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Original article

Short-term effect of different weather conditions upon the behaviour of forager and nurse honey bees (Apis mellifera carnica Pollmann)

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Summary — Nurses and foragers were observed around noon and around midnight during good and bad weather conditions. Foragers were very busy on sunny days with almost no periods of inactivity. More than 60% of the observation period around noon they spent outside the hive. When foragers were prevented from flight by the lack of light or by bad weather, they showed long periods that were defined as unproductive and trophallactic contacts were reduced. Nurses aged 7–9 days showed a less pronounced behavioural difference between day and night but were highly sensitive to weather alterations. They spent less than half of the time nursing the brood during bad weather conditions compared to good weather conditions, although there was no lack of pollen and honey in the colony. The same tendency was observed in other nurse-related activities. They were less often fed by other bees during days with bad weather conditions than during days with good weather conditions. These dramatic changes in behaviour could be observed even on the first day of rain. We presume that the decline of activity is at least partly caused by the diminishing flow of food within a colony.

social behaviour / division of labour / weather / day and night

INTRODUCTION

Division of labour in honey bee colonies is based on age polyethism. Individuals pass through a sequence of behavioural phases during their life, lasting 4–7 weeks during the foraging season. Every stage of a bee's life is characterized by the performance of a

set of tasks (Winston, 1987). They start with the cleaning of cells when they are just emerged, continue with the nursing of brood and later are responsible for the storing of nectar and pollen. The most dangerous task, foraging, is undertaken by the oldest bees in the colony (Rösch, 1925,1930; Lindauer, 1952). This sequence is not fixed, but bees

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of certain ages do typically exhibit consistent sets of tasks. The temporal changes in labour activities of the workers correlate to the spatial shift from the central broodnest to the outside of the hive (Sakagami, 1953; Seeley, 1982).

During days with good weather conditions and during nights nurse bees spend most of their time in the broodnest and show similar behaviour during day and night. Foragers have a more cyclic lifestyle, during daytime they fly out, whereas they show large periods of inactivity during night (Crailsheim et al, 1996). They rest either on the combs, outside of the brood area, or on the hive walls. Prolonged rest in forager bees is accompanied by reduced muscle tone, decreased motility, lowered body temperature and raised reaction threshold. It seems very likely that the rest experienced by forager bees at night is sleep (Kaiser, 1988).

Genetic and environmental components, such as predators, diseases, the amounts and type of brood and stored resources, available forage and certainly the weather conditions all influence what a worker will do at any time (Page and Robinson, 1991). Bees can respond to changing environmental conditions by showing plasticity in age polyethism. Different forms of such plasticity have been identified. Young workers in colonies without foragers compress the period of time devoted to nest activities and become premature foragers (Robinson, 1985; Winston, 1987). A shortage of young bees in the colony causes a retarded behavioural development. Behavioural reversion, from foraging to brood care, was reported in honey bee colonies from which young bees were removed experimentally (Rösch, 1930; Robinson et al, 1992).

Juvenile hormone is involved in the regulation of honey bee age polyethism. Low haemolymph titres are associated with nest tasks, higher titres are associated with foraging (Robinson, 1992). Juvenile hormone titres and rates of biosynthesis decrease in foragers in the autumn as foraging drops and bees become less active. Huang and Robinson (1995) mimicked the seasonal decline in juvenile hormone in foragers by placing a honey bee colony in a cold room for 8 days. Their results suggest that seasonal changes in juvenile hormone are related to changes in temperature.

Increasing temperatures enhance flight activity while decreasing temperatures have the inverse effect (Burrill and Dietz, 1981). A sudden onset of cold weather has a negative influence on the development of honey bee colonies. The consequence of the interruption of the pollen supply is a restricted supply of nurses and a decline in brood production (Dustmann and von der Ohe, 1988).

Little information on the behaviour of honey bees inside the hive in response to weather conditions is available. The objective of this study was to investigate the effect of changing weather conditions on the behaviour of nurses and forager bees during days and the following nights.

MATERIALS AND METHODS

Colony

In the summer of 1996 a colony of honey bees (*Apis mellifera carnica* Pollmann) was established in an observation hive. This hive with glass walls (von Frisch, 1967) containing three vertically arranged combs (22 × 42 cm) was located in a closed dark room on the top floor of the Zoological Department of the Karl-Franzens-University, Graz. The bees found their way out through a transparent plastic tube (Ø 40 mm). The room temperature was kept constant at about 23 °C; red light was used for observation.

A queen excluder was fixed above the lowest comb to prevent the queen from laying eggs in it. Three temperature sensors were installed inside the hive, located in the broodnest, at the honeystores and at the lowest comb that contained food, empty cells and the dance floor. All temperatures were registered at the beginning, in the middle and at the end of each observation period.

The colony consisted of approximately 5000 bees. To keep this number constant, an agerelated cross-section of bees was removed from the colony when needed. This was carried out by taking about one third from the foodstores, one third from the broodnest and the last third from the lowest comb where mainly foragers were located.

To provide a sufficient saccharide influx an artificial food source (1 M sucrose solution) was established in July and August about 20 m from the observation hive.

The broodnest area was marked every day on the glasswalls of the hive to facilitate the location of the bees. The surface area was measured every third day with a special screening frame (Dustmann and Ohe, 1988). Open (min 606 cm², max 1 380 cm²) and sealed brood (min 545 cm², max 4 333 cm²), open (min 220 cm², max 2 106 cm²) and sealed honey and bee bread, and empty cells were always available in the colony.

Every third day 30 bees (baby bees) that had emerged in an incubator (34 °C, 60% rh) during the preceding 12 h were marked with powdered artist's pigment mixed with shellac (von Frisch, 1967) on their abdomen and with a special number code on the dorsal surface of their thorax. Subsequently they were introduced into the observation hive. These bees were observed between 7 and 9 days of age when they served as nurses. Pollen foragers (subsequently referred to as foragers) were identified as bees with pollen loads on their corbicula. They were caught with a small vacuum cleaner in front of the hive when they were returning from foraging, marked in the manner described for nurses, and were released outside the colony so they had to fly back to the observation hive on their own. Only the bees that could be detected with pollen again during the following days were used for observations. Later in the summer, when the marked newly emerged bees became foragers, all bees seen at least once with pollen were observed as foragers. The average age of this latter group was 30 ± 6.8 days. Most of them switched from pollen foraging to nectar foraging and back again.

Observations

The observations were made from the end of May (27th) until the beginning of August (4th)

1996, between 1100 and 1500 hours, as well as between 2200 and 0200 hours. Observations were made either during very good foraging conditions (warm and sunny weather, > 40 bees/min exiting the colony) or very bad foraging conditions (cold and rainy weather, see below) and the following nights. The bees were observed with a magnifying glass and additional red flashlight whenever necessary.

Bees were chosen randomly for observation from the group of marked bees that could be detected at the beginning of the individual observation period (focal samples). Each observation period lasted for 1 h per bee. Time of the start and end of each activity and the location of the bee were immediately entered into a computer program created for these experiments. Duration of activities was calculated as the percentage of the period the bee could be located, and frequencies were calculated as events per hour.

Manipulation of weather conditions

To be independent of actual ambient weather conditions, an artificial rain machine was designed. The tube connecting the hive with the environment led into a box made from plexiglass $(40 \times 15 \times 30 \text{ cm})$. Inside the box the plastic tube was replaced by a wire-lettice tube. Above the tube three distributors of an automatic-watering system (Gardena) were fixed, each with ten outlets and a capacity of 60 mL/min. As water hit the wire-lettice tube it dispersed into fine 'raindrops'. The water collected on the bottom of the box, drained into a container where it was cooled, and was then pumped up again to supply the three distributors. The water was changed every day. During employment of the rain machine the temperature inside the plexiglass box was held constant between 12 and 15 °C. The low temperature was necessary to prevent bees from trying to fly out (Mauermayer, 1954; Burrill and Dietz, 1981). The rain machine was used approximately every second or third day for 24 h at a time. We attempted to allow natural weather conditions to indicate when the rain machine was to be used, so that it was always used when it rained outside (25 observation days with rain, 13 with natural and simulated rain, 12 with only simulated rain). The simulated rain was switched on or off at 0200 hours after the last observation period. The entrance to the environment was shaded by an umbrella.

With all three factors, the exclusion of daylight, the regulation of temperature and the simulation of rain, it was possible to keep the bees from trying to fly out.

The weather in the summer of 1996 was very changeable with short spells of fine weather, and was well suited for this experiment.

For good or bad weather conditions, synonyms like 'sunny days' or 'rainy nights' will be used in the following sections.

Classification of behavioural patterns

Absolutely inactive

The bee sits motionless on the comb surface without any movement of antennae or legs, or remains in an empty cell without any detectable movements of her abdomen (Sakagami, 1953).

Idle

The bee sits and moves her antennae and legs or walks around very slowly with no recognizable intended direction with a velocity of less than 5 mm per second.

Patrolling

The bee walks reasonably purposefully across the comb with a speed of more than 5 mm per second if she has nothing in her way.

Nursing brood

The bee has her head and her thorax inside a cell within the brood area for more than 2 s and her abdomen pulsates. The presence of larvae was investigated afterwards. Each visit to a cell was recorded as one action. Time that the bee spends walking from one cell to another was recorded as patrolling.

Inspecting cells

The bee bends her head over a cell and looks into it for less than 2 s (Sakagami, 1953).

Cleaning cells

The bee remains in a cell and movements of the visible parts of the bee can be observed.

Attending the queen

The bee contacts the queen with her tongue or antennae, or feeds her.

Trophallactic contacts (donating and receiving)

One bee (recipient) puts her tongue between the mandibles of another one (donor) for more than 2 s.

Visiting pollen and honey cells

The bee inserts her head and thorax into a cell containing honey or pollen, during which her abdomen moves.

Manipulating wax

The bee manipulates the wax on brood caps, cells or frames in any way.

Flights

The bee leaves the hive through the plastic tube attached to the entrance and takes off.

Other activities

Other activities include various behaviours such as grooming or dancing.

Statistics

Means and standard deviations are given. The sample size comprised 26–27 observation periods for nurses and foragers, during the day and night and during both good and bad weather conditions for each. Data were tested by the Mann-Whitney U-test, as data could not be proven to be distributed normally. The level of statistical significance was set at P < 0.05.

RESULTS

Temperature (fig 1)

The temperature of the room where the hive was located was kept constant between 22

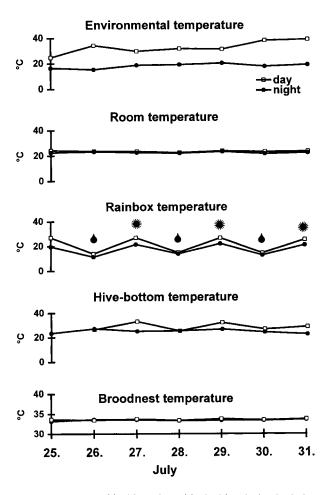


Fig 1. Various temperatures measured inside and outside the hive during both day and night, with 1 week as an example. Temperatures were registered three times within each observation period. Means were calculated from these data (•, bad weather conditions; •, good weather conditions). One data point is missing for the hive-bottom temperature as the thermometer did not work on one occasion.

and 25 °C at all times. The temperature of the broodnest region was regulated by the bees to 33.5 °C (\pm 0.2).

Inside the rainbox, in front of the hive entrance, there was a rise in temperature on days with good weather conditions and a drop during days with bad weather conditions. The same tendency was observed during nights with good or bad weather conditions. Fluctuations in temperature could also be recorded inside the hive in the non-broodnest areas (hive-bottom temperature). The course of the daily temperature curves in the non-broodnest areas is related to the

simulated temperature inside the rainbox. Little variability is seen during nights.

Location in the hive (fig 2)

During all weather conditions nurses spent more than 54% of the observation time in the broodnest area. Despite some variations there was no significant difference between day and night or good and bad weather conditions. They spent most of the remaining time on the honeystores (about 30%), although on rainy nights this time increased up to 45%. Nurses spent only 7% of the observation period on the lowest comb, below the queen excluder, during sunny days and nights and were very seldom seen there during rainy days, and never during rainy nights.

Foragers spent most of their time below the queen excluder, where they were crowded together in clusters and very quiet. Only during sunny days did they become more active. During nights with good or bad weather conditions they were also seen on the honeystores and the broodnest occasionally.

Absolutely inactive (fig 3a, b)

On rainy days nurses spent significantly more time inactive than they did on sunny days. Periods of inactivity during days with good weather conditions are very rare. During nights they were less active under bad than under good weather conditions. There was a significant difference between sunny days and the following nights while there

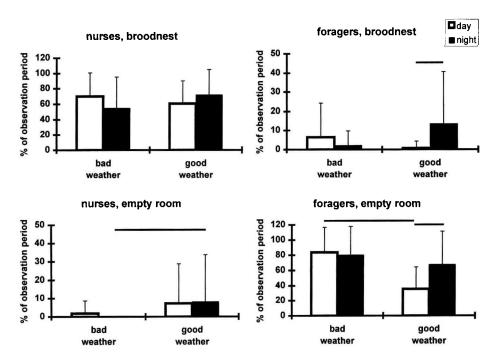


Fig 2. Location of bees observed in various regions of the hive. Length of stay is shown in percentage of the observation period. Means and standard deviations are shown. Horizontal lines above columns indicate a significant difference. The level of statistical significance was set at P < 0.05.

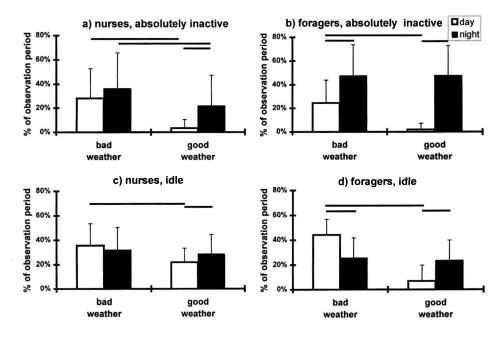


Fig 3. Comparison of inactive and idle activities in nurses and foragers. Means and standard deviations are shown. Horizontal lines above columns indicate a significant difference. The level of statistical significance was set at P < 0.05.

was no difference between rainy days and the following nights.

As expected, foragers were very busy on sunny days with almost no periods of inactivity (fig 3b). They were less active on rainy days and spent almost half of their time inactive during nights under all conditions.

Idle (fig 3c, d)

This behaviour in general was seen more often during days with bad weather conditions than during days with good weather conditions for both nurses and foragers. No significant differences could be found between nights in general. On sunny days nurses and forager bees were less idle than during the following nights. During days

with bad weather conditions foragers showed this behaviour very often.

Nursing brood (fig 4a)

The time nurse bees spent on nursing activities was equal irrespective of the time of day, but it was significantly different according to the weather. During rainy periods nurses spent less than half as much time nursing brood as they did during sunny periods. Foragers were never observed to nurse brood.

Inspecting cells (fig 5)

Independent of the time of day this behaviour was exhibited regularly by nurses

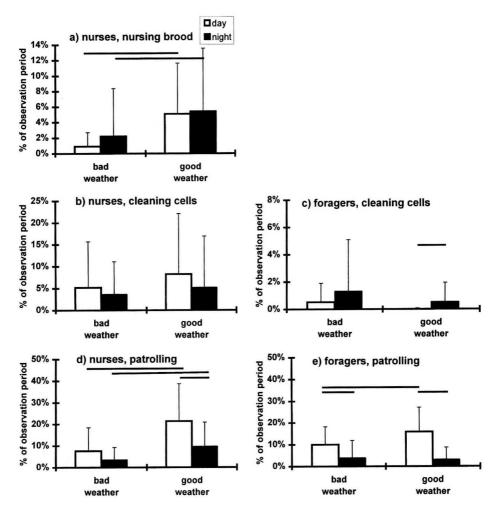


Fig 4. Typical activities of nurses and foragers, means and standard deviations are shown. Horizontal lines above columns indicate a significant difference. The level of statistical significance was set at P < 0.05.

and foragers. Most of the time nurse bees inspected brood cells, sometimes pollen or honey cells; foragers mostly inspected cells on the dancing floor below the queen excluder (data not shown). Significant weather-dependent differences were perceptible only in nurse bees. During bad weather conditions nearly half as many actions per hour were observed compared

to good weather conditions. There was no such difference in forager bees.

Cleaning cells (fig 4b, c)

Nurse bees as well as foragers were observed cleaning cells. There were no significant differences in this behaviour in

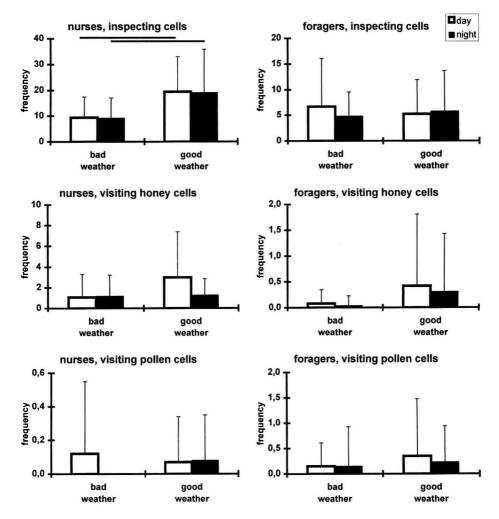


Fig 5. Comparison of food visiting activities and cell inspection. The mean numbers of visited cells per hour and standard deviations are given. Data were shown when at least two bees were observed performing these tasks. Horizontal lines above columns indicate a significant difference. The level of statistical significance was set at P < 0.05.

nurses. Foragers performed this duty to an extremely low extent.

Attending the queen

Nurse bees cared for the queen especially during good weather conditions. During the 53 h of good weather observations they were observed attending the queen eight times during days and ten times during nights. During the 52 observation hours in bad weather conditions this behaviour was performed by the focal bees only three times during days and never during nights (data

not shown). Foragers were never seen to attend the queen.

Patrolling (fig 4d, e)

On sunny days nurse bees showed this behaviour more often than during rainy days. They also did so during nights with good or bad weather conditions. In foragers this behaviour was also observed significantly more often during sunny days than during rainy days, during days the patrolling activity was significantly higher than during both types of nights. The highest patrolling activity in nurses and foragers was always seen during sunny days.

Trophallactic contacts (donating and receiving) (figs 6 and 7)

During sunny days a higher percentage of nurses received food, the transfer lasted longer and the frequency was higher than during rainy days (figs 6a and 7a). No significant differences in the duration could be found during nights with good or bad weather conditions, nevertheless the fequency was lower during good weather nights than good weather days. During days and nights with good and bad weather conditions the donating of nurses was similar (fig 6c) regarding time and percentage of nurses involved, but the fequency of interactions was higher on a good weather night than on a bad weather night (fig 7c).

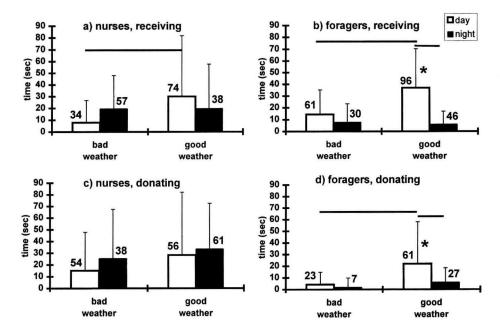


Fig 6. Mean duration of throphallactic activities (donating and receiving) in nurses and foragers. Data from all bees observed are used for calculation, even if they did not show this specific behaviour. Numbers above columns show the percentage of bees performing this task. Horizontal lines above columns indicate a significant difference between the time of day and between the weather conditions, and a pair of asterisks indicates a significant difference between receiving and donating. The level of statistical significance was set at P < 0.05.

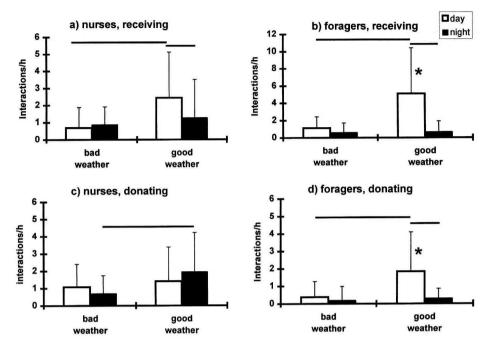


Fig 7. Frequency of trophallactic interactions (donating and receiving) in nurses and foragers. Horizontal lines above columns indicate a significant difference, and a pair of asterisks indicates a significant difference between receiving and donating. The level of statistical significance was set at P < 0.05.

In foragers a significant difference in receiving and donating food between days with good and bad weather conditions was visible. During sunny days the duration of trophallactic activities (both donating and receiving), the frequency of performance (fig 6b, d) and the number of interactions (fig 7b, d) was highest, while similar durations of trophallactic activity and numbers of interactions were recorded on nights with good weather and rainy days and nights. During good weather conditions foragers received food for a significantly longer period and with a higher frequency than they donated food.

Visiting honey and pollen cells (fig 5)

Nurse bees visited honey cells more often during days with good foraging conditions than during rainy days or during nights with good or bad weather conditions. They were very seldom seen in pollen cells.

Manipulating wax

In nurses and foragers there were no significant differences in this behaviour between good and bad weather conditions or between days and nights. In nurses this task was observed between 3.6 and 6.3% of the observation periods, while it was seen in foragers only between 0.2 and 1.3% of the observation periods (data not shown).

Flights

Nurses were flying 0.8% of the observed time during sunny days.

During days with good weather conditions foragers spent 60.2% of the observation periods outside of the hive. In our study 24 out of 27 observed foragers flew out during sunny days, 12 of them also returned during the observation period, six had collected pollen (data not shown). Focal bees did not leave the hive during nights or rainy days.

Other activities

All activities other than those listed above are summarized. Nurses and foragers spent between 15.5 and 24.6% of the observation time on activities that are not described above during days and nights and good and bad weather conditions (data not shown).

DISCUSSION

The temperatures in the rainbox that represent the climate in the environment during rainy periods influenced the temperatures in the non-broodnest regions of the colony. These temperatures in the hive-top (data not shown) and the hive-bottom depended also on the activity of the bees. During sunny days, when there was less inactivity seen in the hive (fig 3a, b), the temperatures rose, and there was a drop in temperature during rainy days. This could be explained by the expansion of the colony at higher temperatures (good weather conditions) and the contraction of the colony at lower temperatures (bad weather conditions) (fig 2). During nights with good or bad weather conditions, there were no correlations to the simulated temperatures inside the rainbox (fig 1), bees were crowded together on or near the broodnest in the center of the colony and showed rather long periods of inactivity. The broodnest temperature was kept very constant independently of the natural or simulated temperature in the rainbox.

The periods of unproductivity (absolutely inactive and idle summed up) were aproximately equal in foragers (about 70% of the observation time) during conditions when flying was not possible. These were days and nights with bad weather and nights with good weather conditions. The two behaviours (absolutely inactive and idle) that contribute to this category do differ. In foragers during nights more inactivity was observed than during days, which is consistent with the observations of Sauer and Kaiser (1995), who established that there is a clear daily fluctuation in the amount of rest. These inactive, sleep-like phases (Sauer and Kaiser, 1995) are not dependent on the activities the bees performed in the course of the previous day. In our experiment they lasted for 48% of the observation period no matter if the bee was able to fly out or had to stay in the hive during a rainy day.

In nurses, inactive periods appear less often during good weather conditions, than during bad weather conditions. These observations are consistent with the observations of Crailsheim et al (in preparation) who demonstrated, using a screening method in the same colony, that the general activity level of workers was lower during bad weather conditions than during good weather conditions and that there was a tendency for younger bees to be more active than older ones.

Nurse-aged bees between 7 and 9 days perform various tasks within a colony. A selection of activities performed by nurses is shown in figure 4a, b, d. Their major duty is the nursing of brood. There is no difference between day and night in this specific behaviour as Crailsheim et al (1996) have already stressed. However, great differences could be observed during good and bad weather conditions as documented in this study.

Dustmann and von der Ohe (1988) have already described the negative impact of a sudden onset of cold weather on the development of a honey bee colony. They presume that the decrease in broodcare is caused by the interruption of the pollen supply and the restricted supply of the nurses. In our experiment there was always enough food, pollen and open honey available in the colony, nevertheless a significant decrease in brood care occurred during bad weather conditions. It should be emphasized that the weather in this study changed almost every day and the bees reacted to these changing weather conditions within a few hours.

Our results are consistent with the observations of Alhaddad and Darchen (1995) who established that the behaviour of foragers and the egg-laying of queens followed the rhythm of the external temperature fluctuations. In our study nurses attending the queen were not observed very often, but a trend towards more actions during good weather conditions was visible.

Our experiment suggests that the activity of the nurses is linked to the influx of food and its passage from bee to bee. Nurses receive food more often and over a longer period on days with good weather conditions than on days with bad weather conditions (figs 6a and 7a). The frequency of donating to other bees is only significantly lower during bad weather nights than during good weather nights (fig 7c). It seems that the flow of nectar diminishes after only one night and causes the decline in nursing activity even on the first day with bad weather conditions and the following night.

Kolmes (1985) found that worker bees experiencing a season of poor nectar and pollen supplies carried out fewer acts related to the acquisition and storage of materials in the hive than did worker bees living in a richer environment. Our experiment showed that even after 1 day of an interruption of nectar and pollen income there was a significant decrease in typical nurse activities, while the unproductive periods increased. These changes in activities may be even

more dramatic during longer periods of bad weather conditions.

When foragers were confined for 6 or 9 days by simulation of rain a delay in caste ontogeny occurred in the experiments of Huang and Robinson (1996). No changes appeared after 3 days. Since our simulated weather conditions changed nearly every day we presume there was no such effect on the division of labour within our observation colony.

Free et al (1989) observed that larvae that were isolated for a while received many more visits from nurses than a control group. When a colony is disturbed by moderate alternations, bees may work harder at some tasks but do not significantly alter median ages of task performance for many behavioral patterns (Kolmes and Winston, 1988). It might be predicted that nurse bees try to compensate for the interruption in the food flow during the following period of good foraging conditions by intensifying their tasks. Thus a reduction of brood care during a short period of low food income as we observed might not harm the colony.

Within a honey bee colony food is transmitted between adult workers. Adult workers donate food to larvae, to drones and to the queen (Ribbands, 1953). Nixon and Ribbands (1952) demonstrated with radioactive tracer methods that a small quantity of food collected by foragers can become widely distributed among the members of a colony within a few hours. In our experiment trophallactic activities of foragers, donating and receiving food, were observed more often during days with good foraging conditions than during days with bad weather conditions. During good weather conditions trophallactic activities occur more often during days than during nights. In nurses the receiving of food was also observed more often during sunny days than during rainy days. It could be supposed that the flow of nectar passes through the whole colony and limits, when not existing, the trophallaxis of both foragers and nurses. This lack of a pronounced difference in nurses might depend on the varying nature of the donated food. Nurses were shown not only to donate carbohydrates but also protein-rich jelly (Crailsheim, 1992).

When we observed bees visiting honey or pollen cells it could not be established with certainty if a bee was really consuming honey or pollen, or just handling it. As the abdomen of the bee was moving we assumed that the bee was manipulating or eating honey or pollen in some way. The time nurse bees spent inside a cell varied from a few seconds to more than half an hour, which results in high standard deviations (data not shown). They were observed visiting honey cells very often, especially during days with good weather conditions (fig 5). Foragers were seen only occasionally in honey cells. If their visiting was for eating, their low frequency could be compensated by the frequent receipt of food by trophallaxis (fig 6).

Lorenz and Crailsheim (1994) described the movement of a pollen bolus through the gastrointestinal tract of honey bees. They found that the pollen passage to the end of the midgut takes about half a day indicating non-frequent pollen consumptions. These results are consistent with our observations where 'visiting of pollen cells' was recorded very seldom in both age groups (fig 5). Pollen then seems to be consumed in rather large amounts.

Our data show that even a very short duration of bad weather has significant results on the honey bee colony. Both age groups of bees increased their unproductive periods, possibly as an early adaptation to times of need. The trophallactic flow was reduced, and the broodcare activities were decreased. It can be presumed that the consequence of longer bad weather periods is even more dramatic. Further experimentation is required to quantify the effects of longer periods of bad weather on the devel-

opment of honey bee colonies and the benefit of management practices that would prevent economic losses due to inclement weather

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Résumé — Effet à court terme des conditions météorologiques sur le comportement des abeilles butineuses et des nourrices (Apis mellifera carnica Pollmann). Au cours de l'été 1996 des nourrices et des butineuses ont été observées entre 11 h et 15 h et entre 22 h et 2 h. Les observations ont eu lieu par beau temps et mauvais temps. Pour ne pas être totalement dépendant des conditions météorologiques réelles, un dispositif expérimental a été conçu, qui arrêtait la lumière du jour, régulait la température et simulait la pluie de façon à empêcher les abeilles de s'envoler. Les abeilles ont été classées comme nourrices en fonction de leur âge (7–9 j), en butineuses d'après leur activité. Des abeilles naissantes ont été choisies au hasard, marquées avec un code comprenant une couleur et un nombre et observées durant une heure. Toutes leurs activités ont été enregistrées immédiatement sur ordinateur.

Les butineuses sont restées le plus souvent dans la partie inférieure de la ruche d'observation à trois cadres (fig 2). Les jours où il faisait beau, elles passaient 60,2 % du temps d'observation en vols de butinage. Ces jours-là, elles étaient aussi très actives dans la ruche alors que, les jours de mauvais temps et la nuit (que le temps fût beau ou mauvais), elles avaient de longues phases d'inactivité (fig 3). Les nourrices, qui se tenaient habituellement près du nid à cou-

vain, étaient plus souvent près du trou de vol les jours de beau temps (7 % du temps d'observation) que les jours de mauvais temps (1,8 %). On n'a pas observé de différences dans le comportement des nourrices entre la nuit et le jour, en revanche de fortes différences étaient visibles entre les jours de beau temps et de mauvais temps. Par beau temps les nourrices passaient 5 % du temps d'observation (jour + nuit) à s'occuper du couvain, par mauvais temps seulement 0.9 % le jour et 2.2 % la nuit (fig 4). Des tendances semblables se sont dégagées pour les autres activités des nourrices, telles que le patrouillage, l'inspection et le nettoyage des cellules (figs 4 et 5).

Cette étude a permis de montrer que les conditions météorologiques exercent une forte influence sur le comportement non seulement des butineuses, mais aussi des nourrices.

comportement social / division travail / condition météorologique / jour et nuit

Zusammenfassung — Der Einfluß von kurzfristigen Wetteränderungen auf das Verhalten von Sammlerinnen und Ammen bei der Honigbiene (Apis mellifera carnica Pollmann). Im Sommer des Jahres 1996 wurden Ammen und Sammlerinnen rund um Mittag und rund um Mitternacht beobachtet. Die Beobachtungen erfolgten jeweils an Tagen mit guten und an Tagen mit schlechten Wetterbedingungen. Um nicht gänzlich von den tatsächlich herrschenden Wetterbedingungen abhängig zu sein, wurde Schlechtwetter mit Hilfe einer speziellen Versuchseinrichtung simuliert. Ausschluß von Tageslicht im Stock, die Regulation der Temperatur und Simulation von Regen ermöglichten es, die Bienen vom Ausfliegen abzuhalten.

Ammen wurden nach ihrem Alter (7–9 d) definiert, Sammlerinnen nach ihrer Tätigkeit. Die beim Schlüpfen mit einem

bestimmten Farben und Nummern Code markierten Bienen wurden zufällig ausgewählt und jeweils eine Stunde lang beobachtet. Alle ihre Tätigkeiten wurden sofort mit Hilfe eines Computers aufgezeichnet.

Sammlerinnen hielten sich meist in den unteren Bereichen des drei Waben-Beobachtungsstockes auf. Schöne Tage nützten sie zu ausgedehnten Sammelflügen, die rund 60% der beobachteten Zeit in Anspruch nahmen. Ebenso waren Sammlerinnen an schönen Tagen innerhalb des Stockes sehr aktiv während sie bei schlechtem Wetter und in den Nächten (Schön- und Schlechtwetter) lange inaktive Phasen zeigten.

Ammenbienen, die sich üblicherweise im Bereich des Brutnestes aufhalten, waren bei Schönwetter länger (7% der Beobachtungszeit) nahe dem Ausflugloch anzutreffen als bei Schlechtwetter (1.8%). Im Verhalten der Ammen konnten keine Unterschiede zwischen Tag und Nacht beobachtet werden, große Unterschiede im Verhalten wurden allerdings bei guten und schlechten Wetterbedingungen sichtbar. Bei Schönwetter verbrachten Ammen 5% der beobachteten Zeit (Tag und Nacht) mit Brutpflege, bei Schlechtwetter jedoch nur 0,9% bei Tag und 2.2% bei Nacht. Ähnliche Tendenzen konnten bei anderen von Ammen ausgeführten Tätigkeiten, wie patrouillieren, inspizieren von Zellen oder putzen von Zellen festgestellt werden.

Mit Hilfe dieses Experimentes konnte gezeigt werden, daß unterschiedliche Wetterbedingungen nicht nur Sammlerinnen sondern auch Ammen in ihrem Verhalten stark beeinflussen.

Sozialverhalten / Arbeitsverteilung / Wetter / Tag und Nacht

REFERENCES

Alhaddad S, Darchen B (1995) Influence des conditions meterologiques sur l'alimentation et la ponte

- d'une reine d'abeilles. CR Acad Sci Paris, Science de la vie/Life sciences 318, 245-248
- Burrill RM, Dietz A (1981) The response of honeybees to variations in solar radiation and temperature. *Apidologie* 12, 319-32
- Crailsheim K (1992) The flow of jelly within a honeybee colony. *J Comp Physiol B* 162, 681-689
- Crailsheim K, Hrassnigg N, Stabentheiner A (1996) Diurnal behavioural differences in forager and nurse honey bees (Apis mellifera carnica Pollm). Apidologie 27, 235-244
- Dustmann JH, Ohe W von der (1988) Einfluß von Kälteeinbrüchen auf die Frühjahrsentwicklung von Bienenvölkern (Apis mellifera L). *Apidologie* 19, 245-254
- Free JB, Freguson AW, Simpkins JR (1989) The effect of different periods of brood isolation on subsequent brood-cell visits by worker honeybees (*Apis mellifera* L). J Apic Res 28, 22-25
- Frisch K von (1967) The Dance Language and Orientation of Bees. Harvard Univ Press, Cambridge, MA, USA
- Huang ZY, Robinson GE (1995) Seasonal changes in juvenile hormone titers and rates of biosynthesis in honey bees. J Comp Physiol B Biochem System Environ Physiol 165, 18-28
- Huang ZY, Robinson GE (1996) Regulation of honey bee division of labor by colony age demography. *Behav Ecol Sociobiol* 39, 147-158
- Kaiser W (1988) Busy bees need rest, too. *J Comp Physiol A* 163, 565-584
- Kolmes SA (1985) A quantitative study of the division of labour among worker honey bees. Z Tierpsychol 68, 287-302
- Kolmes SA, Winston ML (1988) Division of labour among worker honey bees in demographically manipulated colonies. *Insectes Soc* 35, 262-270
- Lindauer M (1952) Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Z vergl Physiol 34, 299-345
- Lorenz W, Crailsheim K (1994) Transport of solids in the gastrointestinal tract of honeybees (*Apis mellifera* L). *Mitt Dtsch Ges Allg Angew Entomol* 9, 313-315
- Mauermayer G (1954) Untersuchungen über die Beziehung zwischen Arbeitsleistung und Lebens-

- dauer bei Arbeiterinnen der Honigbienen. Arch Bienenkd 31
- Nixon HL, Ribbands CR (1952) Food transmission within a honeybee community. *Proc R Soc B* 140, 43-50
- Page RE, Robinson GE (1991) The genetics of division of labour in honey bee colonies. Adv Insect Physiol 23, 117-169
- Ribbands CR (1953) The Behaviour and Social Life of Honey Bees. Bee Research Association, London
- Robinson GE (1985) Effects of a juvenile hormone analogue on honey bee behaviour and alarm pheromone production. *J Insect Physiol* 31, 277-282
- Robinson GE (1992) Regulation of division of labour in insect societies. *Annu Rev Entomol* 37, 637-65
- Robinson GE, Page RE, Strambi C, Strambi A (1992) Colony integration in honey bees: mechanisms of behavioural reversion. *Ethology* 90, 336-348
- Rösch GA (1925) Untersuchungen über die Arbeitsteilung im Bienenstaat, 1. Teil: Die Tätigkeiten im normalen Bienenstaate und ihre Beziehung zum Alter der Arbeitsbienen. Z Vergl Physiol 2, 571-631
- Rösch GA (1930) Untersuchungen über die Arbeitsteilung im Bienenstaat, 2. Teil: Die Tätigkeit der Arbeitsbienen unter experimentell veränderten Bedingungen. Z Vergl Physiol 12, 1-70
- Sakagami SF (1953) Untersuchungen über die Arbeitsteilung in einem Zwergvolk der Honigbiene. *Jap J Zool*, 11 (1), 117-185
- Sauer S, Kaiser W (1995) Pollen foragers of the honey bee (Apis mellifera carnica L) rest in the hive at night. In: Learning and Memory, Proc 23rd (II) Göttingen Neurobiology Conference (N Elsner, R Menzel, eds), Thieme, Stuttgart, Germany, 253
- Sauer S, Kaiser W (1996) The nocturnal behaviour of pollen forager honey bees (Apis mellifera carnica) in an observation hive. Apidologie 27, 317-318
- Seeley TD (1982) Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav Ecol Sociobiol* 11, 287-293
- Winston ML (1987) *The Biology of the Honey Bee.* Harvard Univ Press, Cambridge, MA, USA