the surfaces

The method used to cool is the same as that employed by humans for their air-conditioners—evaporative cooling.

On hot days, specialized workers collect water from moist ground, and also from the edge of open ponds and waterways (Fig. 8.17).

They transport this into the hive, and there spread it as a thin film over the rims or caps of the cells. Martin Lindauer (1918–), a renowned bee researcher, recognized over 50 years ago that when bees ventilate the area with their wings (Fig. 8.18), the air



Fig. 8.19 If a general airing of the hive is required, the bees arrange themselves into a chain of ventilators in front of the hive, to draw out the old air that is too warm, or contains too much carbon dioxide

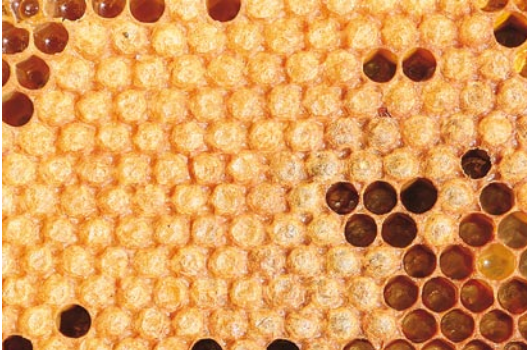


Fig. 8.20 The number of pupae that are adjacent to the empty cells in the brood nest partly determines the time a heater bee will occupy an empty cell. The more pupae in the immediate vicinity of the cell, the longer the cell will be occupied by heater bees

currents produced by this “stationary flying” evaporate moisture, causing the temperature of the hive to sink. Bees sitting either directly on the comb, or at the entrance to the hive create these air currents.

Ventilator bees will organize themselves into some spatial order, and combine their small individual efforts into a highly effective ventilation of the entire nest, should this be required (Fig. 8.19).

The body temperatures of the heater bees, and the time they spend within the cells set the temperature levels of very small, local areas in the brood nest. Both of these depend on the construction of the area around the empty cell.

An empty cell is used for heating only when it borders at least one pupa cell, and in such a case, the heater bee has an average temperature of 33°C. Heater bees raise their temperatures to 41°C if an empty cell is surrounded by the geometrically limited maximum of six capped pupa cells. Intermediate temperatures are applied when the empty cells are bounded by two to five pupa cells.

A clear relationship also exists between the cell surroundings, and the duration of heater cell occupation; those bordered by five or six capped pupa cells are occupied by heater bees for 100% of the time, energetically exhausted bees being immediately replaced by fresh heater bees.

Cells that lie next to only a single pupa cell are occupied during at the most only 10% of any observation period; those neighbored by three capped cells contain heater bees for up to 70% of the time (Fig. 8.20).

“Half-baked” Sisters, or “Genetics Is Not Everything”

In honey, the greater part of the energy stemming from high-energy sugar bonds in plant nectar is converted into heat (Fig. 8.21). This is not the usual, unavoidable loss that accompanies energy conversion and transport, because here the honey is metabolized with the express purpose of releasing heat energy.

What is the fundamental reason for this enormous investment of effort and time, on which so many areas of the biology of bees are focused?

Two possible explanations for the high temperature of the brood nest of honeybees can be considered:

- The first proposal: after winter, a high brood nest temperature enables bees a rapid start in spring, and so to exploit the resources of early flowering plants before their competitors. According to this hypothesis, the higher the brood temperature, the shorter the development time, and the quicker the colony will increase its population. Nevertheless, in any colony during the breeding season, young bees are produced continuously, and so do not follow one another in true generations. Hence, whether individual bees take 1 or 2 days more or less for their development, the situation is the same in terms of continuously replenished population numbers in all colonies. Compared to a brood nest temperature of 35°C, a brood nest temperature of 32°C, in which perfectly normal bees are produced, would enable a considerable economy in energy. So, why is the brood nest temperature so high?

The queen has by far the shortest development time. Her pupa phase lasts, on average, 5 days, compared to 10 to 13 days for a worker. Is the temperature of the queen cell then so much higher than those of the workers? Not in the least. Measurements have shown that the temperature of the queen cell lies at 35°C, heated by bees that cluster around it.

A positive correlation does exist between the duration of development, and the temperature of the pupae; this can be shown for all insects, and has a biochemical basis. As explained above, however, this aspect is unlikely to have been the driving force for the evolution of the heating behavior.



Fig. 8.21 To be precise, one should not describe flowers as the feeding sites of bees, and the collection of nectar as the harvesting of nourishment. Instead, these should be regarded as energy sources, and foraging as the acquisition of energy for the hive. Honey production in the nest is the refinery for the raw materials

- The second proposal for the use of the heating ability of bees is more convincing, particularly in temperate climate zones: honeybees first arose in the tropics, and evolved with brood nests at high and constant temperatures. Pre-adapted with a perfected heating system, they were well prepared to penetrate to temperate latitudes, with their hard winters. Here, they manage to keep the temperature of the outer layers of the closely packed winter cluster from going below 10°C, a temperature limit beneath which bees are no longer able to move. New brood can thus be started early in the year in the shelter of the winter cluster.

The second proposal does not answer the question of why the brood nest temperature of the pupa phase was already so precisely regulated in the tropics. To control the temperature of the pupa there, cooling is more of a problem than heating. Tropical bees, in their hot climates, have correspondingly smaller energy requirements, meaning less honey and storage.

The study described below, of the properties of honeybees that developed as pupae at different temperatures, has provided insights into the importance of social heating by honeybees.

Before manipulating the temperature of the pupae, it is necessary to establish the temperature regime to which the pupae are subjected in the undisturbed brood nest.

Tiny thermocouples installed into the capped cells, without damaging the pupae, produced three interesting results:

- The actual temperatures of the pupae in a natural brood nest are constant over a particular range, but nevertheless do vary slightly about a mean value in many cells. The duration of the single, very gradual variations lies between 30 min and an hour. The amplitude of the variations can be about 1.0°C in either direction about the mean.
- The average temperature of the pupae over time is constant for each individual pupa that was observed.
- The average temperatures of different individual pupae lie several degrees Celsius apart from one another. They range from 33 to 36°C.
- The direction of temperature change during the slow variations is not the same for all pupae, which it would be if the temperature of the entire brood nest varied as a single, inte-

grated unit. Instead, the temperature of an individual pupa may rise, while that of a pupa in a closely adjacent cell will fall.

In summary: worker bee pupae of honeybees (Fig. 8.22) receive individual and different “personal” heat treatments from heater bees.

Do these different treatments have consequences for the resulting bees?

The pupa phase of honeybees lasts about 9 days for the workers, about 10 days for the drones, and about 6 days for the queen. In this time, a bee transforms from a larva into an adult. The essential characteristics of the adult bee are established during this metamorphic change. These are typical of insects, and deviate less from the general basic form than is the case for many insects that are adapted to special ecological niches.

Behavioral plasticity is the distinguishing feature that tops the list for bees. During their lives, worker bees carry out a sequence of different tasks that depend on their age. There is a long list of tasks that bees undertake in an undisturbed colony. Arranged in the order of occurrence, these are: cell cleaning, capping the brood, caring for the brood, serving in the queen’s court, receiving nectar, production of honey, removal of detritus, pollen pack-



Fig. 8.22 Pupae lie on their backs in perfect order in their cells

Fig. 8.23 In principle, each honeybee can carry out any task that has been observed in the hive. The quality of the performance, and the frequency with which the tasks are completed is nevertheless very different for different individual bees. Specialists go into action when the hive needs airing, in order to thicken honey, evaporate water for cooling, or exchange nest air that has a high concentration of carbon dioxide



ing, comb building, ventilation, entrance guarding, and foraging. Behavioral studies employing technology that can focus on single, individual bees have extended the list to include the heater bees, and the filling station bees responsible for providing the energy support for the heater bees (Figs. 8.23–8.26).

Different activities require very different behavior, and behavior is determined by the nervous system. The nervous system of honeybees must therefore possess a highly developed capacity for change. Unusual for insects, the amount of juvenile hormone increases with the age of the bee. As implied by its name, the amount of juvenile hormone is normally highest in young insects, and decreases during the life of the adult. The increasing levels of juvenile hormone during the adult life of bees may be responsible for the older forager bees being better able to learn than are the young hive-bound bees. Bees send their seniors out into an unfriendly world to cope with the dangerous and challenging tasks outside the nest.



Fig. 8.24 Pollen collection is carried out mostly by bees that specialize in this task. Only about five percent of the foragers bring both pollen and nectar back to the hive

Individual bees do not always take part in all the occupations listed above. For example, only a few bees are needed for the queen's court, or to guard the entrance to the nest; bees that are associated with a specific task perform it often, and their sensitivity to stimuli that evoke the task is critical. Highly sensitive individuals will react even to weak stimuli; insensitive bees will react only to strong stimulation, and be correspondingly less active (► Chap. 10).

A list can be drawn up for the frequency with which individual bees are engaged in various activities, and age and the social environment take on a primary role in determining their actual occupation. Here, too, a genetic component plays a role, but even more influential than the direct genetic contribution is the temperature at which the pupae developed into adult bees. Because the climate of the nest is controlled by the heater bees, whose own behavior and genetic disposition are determined by the conditions under which they developed, a highly complex interaction

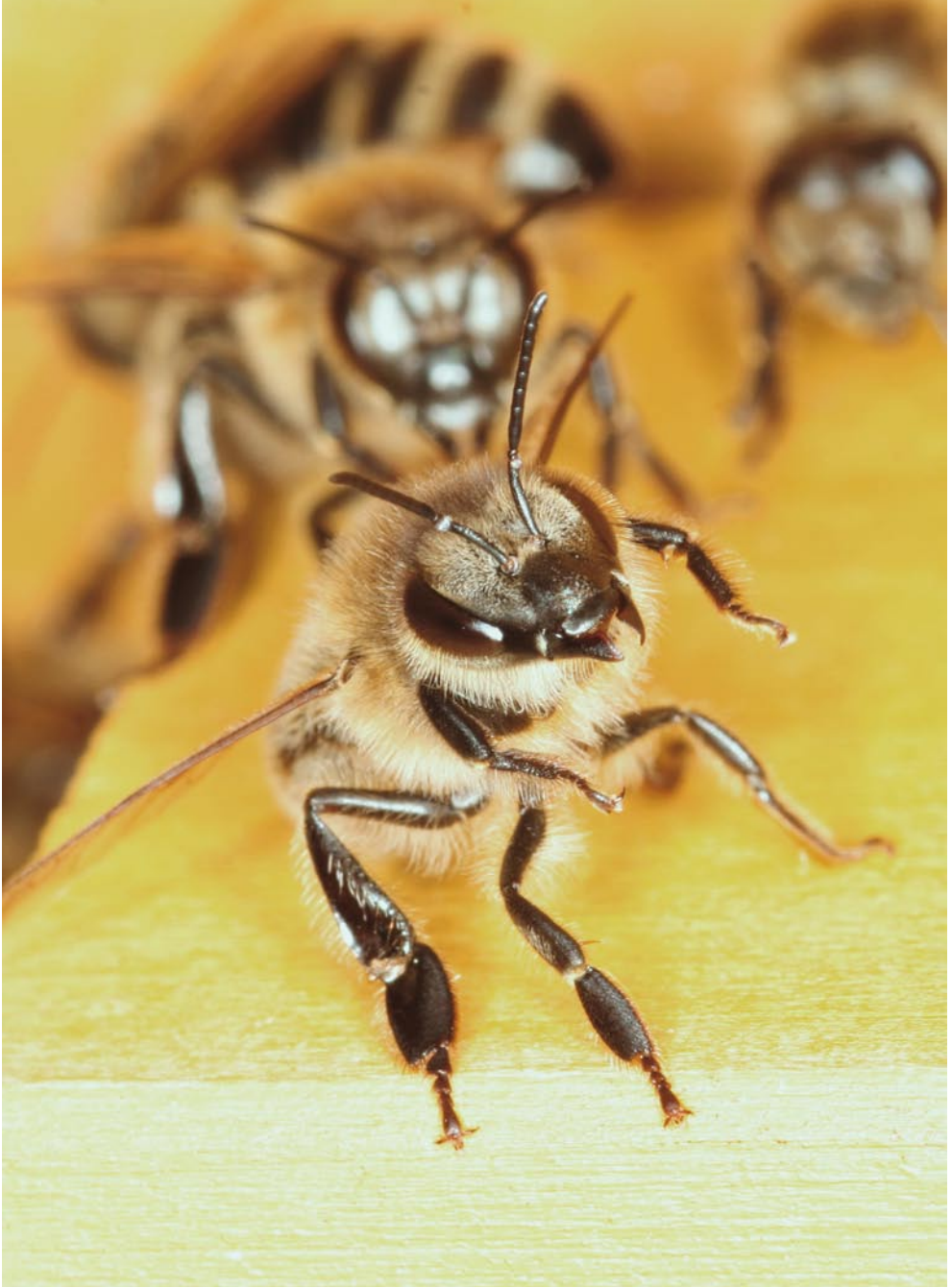


Fig. 8.25 Guard bees deny individuals from other colonies, and all other intruders, entrance to the nest, and will follow any strangers that pass them deep into the nest

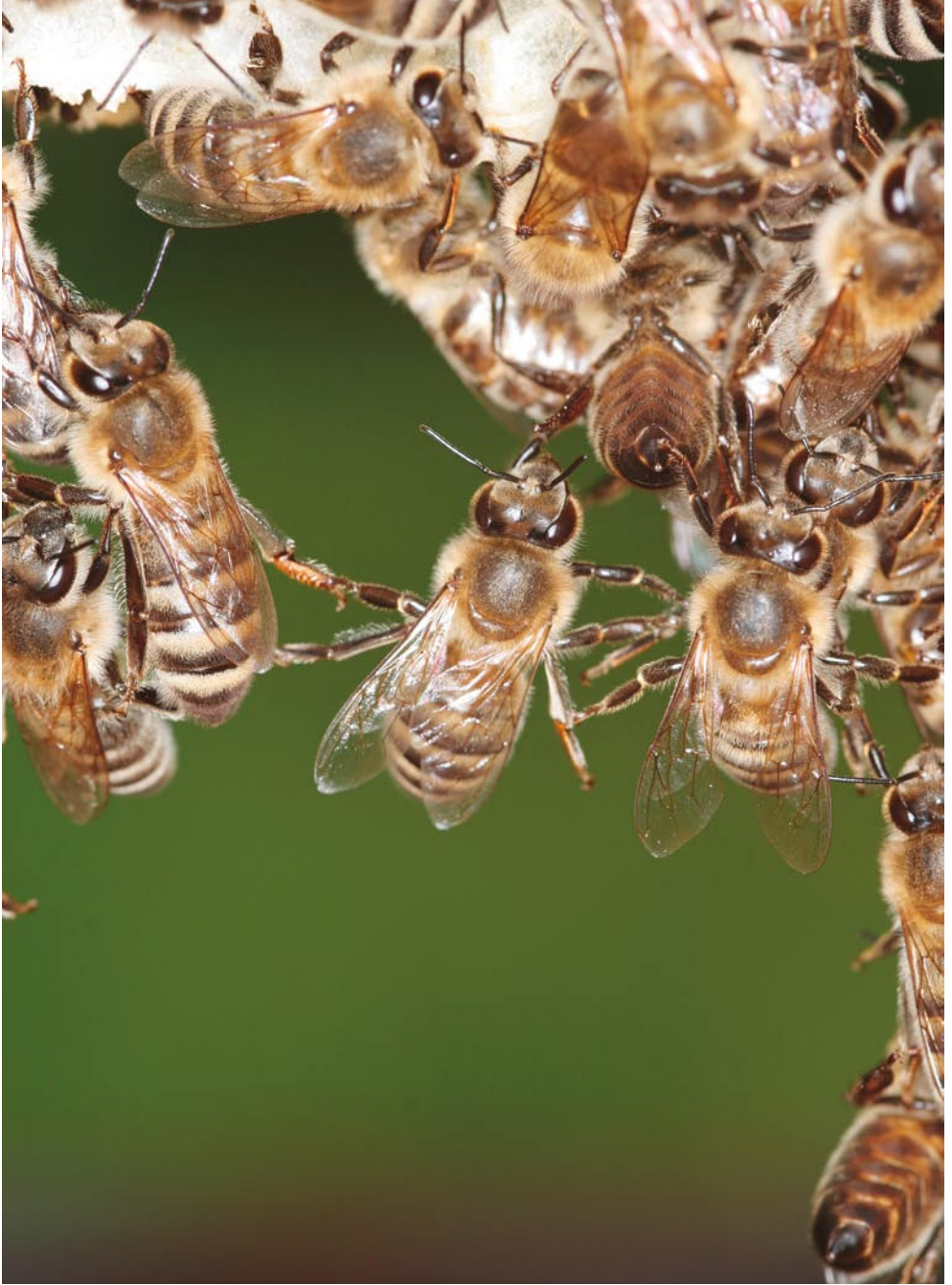


Fig. 8.26 While building combs, bees form living chains, the function of which is completely unknown

of environment and genome provides the colony with a high level of adaptability.

Artificially rearing bee pupae at the different temperatures normally existing in an undisturbed beehive has shown that the frequency of the specific behavioral activities they undertake is dependent on the temperature at which they were raised. Bees that emerge from cooler pupae primarily undertake tasks that differ from those of bees stemming from warm pupae. Communication is critical for the successful foraging of a colony, and bees that can precisely communicate their message turn out to be those that develop at temperatures close to 36°C, the highest that has been found in the brood nest. This group of bees also possesses better learning abilities, and better memories than do their cooler sisters.

The temperature at which bees are raised also influences their lifespan. Adult foragers usually live for about 4 weeks, and are called summer bees by beekeepers. Individuals that survive the winter (winter bees), and are again active in the following season as foragers, can live up to 12 months. Pupae raised at the lowest temperatures in the brood nest are the most likely to become winter bees.

The influence of temperature on metamorphosis is known from many experiments on other insects. Unique to honeybees is that they themselves determine the temperature at which their sisters will develop. The old biological truth that environment and genome together determine the properties of an organism is extended here by honeybees, in their exploitation of a direct feedback between these two shaping forces.





<http://www.springer.com/978-3-540-78727-3>

The Buzz about Bees

Biology of a Superorganism

Tautz, J.

2008, XIV, 284 p., Hardcover

ISBN: 978-3-540-78727-3