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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’.

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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.

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