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Honeybees do not reject dances for 'implausible' locations: reconsidering the evidence for cognitive maps in insects

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Results from a previous study, known as the 'Lake Experiment' (Gould & Gould 1982, *Animal Mind−Human Mind*, Berlin, Springer-Verlag, 269−298), suggest that honeybee, *Apis mellifera*, foragers may assess the locations advertised by the waggle dances that they follow and reject dances for 'implausible' locations that are unlikely to yield food. However, alternative explanations for these results, which do not require bees to use cognitive maps or to evaluate the 'plausibility' of potential food sources, have also been proposed. To address this ambiguity, we repeated the study and used video analysis of dance followers in the hive to determine whether they refused to respond to implausible dances for a feeder on a lake. We found that bees following lake dances were just as likely to leave the hive as bees following control dances for a feeder on land. Bees also took the same amount of time to leave the hive after following dances for both locations, which suggests that their motivation to leave did not depend on the plausibility of the dance they had followed. Contrary to prior findings, our results provide no evidence that honeybees assess the plausibility of information contained in waggle dances or reject dances for locations that are unlikely to yield food. Thus, we conclude that the original Lake Experiment should no longer be cited as evidence that honeybees possess cognitive maps, 'insight' or 'imagination'.

The waggle dance of the honeybee, *Apis mellifera*, is a complex and versatile form of symbolic communication, and the flexibility with which bees use it suggests that they may possess relatively sophisticated cognitive abilities (Gould & Gould 1988; Seeley 2003). Laboratory experiments have shown that honeybees are capable of complex forms of learning, such as distinguishing same−difference relationships (Giurfa et al. 2001), which were previously believed to exist only in vertebrates (Giurfa 2003). However, there have been fewer tests of the cognitive abilities that honeybees use under natural conditions. In

particular, the degree to which honeybees 'understand' or 'interpret' the messages in their dances—as opposed to producing and reacting to them automatically—is still largely unknown.

There is one study that claims to provide evidence that bees assess the 'plausibility' of the dances they follow before responding to them: the 'Lake Experiment' described by Gould & Gould (1982). In this study, honeybee foragers were trained to visit a feeder on a boat in the middle of a lake. When the trained foragers performed dances for this location, no recruits arrived at the lake feeder during 5 of 6 days of training, despite the fact that dances for an equidistant feeder on land elicited heavy recruitment (Gould & Gould 1982). Similarly low recruitment levels to feeders on a lake were also observed in a more recent study by Tautz et al. (2004). The most frequently cited explanation for these results is that 'while still in the hive,

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[dance followers] used the direction and distance information in the dance to position the advertised site on their mental map, determined that it was in the lake and therefore implausibly located, and refused to respond' (Gould 1990). Followers of dances for sites on the shore, however, 'would "picture" a more believable location and act on the information' (Gould & Gould 1988).

Because the Lake Experiment suggests that honeybees use a cognitive map to assess the plausibility of dances, this study has frequently been discussed as potential evidence for cognitive maps in bees (e.g. Gould 1986; Shettleworth 1998). The question of whether bees possess a cognitive map, i.e. an internal representation of the spatial relationship of objects in their environment (Wehner & Menzel 1990), is a long-standing debate that has recently been renewed in the literature (see Menzel et al. 2005).

Beyond its role in the cognitive map debate, the Lake Experiment has also been cited in papers on animal communication and deception (e.g. Fitch & Hauser 2002; Crist 2004) because of its implication that bees can interpret and assess the veracity of messages they receive. Furthermore, some authors have proposed that if bees are actively evaluating the plausibility of information they receive from dances and comparing that information with their own knowledge of the surroundings, then perhaps honeybees have more than just a cognitive map—this suggests that they may possess 'insight' (Gould & Gould 1988), 'imagination' (Gould 1990) or some form of consciousness (Griffin 2001).

Despite widespread interest in the Lake Experiment, most authors acknowledge that the data 'are not sufficient to provide a fully convincing case' (Griffin 2001) and 'can be interpreted in more than one way' (Shettleworth 1998). Indeed, there are a number of alternative explanations for the observed lack of recruits at lake feeders that do not involve bees rejecting dances for implausible locations. Dyer & Seeley (1989) point out that recruits in the original Lake Experiment may have in fact left the hive, but failed to arrive at the feeder because bees flying over a lake surface may become disoriented, lose altitude and drown (von Frisch 1967). Tautz et al. (2004) offer three additional explanations for why recruits in their experiment might have left the hive but failed to arrive at the lake feeder: (1) the indication of distance in the dance directions may have been less precise for lake locations, making them harder for recruits to locate; (2) experienced foragers did not seem to help recruits find the lake feeder, which could have made it more difficult for them to locate it; (3) recruits may have flown over the lake at a different altitude compared to the trained foragers who provided the dance instructions, causing recruits to miscalculate the distance to the feeder.

Knowing only that few recruits arrive at the lake feeders, it is impossible to determine whether bees following lake dances refuse to leave the hive or leave the hive but fail to arrive at the lake feeder for reasons such as those mentioned above. Data on the behaviour of dance followers inside the hive, which were not collected during the original Lake Experiment (Dyer & Seeley 1989; Gould & Towne 1989) or by Tautz et al. (2004), are required in order to discriminate between these possibilities. If bees do not leave the hive after following dances for the lake feeder, this would provide strong support for the hypothesis that they are refusing to respond to dances for implausible locations. However, if as many bees leave the hive in response to lake dances as to land dances, then this hypothesis can be rejected. Our study tested this hypothesis by repeating the original Lake Experiment and videotaping the behaviour of both dancers and dance followers in the hive in addition to recording the number of recruits at lake and land feeders.

METHODS

Study Site and Subjects

We performed this experiment at the Cranberry Lake Biological Station (CLBS) in the Adirondack State Park, Saint Lawrence County, New York, U.S.A. (44°09′N, 74°48′W). This study site is surrounded by more than 20 km of forest and offers very few natural food sources for honeybees. These conditions made it relatively easy to elicit dancing for artificial food sources and guaranteed that nearly all of the dances performed in the hive were for our artificial feeders. In addition, the lack of other honeybee colonies in the surrounding area ensured that every unmarked bee we observed at our feeders was from one of our colonies.

We conducted two trials of the experiment; the methods for both were the same unless otherwise noted. We performed trial 1 on 15−16 August 2006 with a colony of approximately 3000 Italian (*A. m. ligustica*) honeybees (queens from C. F. Koehnen and Sons, Inc., Glenn, California, U.S.A.), which had been brought to the CLBS from the Liddell Field Station in Ithaca, New York, U.S.A., 1 week earlier. During the week leading up to the experiment we permitted the bees to forage freely, both in the surrounding area and at a feeder, which was available twice a day for 2 to 3 h. We housed the colony in a two-frame observation hive, which was kept in a small wooden hut to prevent exposure to the elements (see Seeley 1995, Figures 4.2, 4.4).

We used a second colony of approximately 3000 New World Carniolan (*A. m. carnica*) honeybees (queens from C. F. Koehnen and Sons, Inc.) for trial 2, which took place on 17−18 August 2006. This colony was moved from Liddell Field Station to the CLBS on 15 July and for the following month foraged exclusively on wild sources. This observation hive was housed in a classroom approximately 20 m away from the wooden hut used in trial 1.

Experimental Layout

We trained one group of 20−25 bees to visit a feeder in a 5 m long boat anchored in Cranberry Lake (hereafter, the 'lake feeder') and trained a separate group of bees from the same colony to an equidistant feeder on land (the 'land feeder') (Fig. 1). We labelled all trained bees with shellac-based paint marks; the colour of each bee's thorax indicated the feeder to which she had been trained, and the colours on her abdomen allowed her to be individually identified.
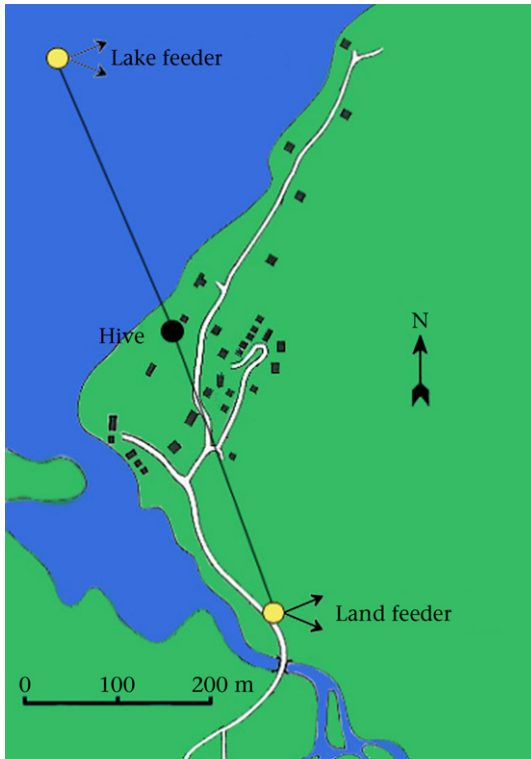
Figure 1. Layout of the hive and the land and lake feeders at the Cranberry Lake Biological Station. Both the land feeder and the lake feeder are 300 m from the observation hive. The lake feeder is 260 m offshore. Arrows emanating from the two feeders indicate the wind direction in the two trials: from the WSW (trial 1) and the WNW (trial 2).

Both feeders provided bees with sucrose solution (0.5–2.5 M). To facilitate training, and to more closely approximate the bees' experience of foraging at natural food sources, each feeder had a distinctive scent, which was present both in the sugar solution and in a reservoir on top of which the jar of solution rested. In trial 1, we used anise scent at the lake feeder and orange scent at the land feeder. We switched the scents in trial 2 to control for any effects the scents might have on the bees' behaviour. The presence of distinct scents tends to increase recruitment levels by enabling recruits to find feeders more easily (Tautz & Sandeman 2003). So, using scents allowed us to better test the hypothesis that bees would not arrive at the lake feeder by increasing the likelihood that bees who left the hive in response to lake dances would then be able to locate the lake feeder.

Both the land and the lake feeder were located 300 m from the hive. At this distance (260 m from the nearest shore), the lake feeder was clearly distinguishable from any location on land, both visually (Fig. 2) and, presumably, via dance instructions obtained from a trained

forager. We chose this distance to maximize the likelihood that bees assessing the location's plausibility would interpret it as an 'implausible' place to find food. At this distance, our feeder should seem even more implausible to bees than the feeder used in the original Lake Experiment, which was located only 165 m from the hive (Gould & Gould 1982).

The angle between our land and lake feeders was approximately 180 degrees, with the result that dances for the two sites pointed in nearly opposite directions (Fig. 1). It was thus highly unlikely that recruits following instructions from a dance for one site would accidentally encounter the other feeder. It was also improbable that bees following dances for the land feeder (hereafter, 'land followers') would mistake those dances as pointing to a location on the water, or that bees following dances for the lake feeder (hereafter, 'lake followers') would interpret those dances as pointing to a location on land. Our design differed slightly from that of Gould & Gould (1982), who placed the land feeder on the shore of the lake, creating a 90 degree angle between the two feeders. The 180 degree angle we used should have made it even easier for dance followers to distinguish dances pointing to the lake from those pointing towards land.

Performing the Experiment

From 0900 hours on the first day of each trial (15 August for trial 1, 17 August for trial 2) until approximately 1400 hours on the following day, we trained bees to visit the land and lake feeders using techniques described by von Frisch (1967). The testing period began at 1500 hours on the second day, at which point the concentration of the sugar solution was raised from 0.5 to 2.5 M to encourage the bees to perform dances for the feeders. During the following 2 to 3 h (trial 1, 2 h; trial 2, 3 h), we recorded all visits to each feeder by both trained bees and new recruits (unmarked bees). Recruits were caught in Ziploc bags to avoid overcrowding at the feeder and to prevent them from returning to the hive to dance.

For 2 h (from 1500 to 1700 hours), we videotaped (Panasonic AGDVC 30) the area of the observation hive in which bees were performing and following dances (the 'dance floor'). These tapes enabled us to analyse the behaviour of both dancers and dance followers, and allowed us to see when followers entered the tunnel leading out of the hive (which we used as an indication that they were leaving the hive). To ensure that all dancing bees could be accurately identified in the videos, throughout each 2 h test period an observer at the hive pointed to each bee that performed a dance and read her identifying paint marks aloud; this information was included on the audio track of the tapes.

Figure 2. Three hundred and sixty degree view from the lake feeder at 300 m from hive (260 m offshore). The location of the observation hive is indicated with an arrow.

Video Analysis

In defining a 'dance', we attempted to minimize our chances of counting bees who had not obtained sufficient information from the dance to be able to leave the hive as having 'rejected' a dance. Because most dance followers that are able to locate a food source indicated by a dance have followed the dance for an average of approximately eight waggle runs (Judd 1995), and followers often do not begin to follow a dance until after the dancer has already performed one or two waggle runs, we defined a dance as a sequence of 10 or more consecutive waggle runs performed by a bee in a particular region on the comb.

We defined a 'dance follower' as a bee that was no more than one bee-width away from a dancing bee, was facing the dancer and followed her movements for at least two complete waggle runs (a.k.a. 'dance circuits'). This allowed us to avoid counting as dance followers bees who simply happened to be walking past the dancer (we ignored bees that followed only one circuit). It also prevented us from biasing our analysis against any bees that recognized quickly that the dance indicated an implausible location and rejected it after following only a small number of waggle runs (we counted any bee that had followed at least two waggle runs as a dance follower).

Across both trials, 228 land and 201 lake dances—performed by 33 land and 37 lake bees—satisfied the criteria described above. For each of these dances, we noted the dancer's identity and feeder. For a randomly selected subset of dances (50 land and 51 lake dances, performed by 23 land and 22 lake bees), we counted the number of waggle runs performed during that dance (a measure of the quality of the food source; Seeley & Towne 1992) and the mean duration of the waggle run (a measure of the distance to the food source; averaged over five dance circuits). Then, for the first two followers of each of these dances, we noted the number of dance circuits they followed, the next action they performed (whether they left the hive, followed another dance, or moved off-screen) and the time that elapsed before the next action. If the bee's next action was to follow another dance, we noted the identity and feeder of the dancer. We performed all video analyses using Final Cut Pro version 4 (Apple, Inc.).

Statistical Tests

We performed all statistical tests except power analyses using SAS version 8.02 (SAS Institute 1999). For analyses of dance data (i.e. number of circuits/dance), we treated multiple dances performed by the same dancer as subsamples of that dancer (experimental unit) to avoid pseudoreplication. From the perspective of a dance follower, however, each dance represented a discrete and unique set of information, so the dance, rather than the dancer, was treated as the experimental unit. Thus, for analyses of dance followers (i.e. number of dance circuits followed), we treated followers of different dances as independent, whereas we treated followers of the same dance as subsamples of that dance.

When numerical data met normality assumptions, we performed two-way ANOVA tests (trial and feeder effects; Proc GLM). Where effects were significant, we separated the means with a Tukey standardized range test. For data that did not initially meet normality assumptions, we either log transformed or averaged the data for each bee to improve normality, or we used a nonparametric Wilcoxon test. The reduced power of the nonparametric tests made it necessary to pool data across trials and ignore subsampling effects. We performed chi-square tests for categorical data (Proc FREQ). All P values are for two-tailed tests; α values for all tests were set at 0.05. Means are reported as $LS_{mean} \pm$ standard error. To avoid type 2 errors and maximize our chance of detecting significant differences between the land and the lake followers, we did not apply Bonferroni corrections for multiple tests performed on the same data set.

We performed power analyses using G*Power version 3 (Faul et al. 2007). Reported values are from post hoc power tests based on our total sample size and degrees of freedom. Estimates of small, medium and large effect sizes for ANOVA tests (small, $f = 0.1$; medium, $f = 0.25$; large, $f = 0.4$) and chi-square tests (small, $w = 0.1$; medium, $w = 0.3$; large, $w = 0.5$) were based on Cohen's (1988) recommendations.

To ensure that followers could be accurately classified as leaving the hive in response to the dance they had followed (as opposed to leaving the hive to scout for new food sources or to return to a previously visited food source), our analysis included only bees that left the hive within 130 s after they had stopped following the dance (this eliminated only the largest 3.5% of values). Similarly, for analysis of bees that followed second dances instead of leaving the hive, we only included bees who began following that dance within 130 s after they had stopped following the first dancer.

RESULTS

Behaviour of Dance Followers in the Hive

Bees following dances for the lake site were just as likely to leave the hive as bees following dances for the land site (Table 1; chi-square test). Our power for this test ($N = 178$) was 0.27 for a small effect size, 0.98 for a medium effect size and 1.0 for a large effect size. There was no difference

Table 1. Number of land and lake followers that left the hive

Dance	Left hive	Trial 1	Trial 2	Both trials
Land	Yes	31	27	58
	No	15	17	32
Lake	Yes	32	21	53
	No	15	20	35
	χ_1^2	0.005	0.89	0.34
	P	0.94	0.35	0.56

All data are for bees that left the hive within 130 s after they stopped following the dance.

between land and lake bees in the amount of time it took for the bees that left the hive after following a dance to exit the hive (Fig. 3; two-way ANOVA with subsampling and log transformation: feeder effect: $F_{1,75} = 0.0$, $P = 0.95$; trial effect: $F_{1,75} = 0.01$, $P = 0.93$; trial*feeder interaction: $F_{1,75} = 3.11$, $P = 0.08$; subsampling effect: $F_{75,32} = 1.28$, $P = 0.22$). Our power for this test ($N = 111$) was 0.18 for a small effect size, 0.74 for a medium effect size and 0.99 for a large effect size.

Bees following land dances tended to follow slightly more dance circuits (7.9 ± 0.37 circuits/follower) than bees following lake dances (6.8 ± 0.37 circuits/follower) (two-way ANOVA with subsampling: feeder effect: $F_{1,97} = 4.1$, $P = 0.047$; trial effect: $F_{1,97} = 0.8$, $P = 0.38$; trial*feeder interaction: $F_{1,97} = 1.4$, $P = 0.25$; subsampling effect: $F_{97,98} = 1.0$, $P = 0.47$). Regardless of the type of dance they were following, dance followers that subsequently left the hive followed more dance circuits on average (8.1 ± 0.35 circuits/follower) than dance followers that did not leave the hive (6.1 ± 0.45 circuits/follower) (Wilcoxon test: $Z = -3.13$, $P = 0.002$).

For those bees that followed a second dance instead of leaving the hive, the location (land or lake) of the first dance they had followed made no difference in the amount of time it took them to begin following a second dance (Wilcoxon test: $Z = -0.74$, $P = 0.46$). However, the second dance they followed was significantly more likely to be for the same feeder as the first dance they had followed than would be expected by chance (Table 2; chi-square test).

Dance Information

Dancers for the lake feeder and for the land feeder performed the same average number of circuits per dance (Fig. 4; two-way ANOVA with subsampling and log transformation: feeder effect: $F_{1,39} = 0.002$, $P = 0.96$; trial effect: $F_{1,40} = 0.41$, $P = 0.52$; subsampling effect: $F_{40,58} = 1.39$, $P = 0.12$; trial*feeder interaction: $F_{1,40} = 1.42$, $P = 0.24$). Our power for this test was 0.17 for a small effect size, 0.70 for a medium effect size and 0.98 for a large effect size.
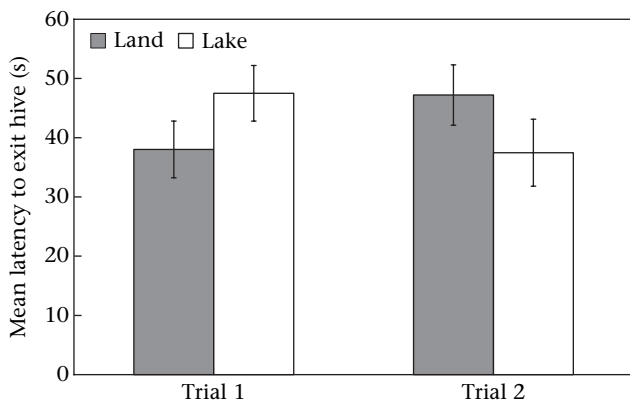
Table 2. Location advertised by first and second dances followed

First dance	Second dance	Number of followers
Land	Land	22
	Lake	5
Lake	Land	6
	Lake	19
χ_1^2		17.26
P		<0.0001

Data are for both trials combined; tests were not performed for the two trials separately because sample sizes were too small. Data are for bees that did not leave the hive after following the first dance, but instead followed a second dance within 130 s after they had stopped following the first dance.

The average duration of waggle runs was significantly greater for bees performing dances for the lake feeder (0.96 ± 0.02 s) compared to bees performing dances for the land feeder (0.72 ± 0.02 s) (Fig. 5; two-way ANOVA averaged across dances for each bee, no transformations: feeder effect: $F_{1,40} = 51.51$, $P < 0.0001$). In addition, the average waggle run duration was slightly greater for bees from trial 2 (0.88 ± 0.02 s) compared to bees from trial 1 (0.80 ± 0.02 s) (Fig. 5; trial effect: $F_{1,40} = 5.48$, $P = 0.02$). (The trial*feeder interaction was not significant: $F_{1,40} = 1.99$, $P = 0.17$.)

Recruitment to Land and Lake Feeders

We captured new, unmarked recruits at the lake feeder in both experimental trials (Fig. 6). When we pool our data across both trials, there is no significant difference in the numbers of recruits that arrived at the land feeders compared to the lake feeders (87 versus 99; chi-square: $\chi_1^2 = 0.77$, $P = 0.38$).

There was, however, a strong interaction between trial and feeder associated with the change in scents from trial 1 to trial 2 (Fig. 6). In trial 1, many more recruits arrived at the lake feeder (90 recruits, anise scent) than at the land feeder (19 recruits, orange scent), whereas in trial 2 far
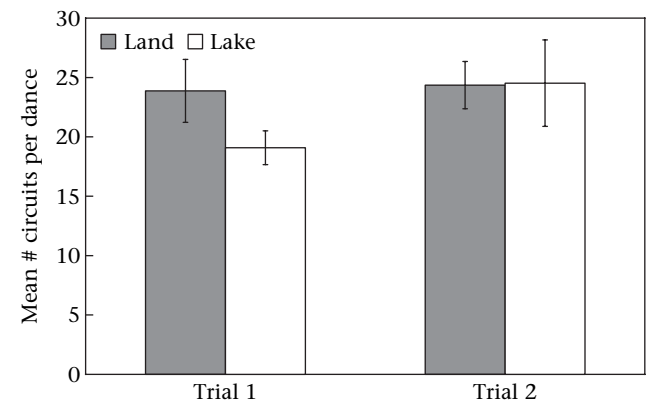

Figure 3. Mean number of seconds (±SE; before log transformation) between the time when a follower stopped following a dance and the time when she exited the hive. Latency to leave the hive did not differ between bees following land and lake dances ($P = 0.95$).

Figure 4. Mean number of circuits per dance (±SE; before log transformation), performed by bees trained to visit the land and lake feeders in trials 1 and 2. Dances did not differ between land and lake bees ($P = 0.96$).
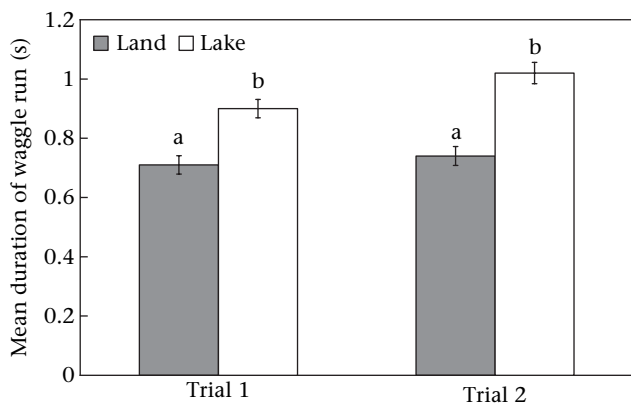
Figure 5. Mean duration (±SE) of dancing bees' waggle runs in trials 1 and 2. Dances for the lake site were significantly longer than dances for the land site ($P < 0.0001$); significant differences are indicated by the letters above the bars.

more new recruits arrived at the land feeder (68 recruits, anise scent) than at the lake feeder (9 recruits, orange scent). Across the two trials, there was a significant difference in the number of recruits that arrived at anise-scented feeders compared to orange-scented feeders (158 versus 28; chi-square: $\chi^2_1 = 90.86$, $P < 0.001$).

In trial 1, the wind was blowing from the WSW at 12.9 to 20.9 km/h, and in trial 2, the wind was coming from the WNW at 0 to 4.8 km/h. In neither trial was the wind blowing scent towards the hive from either of the feeders. On the contrary, in both cases the wind was blowing the scent almost perpendicular to the direction to the hive (Fig. 1).

DISCUSSION

Behaviour of Followers in the Hive

The critical prediction of the hypothesis that bees reject dances for lake sites is that bees following 'implausible' (lake) dances should leave the hive in response to these
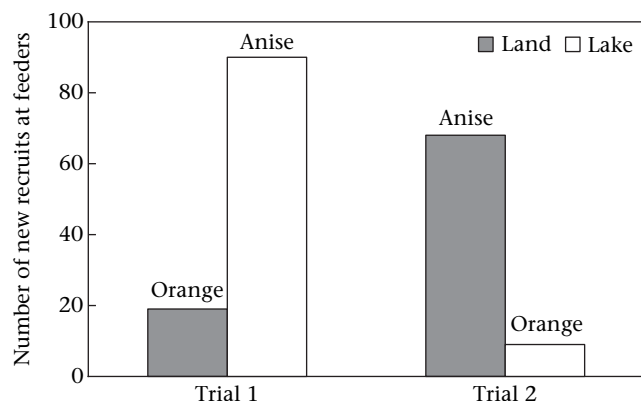

Figure 6. Number of new recruits that were caught at the land and lake feeders in trial 1 (2 h) and trial 2 (3 h). The scent of the sucrose solution that was used at the feeder is indicated above each bar. There was no difference between the numbers of recruits that arrived at the land and at the lake feeders ($P = 0.379$). Significantly more bees arrived at feeders with anise scent ($P < 0.001$).

dances less often than bees following dances for 'plausible' (land) locations. Instead, our data clearly show that bees following implausible lake dances left the hive just as frequently as bees following plausible land dances. If any difference between the land and the lake followers existed, we should have detected it because even for a medium effect size our power was 98%.

Although bees did ultimately leave the hive in response to dances for implausible (lake) sources, if these followers recognized the directions as unusual or potentially misleading, then we might expect them to have been less motivated to leave the hive, and thus have taken longer to leave, than followers of land dances. However, for dance followers who left the hive, followers of implausible dances took no longer to leave the hive than followers of plausible dances. Thus, it seems that following implausible dances did not cause bees to appear 'confused' or 'uncertain'. Instead, they appeared just as motivated to leave the hive as followers of dances advertising a plausible location, which suggests that they did not interpret the lake location as being implausible at all.

If not all bees were equally able to distinguish between plausible and implausible dances, and the lake followers that remained in the hive were the only ones that recognized the location as nonsensical, then we might expect to see a behavioural difference between the land and the lake followers that remained in the hive. In particular, bees that had followed lake dances might begin following a second dance more quickly, because their reason for not responding to the first dance was its implausibility, not a lack of motivation to forage. However, lake followers took no less time to follow a second dance than did land followers. Thus, we have no evidence to suggest that the lake followers that remained in the hive did so because they interpreted the dance they had followed as implausible.

Regardless of the plausibility of the first dance they followed, there was a strong tendency for bees that followed second dances to follow a dance for the same location as the first dance they had followed. This effect could potentially result from dances being distributed in such a way that a bee randomly following the next dance she encountered would tend to follow multiple dances for the same site. However, dances did not seem to be clumped together on the dance floor according to the site that was being advertised. Nor did bees seem simply to follow the next dance that they encountered; instead, they often travelled long distances across the dance floor before following a second dance, sometimes walking directly past one dance to follow a more distant one. An alternative explanation for this result is that, although bees did not seem to assess the plausibility of the locations indicated by dances they followed, they were capable of discriminating between dances for different locations and were actively seeking out multiple dances for the same source.

Dance Information

The fact that we found no difference in the average number of circuits per dance for land and lake feeders

suggests that dancers for the land feeder were not advertising their site more enthusiastically than dancers for the lake feeder (or vice versa). Thus, if followers are responding to dances based on the advertised quality of the food sources (as indicated by the number of waggle runs per dance), followers' responses should not be biased towards one feeder or the other.

Honeybees' 'odometers' have been shown to run at slower speeds over water than over land (Tautz et al. 2004) because of the lower optic flow they experience when flying over water, so we expected that the distance to the feeder (indicated by the duration of the bees' waggle runs) would be shorter for bees trained to the lake feeder. However, we found the opposite: waggle runs of bees trained to the lake feeder were significantly longer than those of bees trained to the land feeder. There are a number of possible reasons for the discrepancy between our results and those of Tautz et al. (2004). There might be differences in the relative amounts of visual contrast (and, therefore, optic flow) at our two study sites. This difference could result, for example, from there being more waves on our lake (greater visual contrast) or fewer shadows on the path along which our land bees flew (less visual contrast). Alternatively, the difference between our findings and those of Tautz et al. (2004) could result from the bees in the two studies flying at different relative altitudes, which could provide them with different amounts of optic flow.

Recruitment to Land and Lake Feeders

Although there was quite a strong effect of scent on recruitment levels (discussed below), when we pooled the data across trials there was no significant difference between the numbers of recruits arriving at the land and at the lake stations. This suggests that the location of the feeder (on the lake or on land) did not have a significant effect on recruitment levels. Moreover, in both trials recruits were able to locate the feeder on the water successfully. This finding contrasts with the results of both Gould & Gould (1982) and Tautz et al. (2004), who reported either no recruits or very low recruitment levels to feeders on the water compared to those on land.

The fact that our recruitment results do not match those of Tautz et al. (2004) may be due to scent differences, especially because our feeders' scents seemed to have a greater impact on recruitment levels than their locations (see Discussion). Because they were studying the behaviour of trained foragers, rather than recruits, Tautz et al. (2004) used unscented feeders, which is likely to have resulted in an overall decrease in recruitment levels. If there were few recruits to begin with, and the bees had slightly more difficulty locating a feeder on the water than they did locating a feeder on a lake, this could have led Tautz et al. (2004) to observe no recruits at all at the lake feeder.

It is difficult to interpret the relationship between our recruitment results and those of the original Lake Experiment, because we cannot be positive that scent was used in that experiment, and data on the exact number of bees recruited to land compared to lake feeders do not exist (Fred Dyer, personal communication). However, it is clear that our results do not match reports that 'no recruits came' to a feeder on a lake (Gould 1984). On the contrary, recruits arrived at the lake feeder in both trials of our experiment, and in trial 1 over 90 recruits arrived over the course of 2 h. Thus, while it is difficult to determine the extent to which our results disagree with the existing data from the original Lake Experiment, we found no evidence to support the claim that very few bees arrive at lake feeders compared to equidistant feeders on land.

Effects of Feeders' Scents on Recruitment Levels

We chose to use scented, as opposed to unscented, feeders for a number of reasons. The first of these is that scents greatly facilitate training, (von Frisch 1967, p. 17) and are specifically recommended when training bees over water (von Frisch 1967, p. 111). The second reason is that under natural conditions, bees rarely pollinate unscented food sources (von Frisch 1967, p. 48), and thus the behaviour of bees being recruited to unscented feeders is rather different from their behaviour when flying to scented feeders (Tautz & Sandeman 2003). Under ordinary conditions, bees that are recruited to unknown food sources tend to rely on both dance information (to locate the general vicinity of the food source) and scent (to pinpoint the food source's exact location; Dyer 2002). When no scent is present, recruits are known to have a much more difficult time locating feeders, resulting in very low recruitment levels (Tautz & Sandeman 2003; Riley et al. 2005).

Our use of scents also makes sense in the context of previous studies. Tautz et al. (2004) did not need to use scents because they were not studying the behaviour of recruits—they were studying the behaviour of trained foragers, who had already visited the feeder and thus did not need scents to locate it. However, Fred Dyer, who performed the original Lake Experiment described by Gould & Gould (1982), is fairly certain that scents were used during the experiment (personal communication). In our study, the aim of collecting recruitment data was to test the hypothesis that recruits would not arrive at the lake feeder, and using scents gave us the best chance of falsifying this hypothesis by providing us with higher recruitment levels overall.

It turned out that the scent of the feeders (anise versus orange) had a more dramatic effect on recruitment levels than the location of the feeders (land versus lake); across both trials, significantly more bees arrived at the anise-scented feeder than at the orange-scented feeder. The difference in recruitment levels was not the product of dance followers in the hive responding preferentially to dancers that smelled of anise, because in both trials bees following dancers with either scent were equally likely to subsequently leave the hive. Instead, the higher recruitment levels to anise-scented feeders are probably the result of recruits being better able to locate anise-scented feeders after leaving the hive. This is consistent with the fact that bees recruited by a dance to visit an unknown food site are known to use scent primarily to pinpoint the precise location of the food source once they arrive in the vicinity (Dyer 2002).

Similarly different recruitment levels to feeders with different scents were obtained in a past study in which equal numbers of trained bees performed dances simultaneously for two equidistant feeders with 2.5 M sugar solution, and approximately 4–12 times more recruits arrived at the anise-scented feeder than at a peppermint-scented feeder (T. D. Seeley, unpublished data). Although we used orange instead of peppermint scent, our recruitment results (4.7–7.5 times more recruits to anise in trials 1 and 2, respectively) are consistent with these earlier findings. Our observation that substantially different recruitment levels can occur at otherwise equally desirable feeders with different scents may be important to consider in future studies involving honeybee recruitment.

Conclusions

Based on our initial hypothesis that bees reject dances for 'implausible' locations, we made the following three predictions: (1) bees following lake dances should be less likely to leave the hive than bees following land dances; (2) followers of lake dances should take longer to leave the hive than followers of land dances; (3) very few, if any, recruits should be observed at the lake feeder. None of these predictions were supported by our data. Thus, we can confidently reject the hypothesis that honeybee foragers are rejecting dances for implausible locations that are unlikely to yield food.

There are a number of hypotheses that could explain why bees might not reject dances advertising a location on a lake. One possibility is that bees do not have a cognitive map, and thus do not recognize the dances as pointing to a location on a lake. A second possibility is that bees have a cognitive map, but either they use it only for navigation outside of the hive or it is overridden by other cues, such as odour, when they follow a dancing bee. A third explanation is that bees can use a cognitive map to determine that the dances indicate a location on the lake, but they do not interpret lakes as being implausible places to find food, either because they are not assessing the plausibility of dances at all or because they do sometimes find food on bodies of water (in the form of flowering water plants, for instance). Last, it is possible that dance followers recognize the lake as being an unusual, even implausible, place for a dance to indicate, but because 'there is no evidence of lying by dancers, and no advantage to dissimulation in a colony of non-reproductive sisters' (Gould 1990), they respond to the dances because they have no reason to believe the signal is in error.

Our data do not allow us to discriminate among these alternative hypotheses, so we cannot currently determine why dance followers did not reject dances for implausible lake sources. Consequently, although our study offers no evidence that bees possess cognitive maps, it also does not allow us to reject that hypothesis. However, if our bees did have cognitive maps, they clearly were not using them to reject dances indicating food sources that were implausibly located in the middle of a lake. On the contrary, we found no evidence that the bees, either before or after they left the hive, had any hesitation about responding to dances for locations on the lake. Thus, we conclude that the original Lake Experiment (Gould & Gould 1982), upon closer examination, does not provide convincing evidence that honeybees assess the plausibility of information contained in waggle dances and use this information to reject dances for implausible locations.

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