

ORIGINAL PAPER

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Honeybees establish specific sites on the comb for their waggle dances

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Abstract Successful honeybee foragers perform dances on the surface of the comb where they interact with nectar receivers and dance followers. We have recorded the sites at which dances take place in large ten-frame hives and in two-frame observation hives. We find that dancing bees are most commonly found on particular combs in large hives and in particular areas on the combs in the observation hives. Although the site where dances take place may change from day to day, dancers will keep to the same site during the foraging period in any one day. Furthermore, if an established dance site is artificially relocated in the hive during the day, dancers seek these sites out before commencing their dances. We conclude that the dance sites are labelled in some way and so promote the congregation of both dancers and dance followers at the same site.

Key words Honeybee · Waggle dance · Dance site

Introduction

The recruitment of nestmates to a food source by foraging honeybees includes the performance of the so-called waggle-dance on the surface of the combs in the darkness of the hive (von Frisch 1965). Dancing foragers give up nectar to their nestmates at the dance site and also appear to pass on information about the location of the food source to potential foragers.

To be effective, such dances must take place in the close vicinity of bees ready to receive nectar or those about to forage. It follows that the recruitment process would be aided by the establishment of a particular site

on the comb which could be recognised in some way by both dancers and dance followers. Some support for this hypothesis comes from the fact that in two-frame observation hives, dancing bees are commonly found at sites on the lower comb near the entrance of the hive (von Frisch 1965; Visscher and Seeley 1982; Seeley 1989, 1994; Seeley and Towne 1992; Tautz 1996).

The experiments described here set out to test this supposition both in large ten-frame hives and in two-frame observation hives. The results support the existence of some marker that fixes the location of the “dance floor” for the duration of a days foraging and so helps both dancers and dance followers to congregate at the same site.

Materials and methods

Experiments were carried out using regular ten-frame hives and two-frame observation hives. Observations with the ten-frame hives were made in August 1995 and in April 1996. The experiments with two-frame hives took place on warm days in mid-September and mid-October 1995 when almost no flowers were blooming nearby. Hence, no dances, except those elicited experimentally, took place in the observation hives. All experiments were performed at the Würzburg University bee station.

All experiments were repeated, and the results confirmed, in 1996.

1. Ten-frame hives

To locate dance sites in regular ten-frame hives we first trained and marked bees living in two such hives to a feeder 150 m away. Once the bees had started to collect from the feeder, frames were carefully lifted, one at a time, from the hives and examined for dancing bees. The frames were lifted in order starting at one end and working through to the other and the locations of the dancing bees recorded.

2. Two-frame hives

A two-frame observation hive was modified by locating the entrance halfway up the side so that bees entering the hive had equal access to both upper and lower combs. The combs consisted en-

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tirely of empty uncapped cells and about 30% of the circumference of each comb was free of the wooden frame.

A queenright honeybee (*Apis mellifera carnica* Pollm.) colony of about 2500 individuals was housed in the hive. After an adjustment period of 1 day the bees were trained to a feeder containing $2 \text{ mol} \cdot \text{l}^{-1}$ non-scented sugar solution, 150 m west of the hive. Bees in the observation hive were exposed to daylight but not to direct sunlight. The location of dancing bees was recorded each morning over 10 successive days preceding the experimental period. Twenty forager bees were marked for the experiments and allowed to visit the feeder and to return and dance in the hive. The feeders were then closed, all the bees in the observation hive were shaken onto a board in front of the hive and the combs exchanged so that the upper comb became the lower comb and the lower, the upper comb. The bees were then allowed back into the hive, feeders re-opened and the sites of the dances again recorded after the combs had been exchanged. In all, the combs were exchanged seven times over a 3-day period.

Results and discussion

The frames containing the combs in ten-frame "Kaltbau" hives that were used in these experiments are arranged at right angles to the front wall. The entrance slot extends along the entire length of this wall, providing entering bees with unimpeded and equal access to all frames. Nevertheless, the dancing bees were not found evenly distributed throughout the hive. Instead we found most dancers on the combs near the center of the hive congregated on areas of its lower half that was nearest to the entrance and where the junction between frame and comb was interrupted by gaps gnawed in the comb by the bees.

The locations of unmarked dancing bees in the two-frame observation hive were recorded over a 10-day period. On six occasions, sites were established on the lower comb and on four occasions on the upper comb (temporal sequence: lower, lower, lower, upper, lower, upper, lower, lower, upper, upper) and maintained for the day. The sites were always in an area of about 100 cm^2 close to the entrance.

The relocation experiments took place over 3 days. On the first day, 20 marked forager bees were trained to a feeder 150 m away. These quickly established a dance site on the lower comb and ten dances were recorded over a period of 10 min (Table 1, first line). The feeder was closed and the combs exchanged as described (methods) and the feeder re-opened. This operation took 10 min. The marked foragers visited the feeder again, returned to the hive, walked slowly through the hive and started dancing as soon as they reached the dance site, now in its new position on the upper frame of the hive (Table 1). Subsequently, arriving foragers proceeded directly to the dance site on the upper frame and 15 dances were recorded in the next 10 min. Two dances took place in this period on the lower frame.

The combs were exchanged again 10 min later with the result that 29 dances were recorded on the lower frame and 3 on the upper comb (Table 1, Fig. 1). The combs were exchanged twice in the next 80 min and each exchange was accompanied by an appropriate relocation

Table 1 Dances performed by all 20 marked dancers on the combs of a two-frame observation hive. The columns show the date and duration of the observations and the numbers of dances observed on the upper and lower combs. On 12.09.95 bees were allowed access to both sides of the comb. At 1130 hours on that day the bees were removed from the hives and then allowed to return but the combs were not exchanged

Date/time		Dances on upper frame	Dances on lower frame
11.09.95			
14.00–14.10		0	10
14.10–14.20	exchange of frames		
14.20–14.30		15	2
14.30–14.40	exchange of frames		
14.40–15.10		3	29
15.10–15.20	exchange of frames		
15.20–15.50		42	7
15.50–16.00	exchange of frames		
16.00–16.30		4	32
12.09.95	both sides of each	26 (front)	11 (front)
10.20–10.50	frame accessible to the bees	0 (rear)	2 (rear)
10.50–11.00	exchange of frames		
11.00–11.30		13 (front) 5 (rear)	34 (front) 0 (rear)
11.30–13.30	no exchange		
13.30–14.00		1	22
14.00–14.10	exchange of frames		
14.10–14.40		21	6
12.10.95			
11.30–11.40		17	0
11.40–11.50	exchange of frames		
11.50–12.20		2	61

of the dancers who kept to the site originally established at the beginning of the day, regardless of whether it was at the top or the bottom of the observation hive. (Table 1, Fig. 1).

On the following day the experiment was repeated. The foragers danced both on the upper and on the lower combs, but more dances were observed over a 30-min period to occur on the upper comb. After exchanging the combs, more dances were recorded on the lower comb (Table 1) and later in the day the lower comb was still favoured over the upper comb (22 to 1). After exchanging the combs, 21 dances were recorded on the upper comb and 6 on the lower (Table 1). The experiment was repeated 1 month later with the same clear result (Table 1). Of the 365 observed dances, 316 dances were recorded on the established dance site irrespective of its position in the observation hive.

Within 1 foraging day, the location of the dancing bees in two-frame observation hives remains fairly stable, slight shifts being perhaps due to changing distances between the nest and the actual food sources (Körner 1939; Seeley 1994). This could be explained by the spatial orientation of the dance site in relation to the entrance to a regular observation hive, close to the bottom of lower comb. In large hives, we have found a similar constancy of dance sites but again, we cannot disassociate this finding from purely spatial cues.

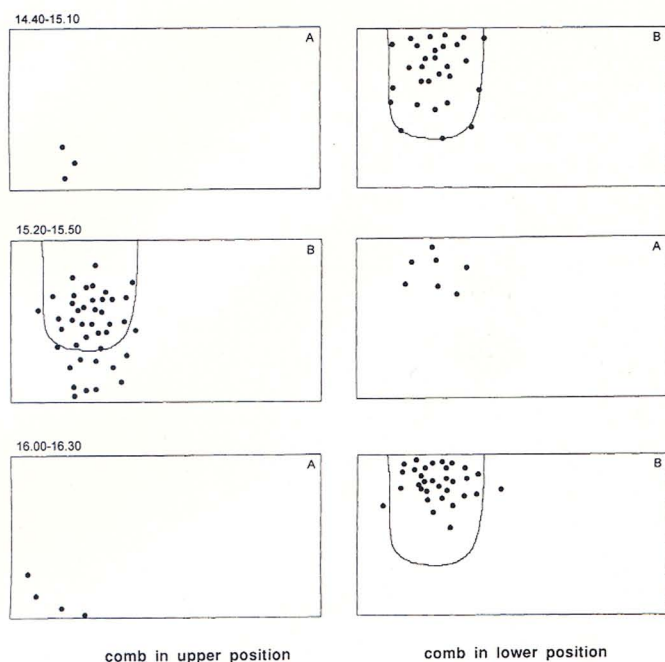


Fig. 1 The location of dances on the combs over three periods recorded in Table 1, showing the relocation of the dances that follow exchanging the combs. All bees were removed from the hive before each comb exchange. *A* and *B*: the two combs in the observation hive. Comb "B" is in the lower half of the hive from 1440–1510 hours and from 1600–1630 hours (*right column*), and in the upper half from 1520–1550 hours (*left column*). The area that was established as dance site during the first observation period (comb "B" from 1440–1510 hours) was marked throughout this figure. Each dot marks the site of the first waggle run of each dance

Modifying the observation hive so that the entrance allowed equal access to the upper and lower frames resulted in an almost equal division of dance sites on the upper and lower combs which could be interpreted to mean that ease of access is a dominant feature. However, the repeated insistence of returning foragers to dance on an established site, regardless of the continual relocation of that site, suggests that the returning foragers are using more than just spatial information to find it.

The behaviour of foragers returning to the hive immediately after a comb exchange points to the presence of chemical cues. These bees walk slowly about over most of surface of the combs until they come across the site of the first dances, before they dance. On their return from subsequent sorties they head directly for the site, perhaps indicating that spatial cues are indeed important after the first rediscovery of the dance site. A convenient chemical cue to use would be the odour of the flowers

collected by the bees; however, our results do not support this possibility because the feeding sites we used were not scented and the experiments were conducted at a time when few natural blooms were available. Also, the constancy of dance sites used by bees that could have been foraging in very different regions, would suggest that the dance site is not specific to the location of the food source (Seeley 1994).

The rediscovery of the dance site by foragers after a comb exchange could be better explained by the existence of a *marked* site. Bees mark the entrance of their nest with chemical footprints (Butler et al. 1969, 1970) probably secreted from Arnhart glands in their feet (Chauvin 1962). In another context, footprint marking of flowers visited by bees is also suspected (Josué Núñez, personal communication). A chemical marker at a dance site could be reinforced by each dancing bee throughout the day but would fade overnight. This would allow the location of the dance site to be changed from day to day to accommodate changing nest conditions such as the enlargement of existing combs, building new ones, changing the contents of the cells, or capping them.

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