Insectes soc. 46 (1999) 34–40
0020-1812/99/010034-07 $ 1.50+0.20/0

Insectes Sociaux

Research article

The behaviour of drifted nurse honey bees

K.J. Pfeiffer and K. Crailsheim *

Institut für Zoologie, Karl-Franzens-Universität Graz, Universitätsplatz 2, A-8010 Graz, Austria, e-mail: crailsheim@kfunigraz.ac.at

Received 16 December 1997; revised 10 March 1998; accepted 19 March 1998.

Summary. The behavioural patterns of nurse bees that had drifted into a neighbouring colony differed from those of non-drifted sister bees of the same age living in the same colony. Drifted bees spent significantly more time inactive and performed brood care tasks less frequently. Our results show that drifted bees contribute less to the benefit of a colony but have no lower individual benefit, and partly explain a prolonged longevity of drifted bees.

Key words: Apidae, nurse honey bees, drifting, behaviour.

Introduction

Drifting of honeybees is influenced by many environmental and apiary layout factors (Betts, 1932; Free, 1958; Free and Spencer-Booth, 1961; Cooke, 1962; Jay, 1965, 1966a, 1966b, 1968; Jay and Dixon, 1988). If no suitable steps to reduce drifting are carried out, drifting may lead to spread of disease, loss of bees to other colonies and reduced honey production (Goodwin et al., 1994; Jay, 1969a, b). A model by Pfeiffer and Crailsheim (1998) showed that the population in an apiary consisting of unmarked hives standing in a row can consist of up to $42 \pm 6\%$ drifted bees.

In a comparison of bees that had drifted by their 9th day of life to bees that had not drifted, significantly more of the drifted bees survived until their 25th day of life (Pfeiffer and Crailsheim, 1996). Major factors that have been shown to influence life expectancy of worker bees are brood rearing (Woyke, 1984; Harbo, 1993) and foraging effort (Mauermayer, 1954; Neukirch, 1982; Wille et al., 1985). Worker mortality is also affected by colony energy requirements and colony growth (Beauchamp, 1992). Thus there are two hypotheses regarding work load influencing the life expectancy of honeybees, one associated with brood rearing and the other one with foraging. These hypotheses involve two taskgroups within the system of division of labour (Rösch, 1925, 1930; Lindauer, 1952; Sakagami, 1953; Seeley, 1982) in the colony: the nurse bees and the foragers. We are using the term "nurse bees" in a broad sense as the bees can be rather flexible in their behaviours during the pre-10 day period (Winston and Nelson Punnett, 1982).

The aims of our study were to compare behavioural patterns of drifted and non-drifted bees and to investigate whether there is reduced activity by drifted bees during their nurse period that could cause higher life expectancy.

Materials and methods

Four commercial colonies (each consisting of approximately 15000–20000 bees) of the same colour and height were set up in a row with entrances facing south. A two-frame observation hive was provided and equipped with a front-blind of the same colour and size as the commercial bee hives. The observation hive was put in the middle of the row so that it was the central hive. All five colonies were queenright and well provided with food at all times during the experiments.

A cohort of newly emerged bees, all daughters of a single queen which was not related to the queen of the observation hive, were marked individually and divided into two groups. One group (5%) was introduced into the observation hive (between 20 and 40 bees) – these were the non-drifted bees – and the other part (95%) into several neighbouring colonies (approximately 200 bees per colony). The marked bees that drifted into the observation colony during the following 6 days constituted the group of drifted bees. A third (control) group of newly emerged bees (20–40 individuals) were taken from the observation colony, marked and re-introduced into the observation colony.

One individual bee from each group was observed from its 7th to its 9th day of life in half-hour periods for 2 hours per day. All observed activities of the bees were recorded with a computer program. Recordings were usually started at 9:00 a.m. For each half hour a bee of a different group was observed. For example, a non-drifted bee was observed for the first half hour, then a drifted bee in the next half hour and a control bee for the next. This cycle was repeated three times per day, so that four observation periods of each bee were recorded per day. Observations ended at 4:00 p.m. On the following observation day the sequence of observing bees was altered, starting for example with the control bee followed by the non-drifted bee and then the drifted bee, to compensate for possible circadian effects.

* *Author for correspondence*.

Seven series of three-day observations were made between June and July. Normally only one bee of each of the three groups was observed in one series. Only if a focus bee was lost during an observation series it was replaced by another one (drifted bees: 5 times; non-drifted bees: 2 times; control bees: 2 times). Only individual bees that underwent at least 6 observation periods were included in the data pool and the analysis. In total 61 observation periods of drifted bees, 77 of non-drifted bees and 78 of control bees were analysed. The total number of bees was 20.

The recorded behavioural patterns of the bees were analysed with a computer program specially designed for these experiments. Activities were analysed singly and also as pooled into groups. Results were expressed as percentage of total observation time for some behavioural categories (inactivity, brood care and other behavioural patterns), and as percentage of the time a bee was active in the hive for other categories (trophallactic contacts, antennal contacts, contacting the queen and aggressive behaviour). Results are given with the standard error of the mean. Because our data are not distributed normally we used the Mann-Whitney U-test for statistical calculations. Significance was set at the $p < 0.05$ level.

The following list shows the observed behavioural patterns and their grouping for analysis.

Location

The time spent on the brood nest was recorded, as well as the time spent in other areas of the hive.

Inactivity

We classified as inactivity time spent motionless in an empty cell, on the comb or on another part of the hive and time spent idle. A bee was considered idle if she was standing and moving antennae or legs or was walking with an estimated velocity of less than 5 mm per second (Crailsheim et al., 1996).

Brood care

Brood care was defined to include nursing brood, inspecting a broodcell and patrolling on the broodnest. A bee was recorded as nursing brood if she had her head inside a broodcell for more than 5 s and she was not motionless (Crailsheim et al., 1996). Broodcell inspection was defined as inserting the head into a brood cell for less than 5 s. Patrolling was recorded when the bee was walking across the comb with an estimated velocity of 5–10 mm per second (Crailsheim et al., 1996).

Trophallactic contacts

In trophallactic contacts, donating food was distinguished from receiving food. A food recipient was identified as the bee with its tongue between the mandibles of a donor for more than 2 s (Crailsheim et al., 1996).

Antennal contacts

Active antennal contacts were distinguished from passive ones. In an active contact, the focus bee was touching another bee with her antennae. In a passive contact, the focus bee was being touched by the antennae of another bee on any part of the body. This category did not include DVAV dances, contacts to the queen and antennal contacts during trophallaxis.

Contacting the queen

This category included contacting the queen with antennae or licking the queen's body.

Aggressive behaviour

The focus bee was attacking another worker or drone, or was being attacked by another worker bee.

Other behavioural patterns

Grooming behaviour was distinguished into self grooming, being groomed by other workers, grooming other workers or by performing grooming dances. When visiting honey and pollen cells a bee inserts its head into a cell containing honey and pollen for more than 2 s (Crailsheim et al., 1996). A bee visiting honey and pollen cells was probably consuming food but may have been thickening honey or producing bee bread.

Other behavioural patterns are described briefly. Begging for food: a bee was moving its tongue towards the mandibles of another bee combined with repeated antennal contacts; following dance: when the focus bee was following a bee performing a round or waggle dance; fast running: the focus bee was moving across the comb or other hive parts with more than 10 mm/s; flying: a bee leaves the hive for an orientation or foraging flight.

The following activities listed below were observed but not described in further detail: patrolling outside the broodnest area, inspecting cells outside the broodnest area, cleaning cells, fanning wings, removing debris, manipulating wax, mouthing wax, cementing chinks with propolis and chewing on wooden hive parts.

Results

Location

The three groups did not differ significantly with respect to the time spent in the broodnest area. Drifted bees were present in the broodnest area for $41.7 \pm 4.5\%$ of the total observed time, non-drifted bees for $44.0 \pm 3.5\%$ of the total observed time, and control bees for $51.7 \pm 4.0\%$ (data not further shown).

Inactivity

The drifted bees were inactive significantly more of the time than the non-drifted bees. Figure 1 shows the results for the behaviour pattern "inactive," made up of the behaviours "motionless on comb," "motionless in empty cell" and "idle." Idle time was the main component of inactive time, followed by time spent motionless on comb. Drifted bees were motionless on comb significantly more than non-drifted bees were.

Brood care

Drifted bees spent a significantly lower percentage of their time engaged in brood care than did non-drifted bees (Fig. 2), but there were no significant differences between the groups in the single activities brood rearing, broodcell inspection and patrolling on the broodnest.

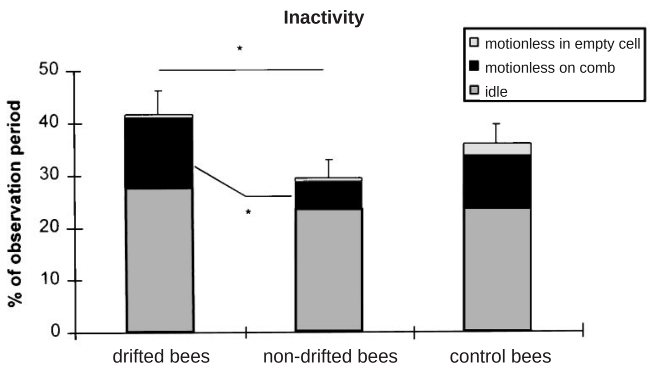

Figure 1. Time spent in inactivity by the observed bees, as a percentage of the total observation period. The three behaviours we defined as inactive are shown as stacked columns. Lines with asterisks between bars or parts of them indicate significance. "Idle" means that a bee was sitting and moving its antennae or legs, or was walking with a velocity of less than 5 mm per second

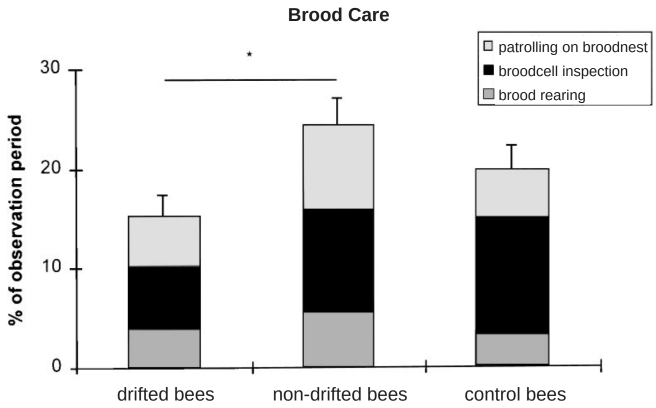

Figure 2. Time spent in brood care activities, as percentage of the total observation period. Lines with asterisks between bars indicate significance

Trophallactic contacts

No significant differences were found in time spent donating and receiving food between the groups, although percentages for drifted bees and control bees were higher than for non-drifted bees (Fig. 3). Control bees fed other bees significantly more often than they received food.

Antennal contacts

The three groups did not differ significantly in time spent in antennal contacts. In each group more active antennal contacts were observed than passive contacts (Fig. 4).

Contacting the queen

The three groups did not differ significantly in time spent in queen contacts. In each group such contacts were infrequent. For drifted bees a total of six contacts with the queen were observed (only $0.41 \pm 0.22\%$ of active time), for control bees five contacts ($0.35 \pm 0.19\%$) and for non-drifted bees just two ($0.09 \pm 0.07\%$) (data not further shown).

Aggressive behaviour

Drifted bees were found to be slightly more aggressive than non-drifted bees and bees of the control group. During $0.22 \pm 0.14\%$ of their active time the drifted bees showed aggressive behaviour against other workers. Both non-drifted bees and control bees were aggressive less than 0.01% of their active time. The difference between drifted bees and bees of the control group was significant. All observed aggression involved workers, except for a single short attack against a drone by a drifted bee.

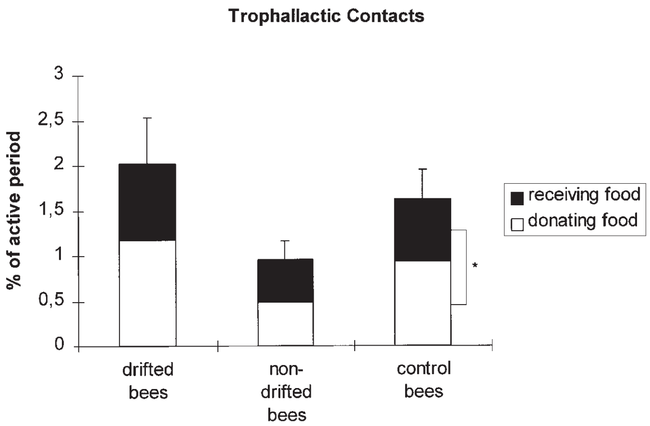

Figure 3. Time spent in trophallactic contacts, as percentage of the active period of the observed bees. No statistical differences between the three groups were found. The significant difference among control bees between donating food and receiving food was not of importance in this study

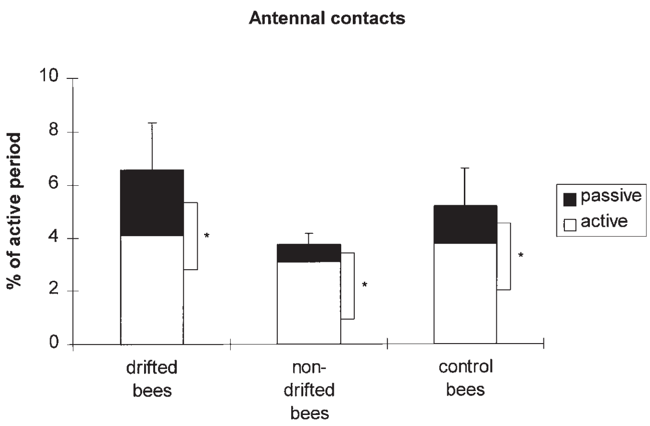

Figure 4. Time spent in antennal contacts, as percentage of the active period of the observed bees. There were no differences between drifted, non-drifted and control bees, but all groups contacted other bees more frequently than they were contacted by other bees

During all observations only one attack against a focus bee was observed. A drifted bee was attacked for 10 seconds by another worker and then was left alone (data not further shown).

Other behavioural patterns

A list of these patterns (for details see Materials and methods) in percentages of the total observation time of the bees can be seen in Table 1. There were no significant differences between drifted and non-drifted bees in any of these behavioural patterns. Significant differences between drifted bees and control bees were found in the following activities visiting honey cells, patrolling outside broodnest area, cell inspection outside broodnest area, fanning wings and fast running. Except of the last activity drifted bees performed these activities at a higher level than control bees. Further significant differences were found between non-drifted bees and control bees in the activities visiting honey cells and patrolling outside the broodnest area. In both cases values were higher in non-drifted bees. No significant differences between the three groups were found in any of the other patterns.

We did not observe any instances of receiving nectar from foragers and subsequent nectar storing, nor did we observed packing pollen or foraging activities by any focus bees.

Discussion

In the present study, drifted nurse bees aged from 7 to 9 days spent significantly more of their time inactive compared to non-drifted sister bees of the same age (Fig. 1). This result, together with the higher survival rate of drifted bees (Pfeiffer and Crailsheim, 1996), corresponds with the results of Schmid-Hempel and Wolf (1988), who found a significant positive correlation between the average amount of time a bee spent inactive in the hive and its life span. However, it is true that we cannot be sure that bees we recorded as inactive were not in fact performing a task such as heating an area of the hive.

Drifted bees were engaged in the set of behavioural tasks we defined as brood care significantly less often than non-drifted bees (Fig. 2). Although Harbo (1986) found that a higher rate of brood rearing did not shorten the life span of workers, he acknowledged that his 22 day test period may have been too short to detect a shortened life span of the bees. In fact, in another study Harbo (1993) showed that brood rearing is somewhat associated with reduced survival of adult bees but that these differences are often not detected when a population is measured immediately after producing one cycle of brood. Woyke (1984) found a negative correlation between total numbers of brood and the length of worker life. He also found a high negative correlation between average brood production per worker and average worker life span, and he concluded that the length of life depends more upon

Table 1. List of behavioural patterns. Means and standard errors on percentage of the total observation time. Arrows indicate significance

Activity	% of total time		
	drifted bees	non drifted bees	control bees
Self grooming	0.24 ± 1.31	10.6 ± 1.34	11.58 ± 1.71
Grooming worker	0.07 ± 0.05	0.04 ± 0.03	0.19 ± 0.19
Being groomed	0.26 ± 0.16	0.6 ± 0.29	0.89 ± 0.47
Grooming dance	0.09 ± 0.06	0.12 ± 0.08	0.01 ± 0.01
Begging for food	0.004 ± 0.003	0.03 ± 0.01	0.003 ± 0.002
Following dance	0.01 ± 0.01	0.03 ± 0.02	0.003 ± 0.003
Fast running	1.25 ± 1.25	1.71 ± 0.83	1.91 ± 0.86
Flying	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.16
Visiting honey cells	2.27 ± 0.98	2.52 ± 0.91 ↔	0.51 ± 0.34
Visiting pollen cells	2.42 ± 0.78	2.21 ± 0.64	1,86 ± 0.57
Patrolling outside Broodnest	3.91 ± 0.67	6.50 ± 1.05 ↔	2.28 ± 0.47
Inspecting cells outside Broodnest	5.48 ± 0.94	3.84 ± 0.65	3.19 ± 0.75
Cleaning cells	0.56 ± 0.44	0.41 ± 0.40	0.69 ± 0.52
Removing debris	0.00 ± 0.00	0.05 ± 0.05	0.00 ± 0.00
Fanning wings	0.34 ± 0.14	0.38 ± 0.19	0.13 ± 0.09
Manipulating wax	1.68 ± 1.08	1.38 ± 0.90	0.23 ± 0.12
Mouthing wax	5.63 ± 1.79	6.56 ± 1.52	7.7 ± 1.53
Cementing chinks	0.00 ± 0.00	0.49 ± 0.31	0.42 ± 0.33
Chewing on hive	0.88 ± 0.47	0.77 ± 0.67	1.17 ± 0.81

larva-worker ratio than upon absolute numbers of brood. Fukuda and Sekiguchi (1966) reported a negative correlation between number of brood cells and life expectancy, and Hassanein and El-Banby (1960) found that the longevity of different races of bees decreases with the brood-rearing rate. These results, together with those we present here, showing that drifted bees engage significantly less often in brood care tasks than their non-drifted sisters, and the findings of Pfeiffer and Crailsheim (1996), who found that more drifted bees than non-drifted bees survived in a 25 day period in summer, indicate that brood care is at least partly involved in life span of adult bees.

Another interesting finding is that drifted and non-drifted bees differed significantly in the time spent motionless on comb (with immobile antennae). Although we cannot directly compare our results with observations of a sleep-like state by Kaiser (1988, 1995), Kaiser and Steiner-Kaiser (1988) and Sauer and Kaiser (1995), we suppose that drifted bees probably 'sleep' more than non-drifted bees, and it would be interesting to investigate this hypothesis further.

There are many possible reasons why drifted bees differ from their non-drifted sister bees in some but not in all tasks. One may be that drifted bees have problems in orientating and adapting to the new environment, possibly because of different odours than those of the colonies where they spent the first days after emergence. Breed and Stiller (1992) found that young bees learn the odour of comb wax within 24 hours after emergence and maintain this knowledge for 5 days even without continuous exposure to the comb. However, prolonged exposure to new cues can modify the behavioural responses of the bees. It may be that the bees in our studies, although primarily adapted to their natal comb, learned the odour of the colonies into which they were experimentally introduced. Thus, the bees that drifted into the observation hive between their 4th and 6th day of life encountered unfamiliar odours, while the non-drifted bees in the same hive probably had become well adapted to those odours. The fact that drifted bees showed slightly higher aggressive behaviour against workers than the bees of the two other groups (significant compared to the control bees) is probably due to this circumstance.

Another possible reason why drifted bees showed different patterns of behaviour than their non-drifted sisters may be that the drifted bees had attained a different physiological age, which means that they probably already had shifted from nurse bees to food storers. We have no proof whether this was true or not, only an indication that the drifted bees were still members of the broodnest caste (Seeley, 1982), because they were performing the identical tasks as the bees of the two other groups, although at lower frequencies. Further, because the drifted bees were not performing food storing activities, we can exclude the possibility that they were food storers rather than nurses, and we did not observe them to take trips outside the hive (Table 1), so we can be sure that they were not yet foragers. Winston and Nelson Punnett (1982) conclude that honeybee workers perform tasks in a temporal sequence during their lifetimes, that the occurrence and timing of these tasks are highly variable, and that for some tasks the ages of task performance may be more predetermined genetically than for others. Although our focus bees undoubtedly belonged to several patrilines because they originated from a naturally mated queen, there seems to be little chance that the drifted bees belonged to one or more special patrilines that could have caused them to spend less time performing certain duties than the non-drifted bees. We cannot completely exclude this possibility, however, because it could be that bees of certain patrilines drifted more than bees of others.

Considering genetic preferences in performing hive tasks, the significantly higher tendency of drifted and non-drifted bees to perform some activities compared to control bees but not compared to each other (see Table 1) may be due to the fact that the drifted and non-drifted bees were related to each other but not to the control bees. However, we have no proof that that the tendency to perform these tasks was determined genetically.

Another conceivable explanation for the increased inactivity of the drifted bees is that this could be a strategy to increase their individual fitness by laying drone eggs. On the other hand, no egg laying by any of the focus bees was observed and we have not checked the ovaries of the drifted bees. Although about 7% of the drone eggs are laid by workers (Visscher, 1996) only about 0.12% of the adult drones produced by colonies were sons of workers (Visscher, 1989). Thus such a strategy would be more important in colonies that have lost their queens.

Another point is that there is a weak positive correlation between the age when workers care for brood and worker population (Winston and Nelson Punnett, 1982). Therefore it seems possible that the drifted bees, who were first introduced into colonies with much larger populations than the observation hive, had already been affected by conditions in the hives from which they drifted away, and therefore were physiologically younger than the non-drifted bees, when they began their activities in the observation hive.

It is interesting that the observed differences between drifted bees and non-drifted bees were significant for some tasks with importance for the colony (for example, brood care and inactive periods), but not for tasks that involve the direct welfare of the individual bee: receiving food or being groomed (Fig. 3, Table 1). However, in case of trophallactic contacts we do not know whether there was a difference in feeding drifted bees and non-drifted bees with either protein or honey (Crailsheim, 1992; Lass and Crailsheim, 1996). Also, no increased aggression against drifted bees was observed. Butler and Free (1952) reported that when young bees were able to enter a foreign colony and to stay there for several hours, they were accepted by the colony. In addition Jay and Dixon (1988) found that very few drifted bees were turned out or killed. These results together with those of the present study (only one single attack against a drifted bee recorded during the whole experiment), and others published elsewhere (Pfeiffer and Crailsheim, 1996) showing that drifted bees have no reduced life span, indicate that drifted bees were not treated worse by other colony members. The fact that 5 drifted bees (vs 2 non-drifted) had to be replaced during the experiment (see Materials and methods) does not necessarily argue against this conclusion. It might have been due to a greater tendency of drifted bees to drift again, as was observed by Pfeiffer and Crailsheim (1998). However, it is possible that drifted bees do not fully integrate themselves into their adoptive colony, resulting in reduced brood care and longer periods of inactivity. This may result in problems for a colony that loses bees by drifting and has a high proportion of foreign bees (Pfeiffer and Crailsheim, 1998).

Jay (1969 a) reported that drifting results in disadvantages in apiary management and has a serious effect on honey production. In a row of colonies with entrances facing in the same direction, he found that the end colonies produced more honey than the centre colonies. He considered that the imbalance in hive populations (more bees in row end colonies as a result of direct drifting) accounts for the imbalance in honey production within the row. Pfeiffer and Crailsheim (1998) modeled severe drifting situations and found that up to $42 \pm 6\%$ of the population of inner colonies of a row can consist of drifted bees. They also showed that in row end colonies only $22 \pm 3\%$ of the population were drifted bees, although the row end colonies had the highest populations because emigration levels were lowest. Emigration rates out of colonies were between 12 and 32% for row end colonies, and between 52 and 91% for inner colonies. Thus it seems that the better development of row end colonies and their higher honey gain compared to centre colonies is not only attributed to a gain of bees by direct drifting (Jay, 1965, 1969 a; Pfeiffer and Crailsheim, 1998), but could also be due to the circumstances that there are more descendants of the queen in the colony and less emigration out of these row end colonies. Simultaneously row end colonies had a lower proportion of drifted bees compared to inner colonies (see above), and considering the results of the present study, that drifted bees at broodcare age spend more time inactive and less time engaged in brood rearing, it is possible that having large numbers of drifted bees lowers the brood production efficiency of the colony and therefore slows colony development. Further indication for this hypothesis is that we found a clear negative correlation between worker-larva ratio and the amount of drifting in experiments with hives standing in a row (Pfeiffer and Crailsheim, 1998).

We conclude that the higher amount of inactivity and reduced brood care performances of the drifted bees results in less contribution of these bees toward the productivity of a colony (brood production), at least during the hive period in general and for the broodnest caste (Seeley, 1982) in particular. Drifted bees do not seem to have any disadvantages for themselves as individuals because they were not treated worse socially (with respect to trophallaxis, antennal contacts, aggressive behaviour, grooming behaviour) by colony members. It might be that drifted bees would eventually be better foragers, but we doubt this possibility considering the negative influence of foraging on life span (Mauermayer, 1954; Fukuda and Sekiguchi, 1966; Neukirch, 1982; Wille et al., 1985; Schmid-Hempel and Wolf, 1988; Beauchamp, 1992) and the fact that the life spans of drifted bees were not found to be reduced (Pfeiffer and Crailsheim, 1996). We believe that it would be of interest to investigate the foraging behaviour of drifted bees.

Acknowledgements

We gratefully thank R. Nowogrodzki for language corrections, editing and for his helpful discussion. We also thank M. Germ for critical comments and K. Steiner for programming. Supported by the Österreichischer Fonds zur Förderung der wissenschaftlichen Forschung.

References

Beauchamp, G., 1992. Effects of energy requirements and worker mortality on colony growth and foraging in the honeybee. *Behav. Ecol. Sociobiol. 31:* 123–132.
Betts, A.D., 1932. Drifting. *Bee World 13*: 70–71.
Breed, M.D. and T.M. Stiller, 1992. Honeybee, *Apis mellifera*, nestmate discrimination: Hydrocarbon effects and the evolutionary implications of comb choice. *Anim. Behav. 43*: 875-883.
Butler, C.G. and J.B. Free, 1952. The behaviour of worker honeybees at the hive entrance. *Behaviour 4*: 262–292.
Cooke, V.A., 1962. Drifting of bees: Effect of hives placed in a circle. *New Zeal. J. Agric. 105*: 407–411.
Crailsheim, K., N. Hrassnigg and A. Stabentheiner, 1996. Diurnal behavioural differences in forager and nurse honeybees (*Apis mellifera carnica* Pollm). *Apidologie 27:* 235–344.
Crailsheim, K., 1992. The flow of jelly within a honeybee colony. *J. Comp. Physiol. 162B:* 681–689.
Free, J.B., 1958. The drifting of honeybees. *J. Agric. Sci. 51*: 294–306.
Free, J.B. and Y. Spencer-Booth, 1961. Further experiments on the drifting of honeybees. *J. Agric. Sci. 57*: 153–158.
Fukuda, H. and K. Sekiguchi, 1966. Seasonal change of the honeybee worker longevity in Sapporo, North Japan, with notes on some factors affecting the life-span. *Jap. J. Ecol. 16:* 206–212.
Goodwin, R.M., J.H. Perry and A.T. Houten, 1994. The effect of drifting honey bees on the spread of American foulbrood infections. *J. Apicult. Res. 33*: 209–212.
Harbo, J.R., 1986. Effect of population size on brood production, worker survival and honey gain in colonies of honeybees. *J. Apic. Res. 25:* 22–29.
Harbo, J.R., 1993. Effect of brood rearing on honey consumption and the survival of worker honey bees. *J. Apic. Res. 32*: 11–17.
Hassanein, M.H. and M.A. El-Banby, 1960. Studies on the longevity of carniolan, caucasian, and italian honeybee workers, with special reference to their foraging behaviour. *Bull. Soc. Entomol. 44*:291–308.
Jay, S.C., 1965. Drifting of honeybees in commercial apiaries. I. Effect of various environmental factors. *J. Apic. Res. 4*: 167–175.
Jay, S.C., 1966 a. Drifting of honeybees in commercial apiaries. II. Effect of various factors when hives are arranged in rows. *J. Apic. Res. 5*: 103–112.
Jay, S.C., 1966 b. Drifting of honeybees in commercial apiaries. III. Effect of apiary layout. *J. Apic. Res. 5*: 137–148.
Jay, S.C., 1968. Drifting of honeybees in commercial apiaries. IV. Further studies of the effect of apiary layout. *J. Apic. Res. 7*: 37–44.
Jay, S.C., 1969 a. Drifting of honeybees in commercial apiaries. V. Effect of drifting on honey production. *J. Apic. Res. 8*: 13–17.
Jay, S.C., 1969 b. Studies on hiving package bees. II. Effects of environmental factors on loss and drifting of bees. *J. Apic. Res. 8*: 91–97.
Jay, S.C. and D. Dixon, 1988. Drifting behaviour and honey production of honeybee colonies maintained on pallets. *J. Apic. Res. 27*: 213–218.
Kaiser, W., 1988. Busy bees need rest, too. *J. Comp. Physiol. 163A*: 565–584.
Kaiser, W., 1995. Rest at night in some solitary bees – a comparison with the sleep-like state of honey bees. *Apidologie 26*: 213–230.

Kaiser, W. and J. Steiner-Kaiser, 1988. Behavioural and physiological changes occurring during sleep in the honey bee. In: *Sleep '86* (W.P. Koella, F. Obál, H. Schulz, P. Visser, Eds.), Gustav Fischer, Stuttgart. pp. 157–159.

Lass, A. and K. Crailsheim, 1996. Influence of age and caging upon protein metabolism, hypopharyngeal glands and trophallactic behavior in the honey bee (*Apis mellifera* L.). *Insectes soc. 43*: 347–358.

Lindauer, M., 1952. Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. *Z. vergl. Physiol. 34*: 299–345.

Mauermayer, G., 1954. Untersuchungen über die Beziehungen zwischen Arbeitsleistung und Lebensdauer bei Arbeiterinnen der Honigbiene. *Archiv für Bienenkunde 31*: 31–41.

Neukirch, A., 1982. Dependence of the life span of the honeybee (*Apis mellifera*) upon flight performance and energy consumption. *J. Comp. Physiol. 146*: 35–40.

Pfeiffer, K. and K. Crailsheim, 1996. Bienenverflug im Sommer und im Herbst. *Apidologie 27*: 315–317.

Pfeiffer, K.J. and K. Crailsheim, 1998. Drifting of honeybees. *Insectes soc. 45:* 151–167.

Rösch, G. A., 1925. Untersuchungen über die Arbeitsteilung im Bienenstaat. I. Teil: Die Tätigkeiten im normalen Bienenstaate und ihre Beziehungen zum Alter der Arbeitsbienen. *Z. vergl. Physiol. 2*: 571–631.

Rösch, G.A., 1930. Untersuchungen über die Arbeitsteilung im Bienenstaat. 2. Teil: Die Tätigkeiten der Arbeitsbienen unter experimentell veränderten Bedingungen. *Z. vergl. Physiol. 12*: 1–70.

Sakagami, S.F., 1953. Untersuchungen über die Arbeitsteilung in einem Zwergvolk der Honigbiene. Beiträge zur Biologie des Bienenvolkes, *Apis mellifera* L., I. *Jpn. J. Zool. 11*: 117–185.

Sauer, S. and W. Kaiser, 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, p. 253.

Schmid-Hempel, P. and T. Wolf, 1988. Foraging effort and life span of workers in a social insect. *J. Anim. Ecol. 57:* 509–521.

Seeley, T.D., 1982. Adaptive significance of the age polyethism schedule in honeybee colonies. *Behav. Ecol. Sociobiol. 11*: 287–293.

Visscher, P.K., 1989. A quantitative study of worker reproduction in honey bee colonies. *Behav. Ecol. Sociobiol. 25:* 247–254.

Visscher, P.K., 1996. Reproductive conflict in honey bees: a stalemate of worker egg-laying and policing. *Behav. Ecol. Sociobiol. 39:* 237–244.

Winston, M.L. and E. Nelson Punnett, 1982. Factors determining temporal division of labor in honeybees. *Can. J. Zool. 60:* 2947–2952.

Wille, H., A. Imdorf, G. Bühlmann, V. Kilchenmann and M. Wille, 1985. Beziehung zwischen Polleneintrag, Brutaufzucht und mittlerer Lebenserwartung der Arbeiterinnen in Bienenvölkern (*Apis mellifica* L.). *Mitt. Schweiz. Entomol. Ges. 58*: 205–214.

Woyke, J., 1984. Correlations and interactions between population, length of worker life and honey production by honeybees in a temperate region. *J. Apic. Res. 23:* 148–156.