The connection between landscapes and the solar ephemeris in honeybees

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SUMMARY

Honeybees connect the sun's daily pattern of azimuthal movement to some aspect of the landscape around their nests. In the present study, we ask what aspect of the landscape is used in this context – the entire landscape panorama or only sectors seen along familiar flight routes. Previous studies of the solar ephemeris memory in bees have generally used bees that had experience flying a specific route, usually along a treeline, to a feeder. When such bees were moved to a differently oriented treeline on overcast days, the bees oriented their communicative dances as if they were still at the first treeline, based on a memory of the sun's course in relation to some aspect of the site, possibly the familiar route along the treeline or possibly the entire landscape or skyline panorama. Our results show that bees lacking specific flight-route training can nonetheless recall the sun's compass bearing relative to novel flight routes in their natal landscape. Specifically, we moved a hive from one landscape to a differently oriented twin landscape, and only after transplantation under overcast skies did we move a feeder away from the hive. These bees nonetheless danced accurately by memory of the sun's course in relation to their natal landscape. The bees' knowledge of the relationship between the sun and landscape, therefore, is not limited to familiar flight routes and so may encompass, at least functionally, the entire panorama. Further evidence suggests that the skyline in particular may be the bees' preferred reference in this context.

Key words: honeybee, sun compass, landmarks, landscape, skyline, panorama, orientation.

INTRODUCTION

Dyer's discovery that honeybees learn the relationship between the sun's daily pattern of azimuthal movement (the solar ephemeris function) and some aspect of the landscape around their nests (Dyer and Gould, 1981; Dyer, 1987) has been useful in efforts to understand the mechanisms of sun-compass orientation (Dyer, 1987; Dyer, 1996), the structures of backup orientation systems (Dyer and Gould, 1981; Able, 1991), the specialized learning mechanisms by which bees acquire their knowledge of the sun's movements (Dyer and Dickinson, 1994; Dyer and Dickinson, 1996; Dyer, 1996; Towne and Kirchner, 1998; Towne et al., 2005; Towne, 2008) and the evolution of the dance communication and its associated orientation mechanisms (Dyer, 1991). However, there remain plausible interpretations of Dyer's original observations that, if correct, could reduce their functional significance and undermine some of the later work built upon Dyer's conclusions.

In his basic experiment, Dyer (Dyer and Gould, 1981; Dyer, 1987) placed a hive beside a conspicuous extended landmark such as a treeline and trained a number of bees to visit a feeder some distance away from the hive along the treeline. After allowing the bees to visit the feeder for a few days under sunny skies, Dyer transplanted the hive to a second treeline that was differently oriented. When the hive was opened at the new site, the transplanted bees mistook the second treeline for the first and flew to a feeder that was placed in its usual location relative to the treeline, although now in a different compass direction. On sunny days, the transplanted bees oriented their communicative waggle dances normally: upward on the vertical comb represented the direction of the sun in the field. Under overcast skies, however, the dances were oriented as if the hive and feeder were still at the first treeline; the bees had learned the relationship between the sun's course and some aspect of the

first site and were using this memory to locate the sun (erroneously) at the second site.

Most authors have either explicitly (e.g. Dyer, 1996; Towne and Kirchner, 1998) or implicitly (e.g. Gallistel, 1998; Towne et al., 2005) taken these observations to mean that most or all field bees usually learn the sun's pattern of movement in relation to the entire landscape panorama around their nests. Only this interpretation, after all, accounts for the apparent ability of recruit bees to interpret cloudy-day dances correctly: the dancers and recruits would be using the same directional frame of reference – the learned relationship between the solar ephemeris function and the landscape – and they could therefore communicate effectively. And Dyer (Dyer, 1984; Dyer, 1987) did indeed observe heavy recruitment in his cloudy-day experiments, although one cannot be certain that the recruit bees used the dance information (instead of, for example, odors) to find the feeder. Dyer reports further that the recruits were able to dance according to a memory of the sun's course in relation to the first treeline. If true, this would indicate that the recruits knew the sun's course in relation to the first treeline, even though they had never visited the feeder there. This would strongly support the inference that most or all bees normally learn the relationship between the sun's course and the entire landscape. However, because Dyer (Dyer, 1984; Dyer, 1987) focused his observations almost exclusively on trained foragers, he reports no detailed observations of recruits.

A plausible alternative to the usual explanation of Dyer's results is that his dancers, which usually had considerable experience visiting the feeder at the first site, had learned the sun's course only in relation to the narrow sector of the landscape along their familiar flight route to the feeder. Dyer himself pointed out this possibility and attempted to test it, although the resultant experiments were inconclusive (pp. 130-137 in Dyer, 1984). Furthermore, there are

possible explanations for Dyer's observations that would not require the bees to have learned the sun's course in relation to the landscape at all. It could be, for example, that the bees had learned the sun's position over time in relation to their own direction of movement or their own body orientation *en route* to the feeder. It is even possible that the bees merely matched their dance angles at the second treeline to those angles that the same bees had performed on sunny days at the first treeline, recalling only the previous dance angles relative to gravity on the comb, although some of the cloudy-day dances occurred at times of day at which the bees had not danced at the first site (pp. 100-101 in Dyer, 1984). It is not clear why bees would perform dances oriented according to memories acquired only while foraging at a single, specific food source because such dances could be interpreted only by the (presumably small) pool of potential recruits that had already acquired similar memories. Still, none of the alternative explanations we have suggested can be definitively ruled out. Dyer (Dyer, 1984) discusses these issues thoroughly and concludes, as we do, that the evidence is inconclusive as to whether most bees normally learn the sun's pattern of movement in relation to the entire landscape panorama.

Therefore, in the present study, we report our efforts to repeat an experiment first attempted by Dyer (pp. 130-137 in Dyer, 1984) to determine whether bees with no specific flight-route training normally learn the relationship between the sun's course and the entire landscape. We transplanted a hive on overcast mornings from the bees' home site to a second site that was a rotated panoramic twin of the first. Only after transplanting the hive did we move the feeder away from the hive and observe the bees' dances, which we expected would reveal whether the bees had learned the relationship between the sun's course and the natal landscape in the absence of specific flight-route training there.

MATERIALS AND METHODS
Bees, training and sites

We used bees of mixed sub-specific background, predominantly *Apis mellifera ligustica* (L.), purchased as 'Italian' bees from sources in southeastern PA, USA. The bees were kept in two-frame observation hives as described in Towne et al. (Towne et al., 2005). In the main experiment (of August 2007), the hive was placed along a sloping treeline several weeks before experimentation started (Fig. 1A; Fig. 2A) (hereafter the 'natal site'). A group of bees from this hive was then trained to visit a pneumatic feeder offering a lightly scented sucrose solution approximately 1 m from the hive entrance [techniques reviewed by Seeley (Seeley, 1995)]. All foragers were individually marked with numbered tags during the daily feeding period, which was approximately 06:00–08:00 h local solar time (LST), and the identities of all marked bees visiting the feeder (typically about 30) were recorded daily.

We maintained the feeder until an overcast morning, when we transplanted the hive and feeder to a twin landscape that was, however, oriented oppositely from the first (Fig. 1B; Fig. 2B) (hereafter the 'test site'). As soon as several of the marked bees started foraging, we moved the feeder away from the hive, in different directions in two different trials of the experiment. We moved the feeder as quickly as possible without losing the foragers, and we moved it in a single direction so that its compass bearing did not change with time. When the feeder was at least 30 m from the hive – the distance at which most of the dances of these bees begin to show discernible orientation (Towne and Gould, 1988) – we began recording the dance directions. Meanwhile, we continued to move the feeder away until it was either 140 m (first trial) or 110 m (second trial) from the hive (white arrows in Fig. 1B).
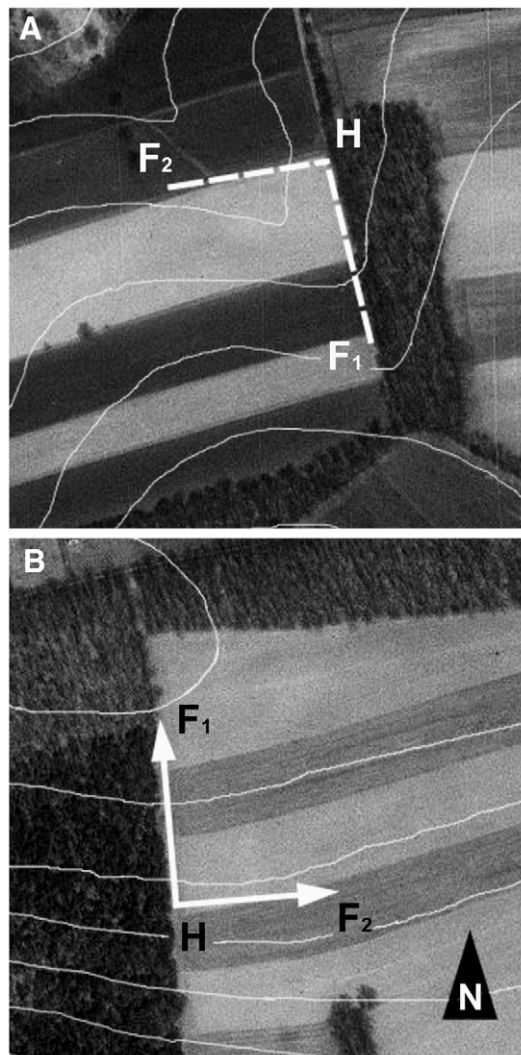

Fig. 1. Aerial views of the natal site (A) and test site (B) for the 2007 experiments. The hive (H) was placed in corresponding locations along sloping treelines at the two sites. The feeder at the natal site A was always directly beside the hive, and the feeders at the test site B were moved toward F_1 (white arrow 140 m northward from the hive) and F_2 (white arrow 110 m eastward from the hive) in the first and second trials of the experiment, respectively. The broken lines at the natal site (F_1 and F_2 in A) indicate the fictive locations of the feeders in the two trials. That is, there were actually never feeders there, but these were the predicted dance directions for bees using a memory of the sun's course in relation to the natal site under clouds at the test site in the first and second trials, respectively. North is indicated by the black arrowhead in B. Adjacent contour lines in both figures are separated by 6.1 m of elevation. The natal site A is at 75 deg. 46′10.5″W, 40 deg. 36′27.9″N; and the test site B is at 75 deg. 47′10.2″W, 40 deg. 37′12.9″N. Photos by the United States Geological Survey, courtesy of the USGS and TerraServer-USA.

A third trial of the experiment (October 2004) was performed using different home and test sites. In this trial, the feeder was established and moved on the day of the test, and the bees were marked with unique patterns of paint on the thorax and abdomen. Other details are given in the Results section. Panoramic images of the sites used in this trial were assembled automatically using Canon PhotoStitch software (Canon, Inc., Lake Success, NY, USA) from 18 individual wide-angle photographs (focal length 36 mm) of each site taken with a Canon camera in PhotoStitch mode. The camera
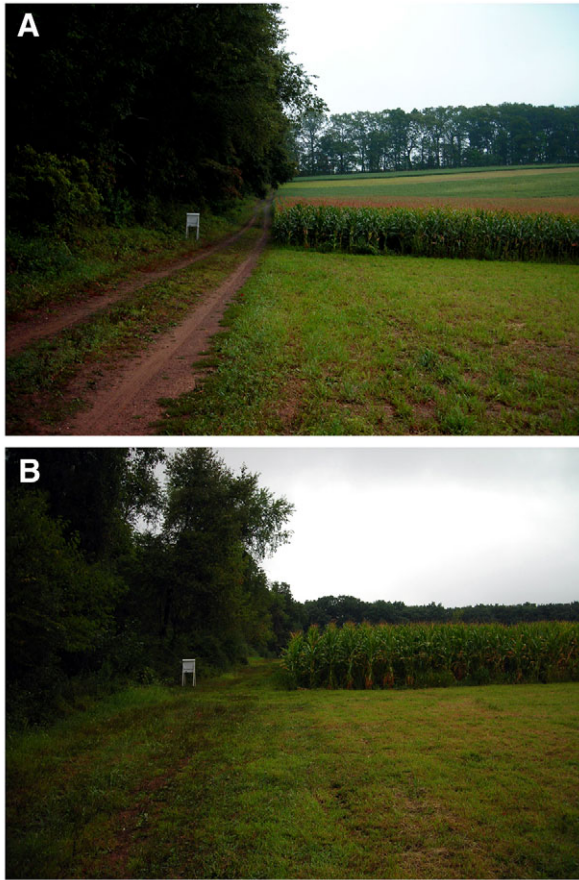
Fig. 2. Views of the hive (white object left of center) in place at the natal site (A, photo facing south-southeast) and test site (B, photo facing north-northwest). The landmarks and topographies of the two sites were similar, including valleys and then distant ridges in the directions opposite from the views shown here. Photos by the authors.

was held in the vertical orientation and rotated around the vertical post of a leveled tripod to ensure that the camera was aimed at the same elevation for all images. The same camera and tripod settings were used for both sites.

The test sites for these experiments were only 1.2 km (2004) or 2 km (2007) from the bees' home sites, within the foraging ranges of naturally sized colonies (Visscher and Seeley, 1982). Although the sites would have, ideally, been farther apart to ensure that all of the bees were initially unfamiliar with the test sites, Dyer (Dyer, 1984; Dyer, 1987) has shown that bees transplanted even smaller distances between panoramically similar sites interpret the new site as the original one as long as there is a cloud cover. Our previous (Towne et al., 2005) and current results (see below) strongly reinforce this conclusion.

Recording and analysis of dance directions

The directions of the bees' dances under overcast skies at the test treeline were recorded to the nearest 7.5 deg. in relation to a vertical plumb line as described in Towne et al. (Towne et al., 2005). The directions were recorded on a small voice recorder by an observer at the hive, and sky conditions were noted regularly by a second observer at the feeder. Each dance direction was scored based on a visual average of at least five wagging runs within a single bout of dancing, one bout being all dancing that occurred between

sequential round trips to the feeder by a single bee. This technique gives measurement errors of less than 8.5 deg. (Towne et al., 2005). No bee was scored more than once after a single trip to the feeder.

Dance directions were analyzed for clustering around predicted directions using the V-test or, when there was no predicted direction, the Raleigh test (Batschelet, 1981). Because sequential dances by a single bee are not independent of each other, we used the mean vector for each bee as a single observation for the statistical analyses, regardless of how many individual dances each bee performed. That is, each bee, not each dance, was weighted equally in the statistical analyses. Furthermore, all analyses included only well oriented dances that occurred before the sun or blue sky first appeared; the few bimodal and disoriented dances (see Results) are reported below but are excluded from the statistical analyses as these dances gave no single direction.

RESULTS

In order to determine whether bees lacking specific experience with a particular flight route can nonetheless recall the sun's compass bearing in relation to that route, we trained a group of individually marked bees to visit a feeder placed approximately 1 m from the hive entrance at the bees' natal site. We then transplanted the hive and feeder to a rotated twin landscape, the test site, on overcast mornings and only then moved the feeder away from the hive and observed the bees' dances. The natal and test sites were both dominated by sloping treelines (Figs 1 and 2) and were oppositely oriented.

The first trial of the experiment occurred on 10 August 2007. The hive was closed at 05:00 h, transported to the test site and opened under overcast skies. As soon as several marked bees began visiting the feeder, which was placed initially at its usual location beside the hive, the feeder was moved slowly up the treeline northward (Fig. 1B, white arrow toward F_1). By 06:52 h, the feeder was 30 m from the hive and we began recording dances. We continued to move the feeder thereafter until it was 140 m from the hive. The dance directions of all 15 bees that danced before the sun appeared are shown in Fig. 3. All of the bees initially oriented their dances as if they were visiting a feeder placed along the treeline to the south at their natal site (Fig. 3) ('natal site' prediction, which corresponds to the broken line extending southward toward F_1 at the natal site in Fig. 1A) ($\varnothing$=183 deg.; N=15 bees that had performed 1–6 dances each; r=0.99; P<0.001, V-test with a predicted direction of 165 deg.; all angles clockwise of north). Soon after the sun started to appear (at 08:04 h), the bees' dances switched to the correct direction for the test site. That is, the bees had begun the day dancing according to a memory of the sun's course in relation to their natal landscape but now re-oriented according to the actual location of the sun at the test site, which was approximately the opposite direction. Two bees performed a single bimodal dance each (Fig. 3, broken vertical lines), indicating both predicted dance directions on alternate wagging runs in a single dance, before switching over completely. The remainder of the day was mostly overcast, and the forecast called for the possibility of overcast weather again the following day, so we left the hive at the test site intending to return for a second trial in the morning. The next morning was clear, however, so we closed the hive and returned it to the natal site.

The dances performed by the transplanted bees under overcast skies indicated a location at the natal site (Fig. 1A, F_1) at which there were few or no resources for bees, so the dancers had almost certainly never foraged there. Nonetheless, all of the dancers knew the sun's azimuth in relation to this route, which suggests that they had learned the relationship between the sun's course and the entire landscape panorama at the natal site.
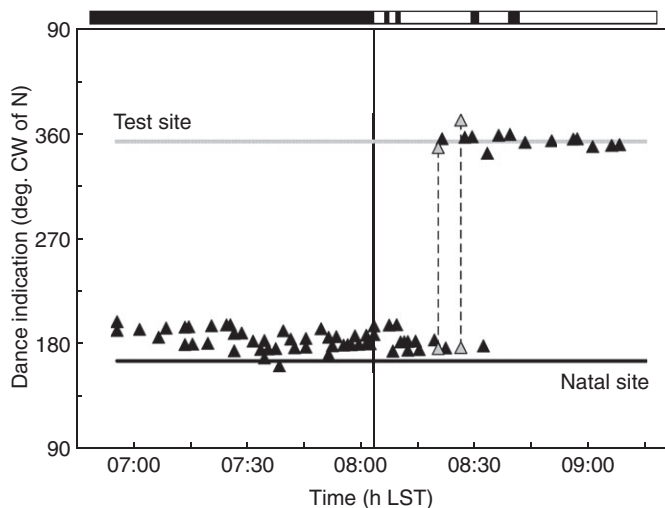
Fig. 3. Dance indications of bees under overcast skies at the test site on 10 August 2007. The bees had no route training at the natal site (Fig. 1A; Fig. 2A), and the hive was transplanted to the test site (Fig. 1B; Fig. 2B) and the feeder moved away from the hive toward the north-northwest (Fig. 1B, arrow labeled F_1) under overcast skies. Times are given in local solar time (LST). Each symbol represents the visual average of at least five wagging runs during a single bout of dancing by one bee; each bee was scored only once after a single trip to the feeder. The direction to the feeder, and thus the correct dance indication for the test site, was 353.5 deg. (horizontal gray line marked 'Test site'). The predicted direction for dances oriented by memory of the sun's course relative to the natal site (broken line toward F_1 in Fig. 1A) was 165 deg. (horizontal black line marked 'Natal site'). The sun first appeared this day at 08:04 h, indicated by a thin vertical line. Gray symbols connected by broken vertical lines show bimodal dances (see text). The sky bar above the graph shows the sky conditions: black indicates complete overcast; white indicates that we could detect the sun. There were no periods of blue sky without sun. CW; clockwise.

The next overcast morning was 16 August 2007, and we again closed the hive at 05:00 h and moved it to the test site. When we arrived, there were some breaks in the clouds so we left the hive closed and waited. The clouds eventually thickened and we opened the hive and put out the feeder under a solid overcast at 08:06 h. Many bees found the feeder immediately, and we were able to move it quickly, this time in a new direction perpendicular to the treeline (Fig. 1B, white arrow pointing east from the hive). By 08:29 h, the feeder was over 50 m from the hive and we started recording dances but continued to move the feeder until it was 110 m away (by 08:55 h). Meanwhile, a steady light rain began to fall.

Fig. 4 shows the dances of the 22 bees that performed a total of 98 dances during the hour-long recording period. A single bee performed two disoriented dances, which had distinct wagging segments that were more-or-less randomly oriented (Fig. 4, shaded triangles on the lower axis). This bee never performed well-oriented dances. The 21 other bees oriented as if they were flying in the corresponding direction at their natal site (Fig. 4) ('natal site' prediction, which corresponds to the broken line extending westward toward F_2 at the natal site in Fig. 1A) ($\emptyset$=271 deg.; N=21 bees, 1–10 dances each; r=0.98; P<0.001, V-test with a predicted direction of 260 deg.).

As in the first trial, most bees danced as if they were indicating a location at the natal site at which they had probably never foraged, suggesting that they knew the sun's course in relation to the entire natal landscape and not familiar flight routes only. A single bee
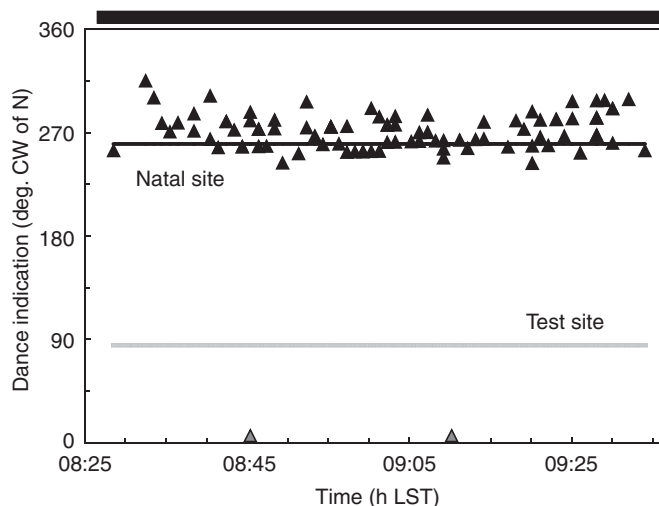

Fig. 4. Dance indications of bees under overcast skies at the test site on 16 August 2007. The hive was transplanted to the test site (Fig. 1B; Fig. 2B) and opened under overcast skies, and the feeder was moved away from the hive, this time toward the east (Fig. 1B, F_2). The direction to the feeder, and thus the correct dance indication was 85 deg. (horizontal gray line marked 'Test site'). The predicted direction for dances oriented by memory of the sun's course relative to the natal site (Fig. 1A, broken line toward F_2) was 260 deg. (horizontal black line marked 'Natal site'). One of the 22 bees performed two disoriented dances (gray symbols on the lower axis). All other symbols and conventions as in Fig. 3.

gave disoriented dances, as if she did not know sun's course in relation to the landscape. Disoriented dances might be expected to occur when bees experience conflicting cues, as when the bee's memory of the sun's course in relation to the landscape conflicts with directly perceived celestial cues (Towne et al., 2005), or when bees have no information about the sun's position. The bee performing disoriented dances on this day was one of seven dancers that had been marked at the feeder only the day before the experiment, so it is possible that she was young and had not yet learned the sun–landscape relationship. However, we do not know the age or history of this bee. Overall, the results of the second trial confirm the results of the first: most bees know the sun's course in relation to any flight route in their natal landscape, even if they have little or no experience flying that specific route.

One of us (W.F.T.) performed a third transplantation experiment on 2 October 2004 that was originally intended to test the bees' ability to orient under overcast skies in completely unfamiliar terrain. The bees foiled the experiment, however, by noticing a similarity between the two landscapes that we did not anticipate, and the results are interesting in the current context. The site from which the bees were transplanted was the floor of a thinly wooded valley (Fig. 5A; Fig. 6A) with pasture on the northern slope and forest on the steeper southern slope. We will refer to this site as the bees' 'home site', not their 'natal site', since the hive was moved there only five days earlier. The bees' actual natal site was a treelined site elsewhere that was entirely unlike the valley. Towne (2008) has shown that bees transplanted between such dissimilar sites will quickly learn the relationship between the solar ephemeris and the new site, however, so the bees in this experiment knew the relationship between the sun and their 'home site' in the valley, even though they were not native to it. The test site for this experiment was a second, broader valley floor (Fig. 5B; Fig. 6B), which was meadow
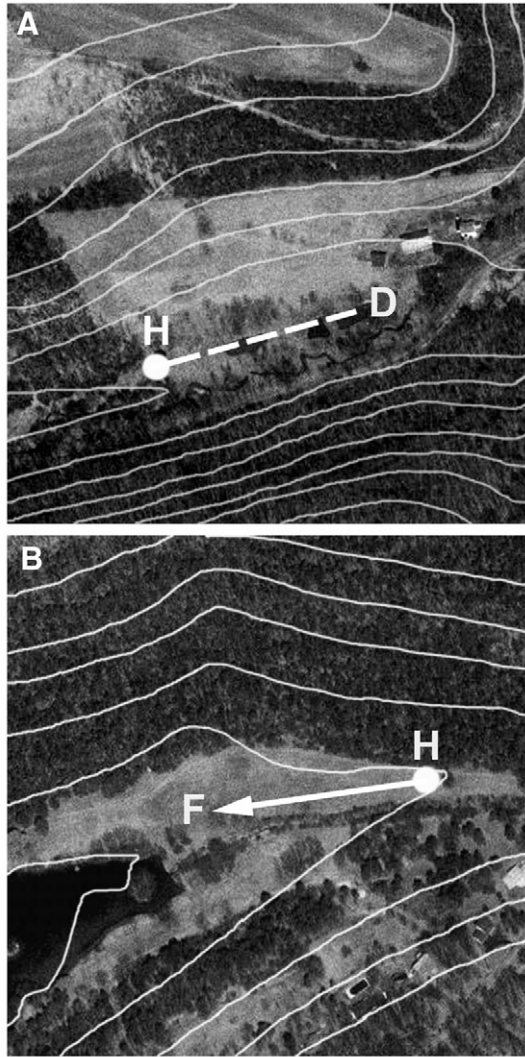
Fig. 5. Aerial views of the home site (A) and test site (B) for the valley floor experiment. The locations of the hive are indicated with white dots labeled H. Both sites were at the bottom of valleys (adjacent contour lines are separated by 6.1 m of elevation) but the landmarks at the two sites were quite different (see also Fig. 6). The bees were given no route training at the home site and were then transplanted to the test site under overcast skies, after which the feeder was moved toward the west (white arrow marked F in B, which is 200 m long). The direction that the bees indicated in their dances (Fig. 7) was roughly opposite the correct direction for the test site and is shown here relative to the home site A by the broken line marked D. The home site A is at 75 deg. 47′43.4″W, 40 deg. 36′41.4″N; and the test site B is at 75 deg. 47′18.8″W, 40 deg. 37′9.6″N. Photos by the United States Geological Survey, courtesy of the USGS and TerraServer-USA.

except for a double row of trees along a stream (just south of and parallel to the white arrow in Fig. 5B) and wooded slopes. The home and test sites seemed quite different to us, especially because the home site contained many isolated trees scattered throughout the valley floor (Fig. 5A; Fig. 6A) whereas the test site contained none.

But when the hive was transplanted from the home valley (H in Fig. 5A and Fig. 6A) to the test valley (H in Fig. 5B and Fig. 6B) under overcast skies, and a feeder was moved away from the hive along the valley floor (F in Fig. 5B and Fig. 6B; direction 262.5 deg.), the bees danced in a direction roughly opposite to the correct direction (Fig. 7) ($\varnothing$=74 deg.; N=30 bees that had performed 1–5

dances each; r=0.99; P<0.001, Raleigh test for uniformity). We later realized that the direction indicated by the dances corresponded to a flight down the valley floor at the home site (D in Fig. 5A and Fig. 6A). That is, the dancers had taken the test valley for their home site and oriented their dances accordingly.

These observations echo the results of the first two transplantation trials reported above (Figs 3 and 4), as these bees had never visited a feeder in the first valley and there were few or no natural resources for bees at the corresponding location there. (There was a feeder at the first valley four days earlier but all of the bees that visited there were marked, and the data in Fig. 7 include only naïve bees that were marked on the day of the observations.) The bees nonetheless knew the sun's pattern of movement in relation to the first valley and expressed that memory under clouds at the test site. Furthermore, in creating the match between the two sites, the bees evidently relied on the skyline panorama, as the two sites shared little else in common (Figs 5 and 6).

DISCUSSION
Bees link the solar ephemeris to the entire landscape

Our main conclusion is that experienced bees know the sun's pattern of movement in relation to an inclusive representation of the landscape, not only familiar flight routes. Dyer (pp. 131-137 in Dyer, 1984) reports the results of three transplantation experiments in which, like those we report in the present study, the bees lacked route training. Two of these experiments gave variable results that are difficult to interpret, probably because there were weak celestial cues available to the bees during the tests. The single test in which Dyer's bees all more-or-less agreed with each other are consistent with the results we report here: under overcast skies at the test site, the bees danced as if they were still at their home site. That is, the bees mistook the test landscape for their home landscape and based their dances on a memory of the solar ephemeris in relation to the latter, even in the absence of flight-route training (the mean error, however, was 46 deg.; more on these errors below). This matches the results of the first two trials we report here (Figs 3 and 4) (mean errors, 18 deg. and 11 deg., respectively). In addition, the experiment in which we transplanted bees from one valley floor to another gave similar results (Fig. 7), although we noticed the matching skyline panoramas (Fig. 6) only after the bees did. Altogether, these results show that bees do not require experience with a particular flight route in order to know the sun's azimuth in relation to it. That is, under overcast skies, experienced bees can probably recall the sun's compass bearing with respect to any flight route in the vicinity of their nests.

Our results, therefore, support Dyer's (Dyer, 1984; Dyer, 1987; Dyer, 1996) inference that most or all experienced bees know the sun's daily pattern of movement in relation to the entire landscape (or skyline) panorama around their nests. To this extent, the several studies that have been built upon Dyer's conclusions – work on the sun compass, backup orientation systems, solar ephemeris learning and the evolution of the dance communication (reviewed briefly in the Introduction) – retain their underpinning. Moreover, our results imply that recruit bees can use the direction information in cloudy-day dances, as dancers and recruits both have similar memories of the sun's compass bearing over time in relation to the landscape. That is, the memories can serve as an effective backup system for recruitment communication on cloudy days (Dyer and Gould, 1981).

It remains possible that experienced bees connect the solar ephemeris function not to the landscape or skyline panorama as a whole but to numerous different flight routes throughout the

Fig. 6. 360 deg. panoramic views of the home site (A) and test site (B) for the valley floor experiment. The two views are more or less oppositely oriented; that is, the center of the panorama is roughly south in A and north in B, which best represents how the bees matched the sites. The location of the hive at each site is indicated with a white dot labeled H. The direction indicated by the bees' dances (D) relative to the home site corresponds to the direction of the feeder (F) at the test site. That is, under overcast skies, the bees mistook the test site for the home site and set their dance angles accordingly (Fig. 7). The photos were taken at corresponding locations 45 m from the hive along the line toward the feeder (test site) or toward the direction indicated by the dances (home site). Note that the skylines of the two sites match closely, especially when one ignores the many trees in the foreground at the home site A (see also Fig. 5).

landscape. Although quite different, these two mechanisms would be difficult to distinguish functionally. That is, both mechanisms could explain our results and both could serve as effective backup systems for cloudy-day communication. The multiple flight-route mechanism, however, would require the bees to connect their solar ephemeris to numerous different routes, while they could connect it instead to a single or a small number of panoramic 'snapshots' of the landscape or skyline acquired in the vicinity of the nest. Collett

et al. (Collett et al., 2006; Collett et al., 2007) have reviewed the content and the use of such snapshots in insect orientation. The landmark snapshots used by bees and other insects to return to learned locations do seem to encompass broad angular views (Graham et al., 2004) (reviewed by Collett et al., 2006), although the question deserves further study (Stürzl and Zeil, 2007). And as we discuss below, such panoramic views could serve naturally as the fixed reference against which the detailed shape of the local solar ephemeris is first acquired.

Bees can clearly link extended boundary landmarks such as treelines and field edges to the solar ephemeris function (Dyer, 1987). Such boundary landmarks, when available, are also used in guiding insects along familiar paths [bees (von Frisch and Lindauer, 1954); ants (Collett et al., 2001)] and in setting the panoramic context for interpreting local cues (Collett et al., 2002). But strong boundary landmarks are unlikely to be conveniently located for connecting with the solar ephemeris in most landscapes, so bees probably rely on panoramic views of the landscape instead.

If bees do normally connect panoramic views of the landscape to the solar ephemeris, exactly what features of the landscape constitute those views? Our valley floor experiment suggests that bees connect the solar ephemeris to the skyline panorama; in this case, our test site shared little else in common with the bees' home site (Figs 5 and 6). And the visual feature of most landscapes that is best suited for use as a directional reference is almost certainly the skyline. First, the skyline can be a precise and reliable directional reference that, because it is distant, is affected little by an individual's exact location (Zeil et al., 2003) (reviewed by Collett and Zeil, 1997; Collett et al., 2003). Second, the skyline's profile will tend to be stable over time and also easily detectable under a wide variety of sky conditions (Möller, 2002; Stürzl and Zeil, 2007). Third, bees routinely use distant panoramic cues to determine the appropriate spatial context in which to search for local landmarks (reviewed by Collett et al., 2003). Finally, ants (Fukushi, 2001; Fukushi and Wehner, 2004) (reviewed by Collett et al., 2007) and bees (Southwick and Buchmann, 1995) have been shown to use the distant skyline in homing after displacements, and ants, at least, can evidently do so using skyline features that protrude as little as 2 deg. above the horizon (Wehner et al., 1996).
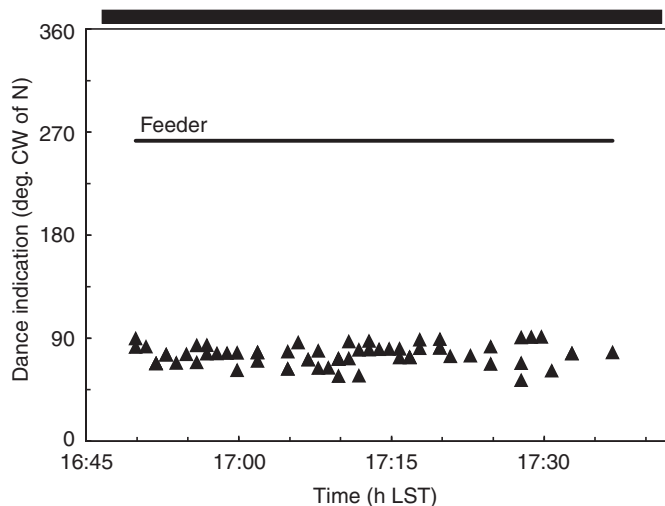

Fig. 7. Dance indications of bees that had been transplanted from their home on the floor of one valley (Fig. 5A; Fig. 6A) to the floor of another (Fig. 5B; Fig. 6B) under overcast skies. The bees had no training at the first valley, and they were marked at the newly established feeder on the day of the test. The correct dance direction for the test site was 262.5 deg. (horizontal black line) but the bees danced in roughly the opposite direction (mean 75 deg.), indicating that they mistook the test valley (Fig. 5B; Fig. 6B) for their home valley (Fig. 5A; Fig. 6A) and danced by memory of the sun's course in relation to the latter. The feeder was 100–200 m from the hive during the recordings. All other symbols and conventions as in Figs 3 and 4.

To test whether the skyline panorama is indeed an important reference to which bees connect the solar ephemeris, it may be possible to predict how bees will respond when transplanted between sites with similar skylines but different landmarks. Our valley floor experiment (Figs 5–7) is one example, although we did not predict the outcome in this case. Or one could transplant bees between sites with similar landmarks but different skylines. The latter experiment, too, might already have been done, also unintentionally: Dyer (Dyer, 1984; Dyer, 1987) and Towne et al. (Towne et al., 2005) have sometimes found that bees transplanted between two sites with similar boundary landmarks have not danced (under overcast skies) exactly as predicted based on the landmarks alone, occasionally erring systematically from the predicted direction by more than 45 deg. In these previous experiments, we accounted for the landmarks at the sites but not the skylines, which may explain why the bees did not perceive the sites exactly as we expected. In the current experiments (Figs 1–4), and in another series of experiments using the same two sites (Towne, 2008), the bees' errors relative to our predictions were small, possibly because both the landmarks and the skyline panoramas were similar at the two sites. The question clearly deserves further study.

In summary, it seems likely that in most landscapes, bees link the solar ephemeris function to the skyline panorama. This does not mean, however, that other directional references, such as boundary landmarks (Dyer, 1987) or the magnetic field, cannot be linked to the ephemeris as well.

On the reference against which the ephemeris is first learned

In the current experiments, we worked with experienced bees that had probably already learned the shape of the local solar ephemeris function. Therefore, our results do not directly illuminate the original acquisition of the ephemeris, unless the landscape is the reference against which the ephemeris is first learned. What, then, do we know about this issue?

Honeybees must first learn the shape of the local ephemeris function against some fixed directional reference, which could be a familiar flight route, the earth's magnetic field, the 'pole point' in the sky around which all celestial cues appear to rotate (Brines, 1980), conspicuous landmarks (Dyer, 1987), or the skyline panorama. The skyline panorama, in particular, can be an excellent directional reference that is insensitive to an individual's exact location, and experienced bees do know the spatial relationship between the solar ephemeris and the skyline (Fig. 6). Landmarks are the only other directional references that we know bees can link to the solar ephemeris (Dyer, 1987). All of this is consistent with the hypothesis that the landscape or skyline is the reference against which the sun's ephemeris is first learned but it does not rule out the possibility that other cues are used as well, or instead. Ants also seem likely to use the landscape as the reference for solar ephemeris learning, although, as in bees, other references cannot be ruled out (Wehner and Lanfranconi, 1981; Wehner, 1996).

The earth's magnetic field seems especially worth considering as a possible reference in this regard. Bees can use both the magnetic field (Collett and Baron, 1994) and celestial cues (Dickinson, 1994) as directional references for learning local landmarks around a feeder, although the bees seem to ignore magnetic cues when the celestial cues are good (Dickinson, 1994). Bees can also learn magnetic and celestial cues simultaneously with respect to the orientation of panoramic views inside small test arenas (Frier et al., 1996). Here, too, the magnetic cues appear to a play secondary or backup role, in that the celestial cues dominate when the magnetic and celestial cues conflict. Nonetheless, as magnetic and celestial cues are both learned with respect to the same views, bees can connect magnetic and celestial cues, at least indirectly (Frier et al., 1996). This supports the plausibility of the magnetic field as a reference for solar ephemeris learning.

However, the landscape, not the magnetic field, is clearly the bees' primary reference for locating the sun under cloudy skies, as Dyer's (Dyer and Gould, 1981; Dyer, 1987) original transplantation experiments have shown. It remains possible that the magnetic field is used as a backup system for locating the sun when the landscape and skyline are not useful. But in one test of this possibility, Dyer (pp. 106-110 in Dyer, 1984) transplanted bees from their home landscape to a dissimilar landscape under overcast skies and the bees failed to locate the sun altogether, as if their backup systems had been exhausted. The bees in Dyer's experiment adopted curious orientations that did not seem to fit any known hypothesis, and it may be that the bees simply matched the two landscapes or skylines in ways that Dyer could not predict. This experiment is clearly worth repeating, but for now it appears that bees do not use the magnetic field as a backup reference for locating the sun on cloudy days, even when the landscape fails to be useful (p. 107 in Dyer, 1984).

Might bees instead use the magnetic field as the original reference for learning the solar ephemeris, then connect the ephemeris to the landscape and then finally rely on the landscape alone as the reference? Yes, this possibility cannot be ruled out, although there is currently no evidence that supports it directly. Considerable evidence, on the other hand, supports the landscape or skyline as the primary reference.

A more likely role for the magnetic field in solar ephemeris learning is that it may serve as a reference by which bees adopt a fixed orientation from which they study the skyline, just as the magnetic field serves in the learning of local landmarks at a feeder (Collett and Baron, 1994), and as it may serve in the learning of natural scenes in general (Frier et al., 1996). Unique to the bees' initial learning of the landscape is the absence of a calibrated sun compass, which, once the latter develops, appears to take over as a primary directional reference for learning visual scenes (Dickinson, 1994). Helping the bees as they first learn the landscape or skyline in the absence of a sun compass, therefore, is a role in which the magnetic field could almost certainly be useful, especially where the landscape and skyline by themselves are directionally ambiguous or difficult. This, in turn, would help the bees to learn the solar ephemeris function, albeit indirectly. This role for the magnetic field seems to be consistent with the available evidence – and the absence thereof for any direct connection in bees between the sun and magnetic field – and with the magnetic field's apparent role as important (Collett and Baron, 1994; Frier et al., 1996) but secondary to celestial (Dickinson, 1994) and other visual cues (Fry and Wehner, 2002) as a directional reference for learning visual scenes in experienced bees.

The evidence taken together, then, suggests that the bees' primary reference for learning the solar ephemeris is the skyline panorama around the nest, at least when, as must happen often, strong landmarks such as treelines are not available near the nest. But other possible references, especially the magnetic field, cannot be ruled out. Studying solar ephemeris learning as it occurs in bees may turn out to be difficult because it probably takes place high in the air, like the learning of other distant panoramic cues (Collett, 1996; Collett and Zeil, 1997). Thus, the problem may be easier to study in ants where the state of our understanding of solar ephemeris learning is similar but where the learning at least takes place on the ground (Wehner and Müller, 1993; Wehner, 1996). Then again, using the honeybees' dances, one can readily measure the

honeybees' knowledge of the solar ephemeris function at any given time, as Dyer and Dickinson (Dyer and Dickinson, 1994) have done in showing that bees innately expect the sun's azimuth in the afternoon to be opposite its azimuth in the morning, for example, or as we (Towne et al., 2005) (Towne, 2008) have done in showing that the learned relationship between the sun and landscape, once acquired, strongly resists revision.

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