

Does swarming cause honey bees to update their solar ephemerides?

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Summary

Spatial orientation in the social insects offers several examples of specialized learning mechanisms that underlie complex learning tasks. Here we study one of these systems: the processes by which honey bees update, or fail to update, their memories of the sun's daily pattern of movement (the solar ephemeris function) in relation to the landscape. Specifically, we ask whether bees that have initially learned the solar ephemeris function relative to a conspicuous treeline at their natal site can later realign the ephemeris to a differently oriented treeline. We first confirm and clarify an earlier finding that bees transplanted passively (by being carried) do not re-learn the solar ephemeris in relation to the new treeline. When they cannot detect the sun directly, as on overcast days, these transplanted bees use a solar ephemeris function appropriate for their natal site, despite days or weeks of

experience at the new site. We then ask whether bees put through a swarming process as they are transplanted are induced to re-learn the solar ephemeris function at the new site, as swarming is a natural process wherein bees transplant themselves. Most of the swarmed bees failed to re-learn, even though they did extensive learning flights (in comparison with those of non-swarmed controls) as they first emerged from the hive at the new site. We hypothesize that the bees' representation of the solar ephemeris function is stored in an encapsulated cognitive module in which the ephemeris is inextricably linked to the reference landscape in which it was learned.

Key words: bee, sun compass, landmark, learning, orientation, swarming, cognition.

Introduction

Since the 1970s, it has become clear that learning in animals is often accomplished by specialized learning mechanisms, the properties of which are specific to the learning problems the animals need to solve (reviewed in e.g. Gallistel, 1990, 2000; Shettleworth, 1998, 2000). Some of the clearest examples of such learning involve spatial learning in social insects (Gallistel, 2000; Shettleworth, 1998; Dyer, 1997, 1998), especially path integration in ants and bees (Wehner et al., 1996; Wehner, 2003), the learning of landmarks around feeders and nests by bees and wasps (Lehrer, 1993; Zeil, 1993a,b; Wei et al., 2002; Collett and Zeil, 1997, 1998; Capaldi and Dyer, 1999; Capaldi et al., 2000), and learning of the sun's daily pattern of movement in ants (Wehner and Lanfranconi, 1981; Wehner and Müller, 1993) and bees (Dyer and Dickinson, 1994; Dyer, 1996). All of this learning occurs in the absence of immediate consequences for the animals, and it is probably best seen as the adaptive collection and processing of information, for later use, by specialized learning mechanisms (Gallistel, 1990, 2000; Shettleworth, 1998, 2000).

Here we focus on one of these systems, namely the mechanisms by which honey bees update, or fail to update, their solar ephemeris functions, that is, their memories of the sun's daily pattern of movement in relation to the landscape. Both bees (Dyer, 1987) and ants (Wehner and Lanfranconi, 1981) do indeed acquire reasonably accurate solar ephemeris

functions for use in their celestial compass orientation. In both cases, the insects begin with an innate expectation that the sun's azimuth in the morning is about 180° from its azimuth in the afternoon (Wehner and Müller, 1993; Dyer and Dickinson, 1994) and fill in the details of the local ephemeris function with experience (Lindauer, 1959; reviewed by Dyer, 1996).

Although it has often been assumed that bees keep their solar ephemerides fully up to date (Gould, 1980, 1984; Dyer, 1987), Lindauer (1971) had suggested, based on a long-distance latitudinal displacement experiment (Lindauer, 1957), that bees might imprint on the solar ephemeris functions at their natal sites. More recently, Towne and Kirchner (1998) have shown that bees can indeed fail strikingly to update their solar ephemerides. Their technique was a minor modification of Dyer's treeline-to-treeline transplantation technique (Dyer and Gould, 1981; Dyer, 1987), in which Dyer transplanted a hive from one treeline (the bees' natal site) to a visually similar but differently oriented treeline (the recipient site). After transplantation, some of Dyer's bees found a feeder at the recipient site placed in its accustomed location relative to the treeline. On sunny days, these bees oriented their communicative waggle dances according to their usual convention: a dance oriented upwards on the vertical comb corresponded to a food source in the direction of the sun in the

field. When Dyer transplanted bees on overcast days, however, bees that found the feeder at the new site usually oriented their dances as if they were still at their natal treeline, relying on a memory of the relationship between the solar ephemeris function and the natal landscape. This is how Dyer and Gould (1981) first showed that bees learn this relationship.

Towne and Kirchner (1998) basically repeated Dyer's procedure, but allowed the transplanted bees to forage under sunny skies at the recipient site for one to several days before observing the same bees' dances under overcast skies. Most of these long-term transplantees danced under overcast skies as if they were still at their natal site; they had not realigned their solar ephemerides to the new treeline, despite ample opportunity to do so. Thus the sun-learning mechanism seems to be surprisingly resistant to revision after the initial acquisition.

Here we extend these observations in two ways. First, we simultaneously compare the orientation of long-term treeline-to-treeline transplantees with the orientation of newly transplanted bees and also with that of un-transplanted bees native to the recipient treeline. The results clarify the effect of experience at the new site.

Second, we ask whether it is important that the bees in Towne and Kirchner's experiments (Towne and Kirchner, 1998) were transplanted passively, that is, carried to the recipient site by the experimenters. Assuming that the bees' learning mechanisms are designed to work under natural conditions, we might expect bees to be able to realign their solar ephemerides only when transplanted under circumstances that mimic natural events. One process by which bees normally transplant themselves is swarming, wherein roughly half of the workers in a colony leave their natal nest and, after a period of living outdoors in a cluster, move to a new nest site some distance away. Thus we hypothesized that bees put through a swarming process as they are transplanted from one treeline to another would, unlike passively transplanted bees, realign their solar ephemerides with respect to the recipient treeline.

Materials and methods

Bees, hives, feeders and schedules of activities (2000–2002)

We used bees of mixed subspecific background, predominantly *Apis mellifera ligustica*, purchased as 'Italian' bees from sources in southeastern Pennsylvania and southeastern Georgia, USA. The bees were kept in two-frame observation hives covered with roofs and wooden sides that allowed the hives to be kept outdoors. The hives were painted white and were mounted on white A-frame stands so that the assembled hives stood 145 cm tall and were visually conspicuous.

In all cases, bees were trained to visit pneumatic feeders offering lightly scented sucrose solutions and were individually marked with numbered, color-coded tags after having been recruited to the feeders at their natal sites (techniques reviewed in Seeley, 1995). The feeders' locations at both sites were marked with conspicuous colored or patterned signs 61 cm square mounted 1 m off the ground on

posts. These signs were intended to help the newly transplanted bees find the feeders at the recipient sites, and they were identical at both sites for any given experiment.

Honey bees rarely survive beyond 3 weeks as field bees (Visscher and Dukas, 1997), and in all experiments reported here, the transplanted bees lived at their 'natal' sites for at least four weeks, ensuring that they had their first flight experience there. In all experiments, feeders were generally set up for two feeding periods every day, typically 7:00 h–9:00 h and 13:00 h–15:00 h local solar time (LST), although the exact time and duration of the feeding periods varied. Hereafter, all times are given in LST.

Field sites (2000, 2001 and 2002)

We used two panoramically similar but oppositely oriented field sites 2.2 km apart. Both sites had conspicuous treelines from which agricultural fields sloped away to valleys about 30 m of elevation below (Fig. 1). In each case, the bottom of the valley was approximately 400 m from the treeline, and the next ridge, beyond the valley (not shown in Fig. 1), was about 400 m farther. The hives and feeders were placed 200 m apart at corresponding locations at the two sites (see H and F in Fig. 1). Hereafter, we refer to these sites as the 'north-facing treeline' (Fig. 1A) and the 'south-facing treeline' (Fig. 1B), even though the correspondences between the two landscapes include not just the treelines but also several broader features of the landscapes and the visually conspicuous hives and signs.

Passive transplantation (2000 control bees, 2001 and 2002)

We transplanted bees passively using two different techniques. In most cases, we captured groups of about 20 marked foragers at the donor site feeder in the late afternoon and carried these bees in small wire cages (2.5 cm×2.5 cm×13 cm) to the recipient hive. The cages were then left inside the recipient hive until the following morning, at which time the bees were released into the hive. This technique prevented most of the transplanted bees from being rejected by their new nest mates, and many of the transplanted bees became regular visitors to the feeder at the recipient site. The second technique by which we transplanted bees passively involved closing the hive at the end of the day and moving the entire hive intact to the recipient site. Many of these bees, too, found the feeder at the recipient site.

Since the recipient site was only 2.2 km from the donor site, within the foraging range of naturally sized colonies (Visscher and Seeley, 1982), some of our transplanted bees were familiar with the area around the recipient site, and typically about 20% returned to the donor site after transplantation. Although the two experimental sites ideally would have been farther apart to ensure that transplanted bees were initially unfamiliar with the recipient site, we were constrained by the available topography and the need to travel frequently between the two sites. Two types of evidence suggest strongly, however, that the transplanted bees we later observed under cloudy skies were indeed initially unfamiliar with the recipient site: (1) these bees had failed to return to their natal site after

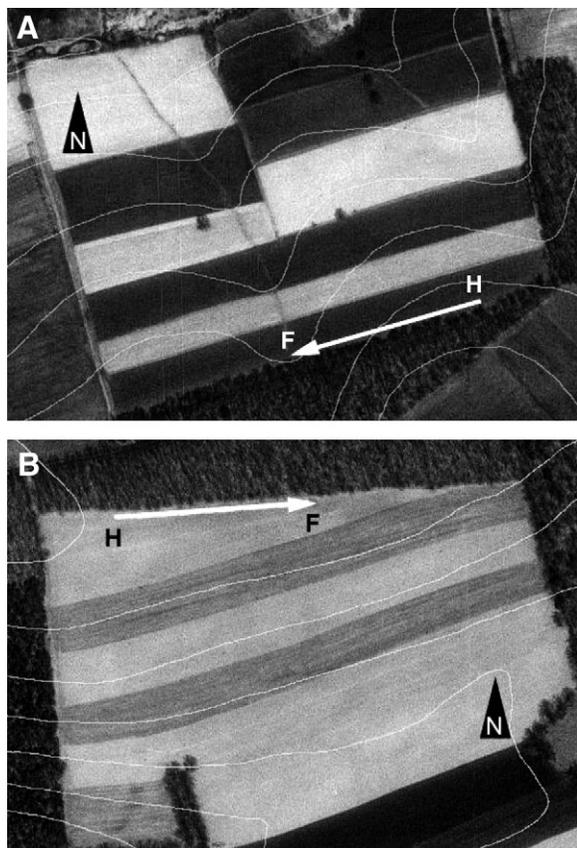


Fig. 1. Aerial views of the field sites indicating locations of hives (H) and feeders (F). White arrows are 200 m long and indicate the bees' outward flights to the feeders. North is indicated by black arrowheads. The agricultural fields adjacent to the treelines sloped downward away from the treelines; adjacent contour lines are separated by 6.1 m of elevation. Different sites served as donor and recipient sites in different experiments. The north-facing treeline (A) is at $75^{\circ}47'12.1''\text{W}$, $40^{\circ}37'6.4''\text{N}$, and the south-facing treeline (B) is at $75^{\circ}47'12.6''\text{W}$, $40^{\circ}36'56.7''\text{N}$.

transplantation, as if they did not recognize the recipient site as part of their former colony's foraging range, and (2) most of these bees later mistook the recipient site for their natal site and oriented their dances accordingly on subsequent cloudy days, as if they had no information about the sun's location relative to the landscape at the recipient site.

Creation, transplantation and re-hiving of swarms (2000)

We transplanted three different colonies by putting them through artificial swarming processes as they were transplanted. In all cases, the swarms' natal site was the south-facing treeline (Fig. 1B). In the few days before the swarms were made, large numbers of bees were individually marked at the feeder at the natal site. As soon as the colonies were transplanted, feeders identical to those at the natal site were set out at the usual location relative to the treeline at the recipient site, and many of the marked, transplanted foragers visited them regularly.

Each of the three swarms was created using all of the roughly 4000 bees from a two-frame observation colony. These swarms were small but within the wide range of sizes that occur naturally (reviewed by Seeley, 1977; Winston, 1987). To make each swarm, the colony's queen was placed in a small wire cage with several attendant workers, and the cage was attached to the center of a wooden cross (45 cm high and 50 cm wide, crosspiece attached 33 cm from the bottom of the vertical member). The cross was mounted on an octagonal plywood platform 50 cm across, held about 1 m off the ground on a metal post. A second octagonal piece of plywood attached on top of the cross provided a bit of shelter for the swarm. After the cage bearing the queen was attached to the cross, the bees from the observation colony were shaken onto the lower platform, and the bees quickly streamed up the vertical member of the cross, many fanning their Nasonov glands, to form a cluster around the queen. Artificial swarms created in this and similar ways begin to seek nest sites and otherwise seem to behave like natural swarms (Lindauer, 1955; Seeley, 1977; Robinson and Dyer, 1993). As soon as each swarm was clustered, the (now empty) hive was moved away, and the swarm was placed where the hive had been.

After they were created, the three swarms were subjected to somewhat different treatments. Swarm 1 was created at noon on 30 June 2000 and was re-hived 7 h later after flight activity for the day had ended. This amount of time in the swarm cluster is short but within the range of that seen in natural swarms. Swarms occasionally find new nest sites quickly, apparently because their scouts sometimes begin searching for nest sites up to 3 days before they depart the parent colony (reviewed by Winston, 1987). While Swarm 1 was clustered, the two frames of comb from the observation hive were replaced with new frames containing only wax comb foundation. To re-hive the swarm, the queen cage was removed from the swarm cluster and placed inside the observation hive atop the upper frame. The glass window of the hive was then folded out to a horizontal position, and the swarm was shaken from the swarm apparatus onto the glass. The bees streamed from the glass into the new hive, many fanning their Nasonov glands. When all of the bees were inside, the hive was closed and transported to the recipient site, and the queen was released. The bees' first flights from the new hive occurred the next morning at the recipient site, and the learning flights of the marked bees were recorded at this time (see below).

Swarm 2 was created similarly at 14:15 h on 28 July 2000, except that the bees on the original frames were liberally smoked with a bee smoker to cause the bees to engorge on honey before they were shaken onto the swarm apparatus (after Robinson and Dyer, 1993). This was intended to mimic the engorgement that occurs in preparation for natural swarming (Combs, 1972). This swarm was carried the same evening, as a swarm, to the recipient site (replacing the Swarm 1 colony) and was allowed to hunt for a new nest site there. We placed an empty nest box with a pheromone lure on a tall post near the swarm in hopes of luring the bees to occupy it, so that the swarming process could run to its natural completion.

Unfortunately, the bees selected instead a natural nest cavity in the wooded area to the northeast of the hive (Fig. 1A) and departed for that cavity at about 14:00 h on 30 July, after 2 days in the cluster (1.5 days at the recipient site). Because the queen was still caged, however, the swarm aborted its relocation effort and straggled back over the next 30 min. While the bees were away, we removed the swarm apparatus, replaced it with a new hive, and transferred the queen cage into it. The new hive had two new frames bearing only comb foundation and had one of its glass sides removed, allowing the bees to enter. After all of the bees had crawled into the new hive, we replaced the glass side and released the queen. The learning flights of these bees upon their first departure were not recorded, as there was too much flight activity around the hive in the middle of the afternoon.

Upon being hived, Swarm 2 abandoned its search for new nest sites, but the swarm did not settle into its new nest as quickly as did Swarms 1 and 3, which were hived at dusk. The bees of Swarm 2 did not immediately spread across the combs but continued to cluster around the queen inside the hive for more than a day after being hived. Also, although the bees of Swarm 2 started to build new comb during their first day in the new hive, they did not build as much during the first few days as did the other swarmed colonies.

Swarm 3 was created at 14:00 h on 8 August 2000 using the same smoking process that was used for Swarm 2. This swarm was left at its natal site and took to the air twice on its second day, 9 August, once at 13:05 h and again at 14:55 h, each time returning to the (still caged) queen after a short period. The swarm remained at its natal site until the end of flight activity that evening, at which time it was re-hived using the same process that was used for Swarm 1 and transplanted to the recipient site. As for Swarm 1, the learning flights of the marked foragers from this colony were recorded at the recipient site the next morning.

In addition to the three swarmed colonies, a control colony that was not put through a swarming process was transplanted intact on 29 June 2000, one day before Swarm 1 was transplanted. The bees from this control colony visited a feeder of their own, and the bees from the two colonies (swarmed and control) were kept separate at the feeders with the help of powder boxes on the entrances of the hives, which dusted the bees lightly with non-toxic paint powder as they passed through, different colors being used for different colonies. In addition, the two feeders were marked with differently colored signs and offered differently scented sugar water.

The control colony was successfully used to measure the learning flights of non-swarmed bees (see below), but the marked bees originally transplanted with this colony turned out not to be useful as controls for the sun-learning aspect of the experiment, as almost all of the bees were lost (presumably dead) by the time the first solidly overcast day occurred at the recipient site 10 days later (the swarmed bees had a much higher survival rate; see below). Subsequently, we used the caging technique to supply the recipient site with groups of non-swarmed control bees as needed.

Recording and analysis of learning flights (2000 and 2001)

Bees and wasps perform learning flights on their first departures from a nest or feeder or when they encounter novel circumstances there, and the flights help the insects to learn the visual features of the targets (Zeil, 1993a,b; Lehrer, 1993; Wei et al., 2002; reviewed by Wehner, 1981; Zeil et al., 1996; Collett and Zeil, 1997, 1998). In the first, hovering phase of learning flights at the hive entrance, bees leap into the air, immediately reverse direction to face the hive entrance, and hover in front of the entrance for several seconds, swinging back and forth through tight arcs within 1–2 m of the entrance. In the second, circling phase, the bees turn from the hive entrance and undertake circling or figure-eight flights of increasing height and diameter within about 5–10 m of the entrance, after which the bees usually leave the hive's immediate vicinity.

The learning flights of individually marked bees were observed as the bees exited the hive for the first time on the morning after they were transplanted. An observer sat beside the hive and watched the bees through the glass as they approached the hive entrance and then departed. The durations of the flights were timed with a stopwatch capable of recording two time intervals after a single starting point, which allowed both phases of each flight to be recorded. The hovering phase started when an individually marked bee left the hive and ended when the bee turned more than 90° from the hive entrance, or when the bee started its circling flight. The circling phase started immediately after the hovering phase and continued until the bee broke the circling/figure-eight pattern and flew away. Some bees were lost to the observer during either the hovering or circling phase of the flight, and only flights for which the entire phase was observed were included in the analysis. Statistical comparisons between the flight durations of the three different types of transplantees were made using the (non-parametric) median test, which is relatively insensitive but entails minimal assumptions about the shapes of the distributions (Conover, 1999; Siegel and Castellan, 1988).

For both phases of the learning flights, the results from Swarms 1 and 3 are not significantly different (Fig. 5Aiii,Biii, black vs shaded; $P > 0.6$ for the hovering flights, and $P > 0.4$ for the circling flights; t -tests), so for statistical comparisons with the results from the non-swarmed bees, the results from the two swarms are pooled.

Dance recording and statistical analysis of dance directions

The observation hives had one-way entrances that diverted all incoming bees to one side of the comb so that most waggle dances occurred on that side. During recording, this side of the hive was covered with four thicknesses of a fabric shroud that prevented dancers from seeing the sky. The sun itself was not detectable through the shroud, even on clear days. Dances were observed under the shroud through the glass side of the hive, and dance directions relative to vertical were estimated using a plumb line for reference. Dance directions were recorded in a notebook as the time on a clock face (e.g. '1:30')

equals 45° clockwise of vertical) to the nearest quarter-hour (7.5°). On one occasion, 14 July 2002, there were too many dances to record this way, so the dances were videotaped (under the shroud) for later analysis. Because sequential wagging runs in a single bout of dancing do not superimpose exactly (von Frisch, 1967; Towne and Gould, 1988; Weidenmüller and Seeley, 1999), each dance direction was estimated based on observing and visually averaging at least five wagging runs. Each bout of dancing was scored only once; a bee had to return to the feeder before her next dance was scored. Each data point in Figs 2–4 and 6–7, then, represents one bout of dancing.

To estimate the errors inherent in our measurement technique, we analyzed dances occurring during four different periods under full sun. This includes 158 dances by 77 bees at two different sites. If we assume that the bees' dance directions varied little (because they were flying under full sun) and that all variation was therefore due to our measurement errors, we can estimate the variability in the measurements by combining all four samples, aligning their means, and calculating the standard deviation of the combined sample. This standard deviation is 8.5°.

Dance directions were analyzed for clustering around predicted directions using the V-test (Batschelet, 1981). All statistical analyses of dance directions from overcast days exclude dances that occurred after the sun or blue sky first appeared to us and also bimodal dances (see Results), as the latter could not be assigned a single direction.

Results

The effect of experience at the recipient site

On several occasions, we have observed long-term treeline-to-treeline transplantees dancing at the recipient site as if they knew the sun's azimuth there, even when we ourselves could not see the sun or blue sky, or when other transplanted bees danced according to the solar ephemeris function appropriate for their natal site (Towne and Kirchner, 1998; our unpublished observations). Such bees could have been using two different mechanisms to orient their dances: (1) they could have been detecting the sun's azimuth indirectly through the clouds using weak skylight polarization cues that are sometimes present even when human observers can detect neither the sun nor blue sky (Labhart, 1999; also von Frisch, 1967, pp. 366–377), or (2) the bees might have re-learned the sun's pattern of movement in relation to the new treeline. In order to separate the effects of fresh celestial cues from the effects of re-learning the sun's course, we simultaneously compared the orientation of three groups of bees with different amounts of experience at the recipient site: long-term transplantees, newly transplanted bees, and natives of the recipient site. We made no attempt to measure skylight polarization cues ourselves, relying instead on the newly transplanted bees (which had little or no opportunity to re-learn the sun's course) to indicate whether celestial cues were available. If these newly transplanted bees could detect polarization cues through the clouds, they would

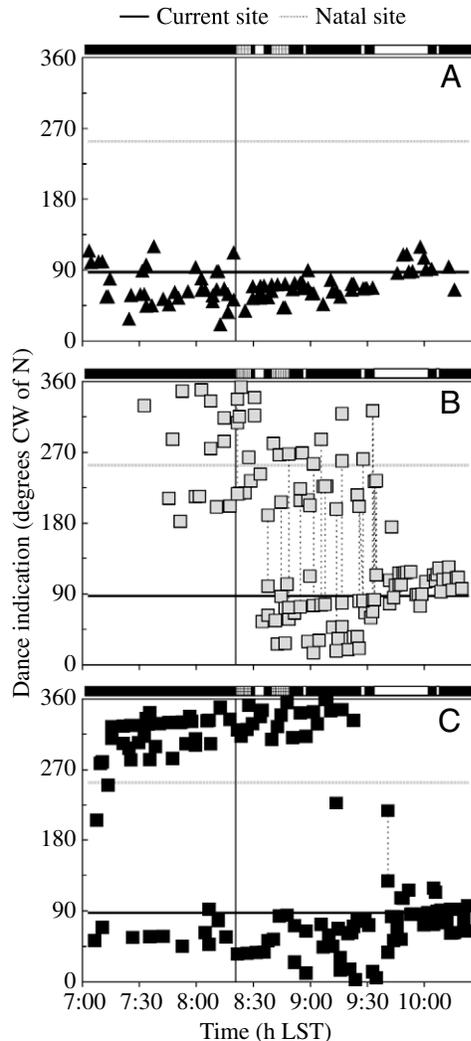
be expected to dance correctly at the recipient site; if not, they would be expected to dance by memory of the sun's course at their natal site.

On several days in July 2002, we transplanted groups of about 20 marked bees native to the north-facing treeline (Fig. 1A) into a hive at the south-facing treeline (Fig. 1B). Meanwhile, a group of marked foragers native to the south-facing (recipient) treeline was trained to visit the feeder there. The transplanted bees adopted into the recipient hive foraged at the feeder alongside the natives under sunny or partly sunny skies for 1–15 days. Then on the day before a predicted overcast, a new cage full of bees was transplanted from the feeder at the north-facing treeline into the recipient hive; these bees would be new to the recipient site when they were released the next morning. If the next morning was indeed overcast, we recorded the dances of all three groups of bees as they visited the feeder at the recipient site.

The results of one such experiment, on 28 July 2002, are shown in Fig. 2. Throughout the recording period, all bees native to the recipient site (Fig. 2A) indicated the correct direction to the feeder ($\bar{\theta}=68.6^\circ$; $N=32$ dances by 7 bees; $r=0.91$; $P<0.001$, V-test, predicted direction 87.5° ; all analyses here and below exclude dances occurring after the sun or blue sky first appeared). The newly transplanted bees (Fig. 2B), by contrast, initially danced according to their memories of the solar ephemeris function relative to their natal treeline ($\bar{\theta}=267.2^\circ$; $N=14$ dances by 4 bees; $r=0.53$; $P<0.005$, V-test, predicted direction 253.5°). This is what Dyer observed on several occasions (Dyer and Gould, 1981; Dyer 1987), and it indicates that these bees were not able to locate the sun using celestial cues. As the sun began to make brief appearances at 8:22, these newly transplanted bees began to switch their dances to the correct direction for the current site. Several did bimodal dances for a while (broken vertical lines in Fig. 2B), indicating both directions on alternate wagging runs. Dyer (1987) sometimes observed such dances under similar conditions.

The results mentioned so far indicate that there were no celestial cues available to the bees before the sun first appeared to us. During this time, the long-term transplantees (Fig. 2C) danced mainly in a direction corresponding roughly to the 'natal site' prediction ($\bar{\theta}=332.9^\circ$; $N=49$ dances by 15 bees; $r=0.66$; $P<0.001$, V-test, predicted direction 253.5°). In the preceding days, these bees had all foraged under sunny or partly sunny skies at the recipient site, and 7 of them had more than a week of experience there. Nonetheless their dances mainly resembled those of the freshly transplanted bees and were appropriate for their natal treeline, not for the current site. Most of these bees had clearly not realigned their solar ephemerides to the new treeline.

Several dances of long-term transplantees (Fig. 2C) corresponded roughly to the 'current site' prediction before the sun first appeared (11 dances altogether by three different bees). It is possible that these bees had realigned their solar ephemerides to the new treeline. But it is also possible that these bees were able to extract celestial cues that we and the



other bees failed to detect. We cannot separate these possibilities based on these data.

Why were almost all of the bimodal dances performed by recent transplantees (Fig. 2B, broken vertical lines) rather than long-term transplantees (Fig. 2C)? This difference is probably attributable to the celestial cues available as these bees first flew out to the feeder. The first dances of the long-term transplantees that oriented by memory of their natal site were performed sooner and indicated directions more northward (average time of first dance 7:26; average direction 290°, $N=12$) than the first dances of the newly transplanted bees that later danced bimodally (average time of first dance 8:15; average direction 196°; $N=3$). Thus these two groups of bees probably first flew out under slightly different sky conditions. The memory of bees using fresh celestial cues evidently operates with a time lag (Lindauer, 1963; Gould, 1984), and bees in transplantation experiments sometimes persevere for a while in dancing in an accustomed direction even after sky conditions change (Dyer, 1987). This is interesting in itself, but for the present purpose it probably means that the differences between the dances of the newly transplanted bees and those

Fig. 2. Dance indications of native and transplanted bees under overcast conditions on 28 July 2002. Each symbol represents the visual average of at least five wagging runs during a single bout of dancing; each bee was scored only once after a single trip to the feeder. The hive was at the south-facing treeline (Fig. 1B), where the direction to the feeder, and thus the correct dance indication, was 87.5° clockwise (CW) of N (Current site, horizontal black line in each panel). The predicted direction for dances oriented by memory of the sun's course at the north-facing treeline (Fig. 1A), to which the transplanted bees were native, was 253.5° (Natal site, horizontal gray line in each panel). (A) Bees native to the current site; (B) newly transplanted bees released on the day of the observations; (C) long-term transplantees, released at the current site 2–15 days earlier. Bimodal dances are indicated by broken vertical lines connecting the two dance directions. The sky bar above each panel indicates sky conditions: black indicates complete overcast; white indicates that the sun was visible; shading indicates the sun peeking frequently in and out. There were no periods of blue sky without sun. The sun first appeared at 8:22 h LST, indicated on each panel by the thin vertical line running the entire height of the graph. Statistical analyses here and below exclude dances occurring after the sun first appeared.

of the long-term transplantees reflect differences in their recent flight experience, not long-term differences in their solar ephemeris functions.

A second result similar to that of Fig. 2 is shown in Fig. 3, taken 1 day before the observations shown in Fig. 2 and involving many of the same bees. In this case, the newly transplanted bees had been transplanted the day before and had one afternoon's experience at the recipient site under mostly cloudy skies, and the long-term transplantees had been transplanted 4–14 days earlier. The bees native to the current site danced correctly (Fig. 2A; $\bar{\theta}=77.9^\circ$; $N=18$ dances by 8 bees; $r=0.95$; $P<0.001$, V-test, predicted direction 87.5°), and both groups of transplantees danced mainly as if they were at their natal treeline (Fig. 2B,C; new transplantees: $\bar{\theta}=281.1^\circ$, $N=40$ dances by 13 bees, $r=0.78$, $P<0.001$; long-term transplantees: $\bar{\theta}=316.3^\circ$, $N=42$ dances by 11 bees, $r=0.48$, $P<0.05$; both V-tests with a predicted direction of 253.5°). Again, the long-term transplantees do not appear to have updated their solar ephemerides at the recipient site.

The results of a third similar experiment, from 14 July 2002, are shown in Fig. 4. New transplantees were released earlier the same day, and the long-term transplantees were transplanted 1–5 days earlier. As in the other trials, the native bees danced correctly from the outset (Fig. 4A; $\bar{\theta}=84.9^\circ$; $N=67$ dances by 7 bees; $r=0.95$; $P<0.001$, V-test with a predicted direction of 87.5°). Both groups of transplanted bees, taken separately or together, were not significantly oriented toward either predicted direction (Fig. 4B,C; for the combined sample: $\bar{\theta}=13.9^\circ$; $N=123$ dances by 14 bees; $r=0.16$; $P>0.1$ for both predicted directions, V-tests) until after the sun appeared toward the end of the observations. Moreover, throughout this period we observed a total of 19 dances by transplanted bees (new and long-term), for which we were unable to discern any orientation at all; we scored them as round dances (7 dances), disoriented waggle dances

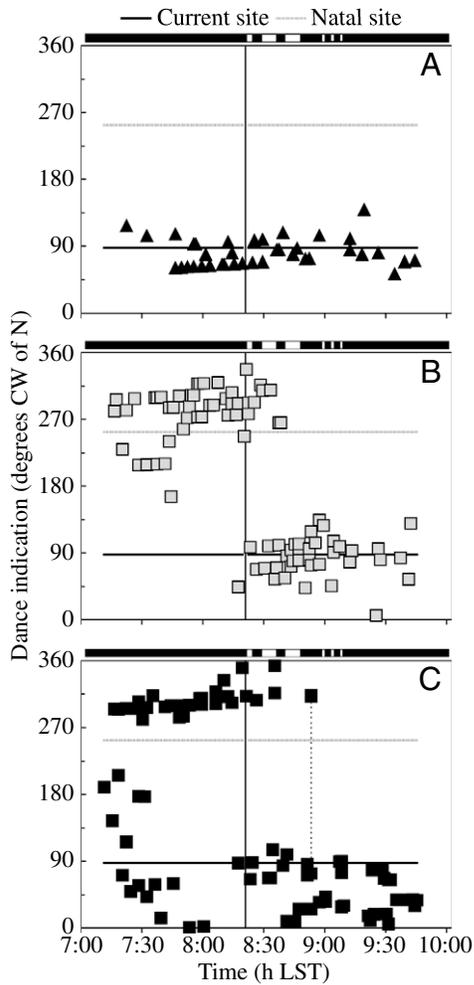


Fig. 3. Dance indications of native and transplanted bees under overcast on 27 July 2002. (A) Bees native to the current site; (B) newly transplanted bees that had less than one full day's experience under mostly cloudy skies at the current site; (C) long-term transplantees. All other symbols and conventions as in Fig. 2.

(9), or something in between (3), depending on whether the dances had wagging segments.

The transplanted bees in Fig. 4 were probably so poorly oriented because they were working with two types of conflicting information, weak polarization or spectral cues (Wehner and Rossel, 1985; Wehner, 1994; Labhart, 1999) penetrating the cloud cover and their long-term memories of the sun's pattern of movement in relation to their natal treeline. Such compromise orientation has been observed before (Dyer, 1987; Towne and Kirchner, 1998) under conditions like this. Indeed, one can see this phenomenon in Fig. 4 toward the end of the observations: many of the dances of the transplanted bees indicated roughly northward (0°) at 10:15 h and then gradually drifted toward the correct direction over the next hour as the sun emerged. (We see this drifting again in Fig. 7B below.) The poor orientation at the beginning of the observation period also calls to mind the scattered orientation seen by Rossel and Wehner (1984; reviewed in Wehner and

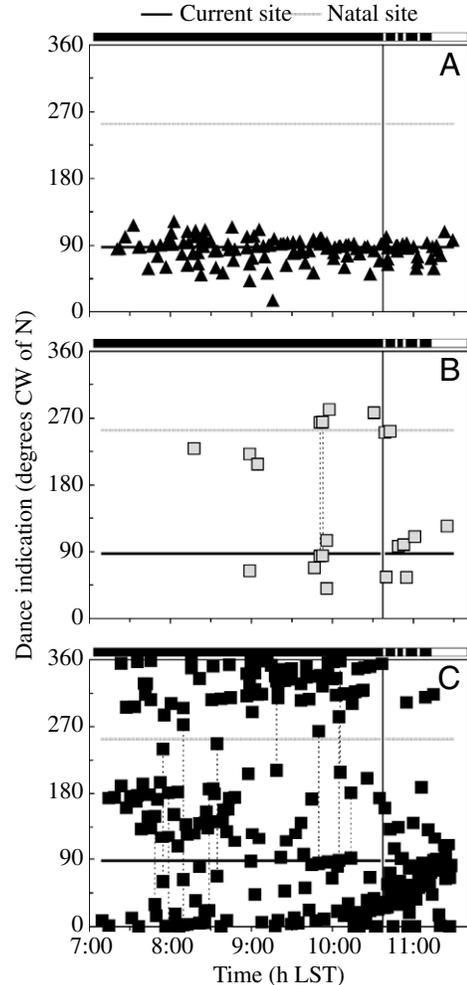


Fig. 4. Dance indications of native and transplanted bees under overcast on 14 July 2002. All symbols and conventions as in Figs 2 and 3.

Rossel, 1985), when bees were given only small patches of unpolarized ultraviolet light with which to orient their dances. Bees take such patches of light to be any point in the anti-solar hemisphere, not necessarily on the anti-solar meridian, and their dances are correspondingly scattered over about 180° .

A noteworthy feature of these results is that all of the bees native to the recipient site (Figs 2A, 3A, 4A) are consistently well oriented throughout, even though the celestial cues were weak or ambiguous. These bees must have been relying on their memories of the solar ephemeris function at this (their natal) site. Further, while the orientation of these bees is very good, it is not as good as the orientation one sees on sunny days, when bees can orient directly by strong celestial cues: The mean vector for all dances of the native bees in Figs 2A, 3A, and 4A combined ($r=0.936$, $N=152$) is significantly shorter, indicating greater scatter, than the mean vector for four periods of recordings made under sunny skies ($r=0.964$, $N=158$; $P<0.01$, Watson and Williams F -test; Batschelet, 1981, p. 122).

Another noteworthy feature of these results is that the

dances of the long-term transplantees oriented by memory of their natal site seem to be consistently skewed by about 45° from the natal site prediction (Figs 2C, 3C, dances at the upper left of each panel). It could be that these dance directions were affected by weak celestial cues, although if this were the case the dances of the newly transplanted bees (Figs 2B, 3B) should have been similarly affected, and they seem not to have been – at least as far as one can tell, given the considerable variability in the dance directions of the newly transplanted bees. Dyer (1987) observed similar skews in some of his cloudy-day displacement experiments, and their cause remains unknown.

Learning flights

To assess the extent to which our transplanted bees initially re-oriented to the recipient site, apart from their solar ephemeris functions, we measured the learning flights of transplanted bees as they first emerged from their hives after transplantation. We measured both the hovering and circling phases of the flights of bees transplanted by the three different transplantation techniques used in this study, i.e. (1) when small groups of bees were transplanted in cages, (2) when whole hives were transplanted intact, and 3) when whole colonies were put through a swarming process as they were transplanted. The caged bees were transplanted in groups of about 20 bees on several occasions during August 2001. The two hives that were transplanted intact were the control colony for the swarm experiments, transplanted on 29 June 2000, and a second colony transplanted on 24 August 2000. The swarmed colonies were Swarm 1 and Swarm 3 (see below), hived on 30

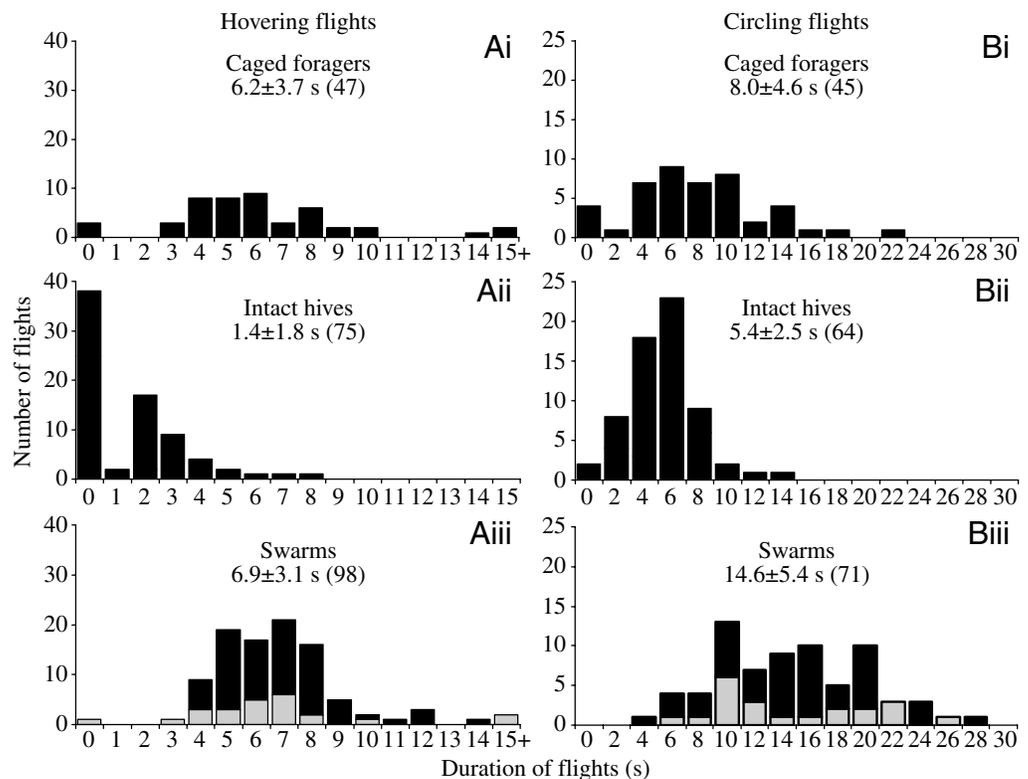
June and 9 August 2000, respectively. The results of all these measurements are shown in Fig. 5.

The bees whose hives were transplanted intact, without swarming, performed fewer hovering flights than each of the other two groups (Fig. 5A), and the hovering flights of the bees from intact hives were the shortest ($P < 0.0001$ for the flight durations of intact hives compared to those of each of the other groups; median tests). Robinson and Dyer (1993) likewise found that non-swarmed bees performed fewer and shorter hovering flights than swarmed bees, although more of their non-swarmed bees performed hovering flights (80% compared to our 51%), probably because our methods for transplanting the colonies were different. Importantly for the present context, Robinson and Dyer also found that the great majority of swarmed bees, but not non-swarmed bees, reoriented quickly to their new nest location, preferring to return to the location at which they were hived over their original nest site only a short distance away. That is, the swarmed bees acted as if they knew that their nest site had changed.

The hovering flights of the caged bees (Fig. 5Ai) were only slightly shorter than those of the swarmed bees (Fig. 5Aiii); the difference is marginally significant ($P = 0.0496$, median test). It is not surprising that the caged bees did substantial hovering flights, since they had spent the night caged in a foreign hive, and learning flights at hives (reviewed by Collett and Zeil, 1998) and feeders (Wei et al., 2002) both tend to be modulated upwards when bees have experienced changes there.

For the circling orientation flights (Fig. 5B), the three groups are significantly different from each other in all pairwise comparisons ($P < 0.0002$ for all comparisons; median tests).

Fig. 5. Hovering (A) and circling (B) learning flights of bees transplanted by three different techniques: caging small groups of foragers (Ai, Bi), moving the entire hive intact (Aii, Bii), and putting the colonies through a swarming process as they were transplanted (Aiii, Biii). Note that the scales of the graphs for the hovering flights (A) and circling flights (B) are different. Also shown in each panel is the mean flight duration \pm s.d. and the sample size, the latter in parentheses. The flight durations for Swarms 1 and 3 are indistinguishable (Aiii, Biii; shaded compared to black), so the results from the two swarms are pooled for statistical comparisons with the other groups (see Materials and methods).



The swarmed bees again performed the longest flights, but in this case their flights were substantially longer than those of the caged bees. This difference can be attributed to the swarming process, which signals to the bees that they have moved to a new nest site (Robinson and Dyer, 1993).

The effect of swarming on relearning the solar ephemeris function

To determine whether swarming causes bees to realign their solar ephemerides to a rotated landscape, we put colonies through an artificial swarming process as they were transplanted from the south-facing treeline (Fig. 1B) to the north-facing treeline (Fig. 1A). The first swarm was created in the early afternoon on 30 June 2000, and it was hived and transplanted at dusk the same evening. A control, non-swarmed colony was also transplanted the day before. Many of the marked bees from both colonies visited feeders 200 m to the WSW at the recipient site (Fig. 1A) in the bees' accustomed location relative to the treeline but now in the opposite compass direction. The feeders offered food in the morning and afternoon for the next 2.5 weeks.

We needed to observe the dances of the swarmed bees on overcast days when the clouds obscured all celestial cues useful to the bees. We ourselves cannot detect all of these cues (see Wehner and Rossel, 1985; Wehner, 1994), however, so we transplanted non-swarmed bees as controls. Because non-swarmed bees do not re-learn the solar ephemeris function at the recipient site (Figs 2–4 above), they should dance correctly at the recipient site only when fresh celestial cues are available; conversely, they should dance by memory of their natal site when such cues are absent. Unfortunately, there was no period of solid overcast until 16 days after the control colony was transplanted, and by then only one (2.3%) out of the 43 marked control bees that had regularly visited the feeder at the recipient site had survived. This is not surprising, as these bees were not necessarily young when they were first tagged at the donor site, and field bees rarely survive as long as 3 weeks (Visscher and Dukas, 1997). Interestingly, however, the swarmed bees showed greater longevity: 23 (32.4%) of the 71 marked foragers survived for at least 16 days after transplantation. In any case, because the non-swarmed control bees had largely disappeared, we resorted to transplanting additional control bees using the caging technique (beginning on 9 July) for the remainder of the study, and it is the caged transplantees that served as the control bees for all cloudy-day dance recordings reported below.

The morning of 15 July was overcast, and the surviving foragers from the Swarm 1 colony and some of the cage-transplanted control bees visited the feeders and danced. The dances were recorded by two observers, one at each colony, and the results are shown in Fig. 6A,B. Before the sun appeared at 8:32 h LST, the dances of the bees from the Swarm 1 colony were oriented mainly according to the 'natal site' prediction (Fig. 6B; $\bar{\theta}=63.7^\circ$; $N=32$ dances by 10 bees; $r=0.71$; $P<0.001$, V-test with a predicted direction of 87.5°); that is, the bees took the current treeline to be their natal treeline and

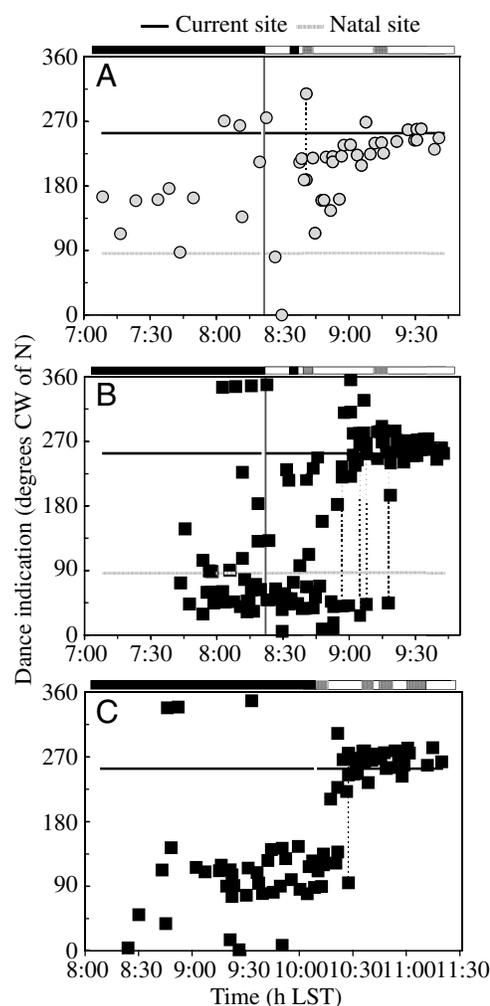


Fig. 6. Dance indications of non-swarmed control bees (A) and Swarm 1 bees (B,C) under cloudy skies. Unlike the previous figures, the three panels are not from the same day: A and B are from 15 July 2000, while C is from 17 July 2000. Sky bars and other conventions as in Figs 2–4, except that shaded regions on the sky bar indicate periods when blue sky was visible but not the sun. Note also that the current (recipient) site is now the north-facing treeline, making the 'current site' prediction 253.5° .

danced accordingly. The control bees (Fig. 6A), from which we were able to record only a small sample during this time, gave more scattered dances, not significantly clustered around either predicted direction ($\bar{\theta}=168.8^\circ$; $N=11$ dances by 6 bees; $r=0.63$; $P>0.1$, V-tests for both predicted directions). After the sun had been out for a while, all of the bees switched over to the dance direction appropriate for the current site, and the Swarm 1 bees performed a few bimodal dances briefly as they made the transition (Fig. 6B, broken vertical lines). The Swarm 1 bees, then, clearly had not realigned their solar ephemerides to the new site, even with over 2 weeks' experience there.

Another overcast period occurred 2 days later. This time we had only one observer to record dances, so we recorded only from the Swarm 1 hive. (Ideally, these experiments would involve three observers, one tending the feeders and one at

each hive, but this day we had to proceed, on short notice, with only two.) The results are shown in Fig. 6C. The results mimic those of 15 July (Fig. 6B): the dances of swarmed bees that occurred before we first saw blue sky are significantly clustered around the 'natal site' prediction ($\bar{\theta}=89.8^\circ$; $N=39$ dances by 9 bees; $r=0.71$; $P<0.001$, V-test with a predicted direction of 87.5°), confirming that the Swarm 1 bees had not realigned their solar ephemerides to the landscape at the recipient treeline.

Bees that experience swarming processes like the one we used for Swarm 1 perform extensive learning flights (Fig. 5) and, importantly, return reliably to their new hive, even when the old hive is available at its original location nearby (Robinson and Dyer, 1993). One might also expect, therefore, that the swarming process would induce bees to realign their solar ephemerides to the landscape around their new nest. But our Swarm 1 bees seem to have retained only their memory of the sun's course relative to their natal landscape.

Then again, there are many stimuli associated with natural swarming that the Swarm 1 bees did not experience and that could possibly trigger re-alignment of the solar ephemeris under natural conditions. These stimuli include, among others, engorgement of the workers with honey before they leave their natal nest (Combs, 1972); the shaking or vibration signals that occur throughout the period in the swarm cluster (Donahoe et al., 2003); wings-together worker piping (Seeley and Tautz, 2001) and swarm warming (Seeley et al., 2003), both of which build during the last hour before take-off; and buzz-running, which may be the final signal for departure (Lindauer, 1955; Esch, 1967). Thus we moved the Swarm 1 colony away and transplanted two additional swarms using modified swarming procedures that included more of the stimuli experienced by bees in natural swarms.

Swarm 2 was created on 28 July 2000 from a colony native to the donor site. This time the bees were liberally smoked with a bee smoker to stimulate engorgement of the workers with honey before they were shaken from the comb. The swarm was then transplanted as a swarm, searched for nest sites, and took to the air 1.5 days later (30 July). Thus the bees experienced all of the stimuli associated with searching for nest sites and lift-off. Because the queen was still caged, however, the swarm aborted its relocation effort and returned. While the swarm was away, we replaced the swarm apparatus with a hive, and the bees moved in. A number of marked bees from this colony then visited a feeder at the recipient site until an overcast period occurred over 2 weeks later on 14 August.

A third swarm was created similarly on 8 August. This swarm was allowed to remain at the donor site until it lifted off for a new nest site the following day. Because the queen was still caged, the swarm returned, and it lifted off and returned again 2 h later. The Swarm 3 colony was finally hived and transplanted to the recipient site at dusk that same evening (9 August), and the bees were allowed to forage at the recipient site for the next 4 days until the first overcast period occurred.

In addition to these two swarmed colonies, 69 control bees were transplanted in cages between 2 and 4 August into the

colony of Swarm 2 after it had been hived at the recipient site. Most of these non-swarmed control bees were adopted into the Swarm 2 colony, although 14 (20.3%, a typical fraction) found their way back to their natal site. Some of the control bees that remained at the recipient site foraged from the feeder there until the first overcast period occurred 10 days later.

The morning of 14 August was mostly cloudy, although small patches of blue sky were available from time to time. Nonetheless, we recorded dances for an hour from about 7:30 h–8:30 h LST, and most bees from both colonies (4 out of 5 from the Swarm 2 colony and 7 out of 11 from the Swarm 3 colony) danced toward the current site prediction, as if they knew the sun's location. By the afternoon feeding period the cloud cover had become complete, and we again recorded dances.

The results from the afternoon period are shown in Fig. 7. Several bees from each colony danced before the sun appeared

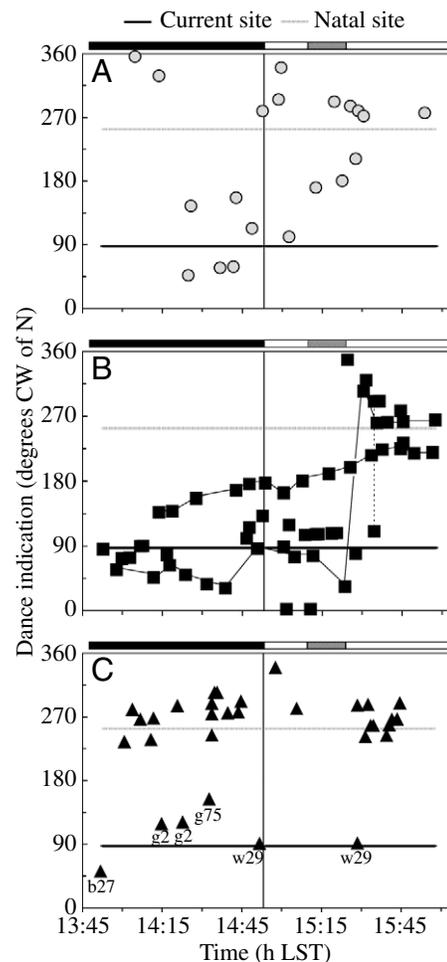


Fig. 7. Dance indications of non-swarmed control bees (A), Swarm 2 bees (B), and Swarm 3 bees (C), under cloudy skies on 14 August 2000. Sky bar and other conventions as in Fig. 6. In B, consecutive dances of the two bees that danced the most are connected by thin black lines. In C, the dances of the four individual bees that indicated only the natal site prediction before the sun became visible are labeled with each bee's identifying tag.

at 14:53 h LST. The results from the control bees (Fig. 7A) are not very useful, as we observed only 9 dances, and these are not significantly clustered, although they are closer overall to the 'natal site' prediction ($\bar{\theta}=59.2^\circ$; $N=9$ dances by 5 bees; $r=0.36$; $P>0.05$, V-test for either predicted direction). The dances of the Swarm 2 bees (Fig. 7B), on the other hand, were consistent with the 'natal site' prediction ($\bar{\theta}=92.6^\circ$; $N=21$ dances by 5 bees; $r=0.76$; $P<0.001$, V-test with a predicted direction of 87.5°). The Swarm 2 bees, then, had not realigned their solar ephemerides in the 2 weeks they had spent at the recipient treeline.

The dances of two Swarm 2 bees that danced throughout much of observation period on 14 August are connected with thin black lines in Fig. 7B to illustrate some typical observations of individual bees not shown in the other figures. The results from these bees show (1) that a given bee tends to dance in a more-or-less consistent direction in sequential bouts of dancing, (2) that different bees sometimes dance in somewhat different directions, and (3) that bees using a memory of the sun's course relative to their natal treeline sometimes shift their dance directions gradually as weak celestial cues become available. Dyer (1987) has noted and discussed each of these in the context of his short-term displacement experiments. The differences between bees could be the result of different recent experience or the result of different thresholds among bees for responding to weak celestial cues. We cannot currently separate these possibilities. And the gradual reorientation evidently represents a compromise between two different memories, one old and one fresh. There seems to be much more to learn about how individual bees integrate memories to select dance directions.

While the Swarm 2 bees clearly failed to realign their solar ephemerides to the recipient site, the Swarm 3 bees observed on the same day gave mixed results (Fig. 7C): The dances of the Swarm 3 bees were clustered around the 'current site' prediction overall ($\bar{\theta}=267.6^\circ$; $N=19$ dances by 10 bees; $r=0.48$; $P<0.005$, V-test with a predicted direction of 257.5°), although 4 out of the 10 bees indicated only the 'natal site' prediction (these dances are labeled with each bee's individual tag number in Fig. 7C). Thus there seems to be a difference between the Swarm 2 and Swarm 3 bees, for which there are a few possible explanations. First, it may be that some of the Swarm 3 bees had realigned their solar ephemerides in the 4 days they had spent at the recipient site, although some (4 out of 10) had not. While the swarming processes used for Swarms 2 and 3 differed somewhat, both swarms selected and departed for new nest sites, and both aborted their departures because the queen was still caged. The two swarms differed mainly in the way they were hived: Swarm 2 was hived in the afternoon as it returned from an aborted departure, and the bees seemed to take a couple of days to fully settle into the new hive, while Swarm 3 was hived in the evening after an aborted departure. It seems possible, but unlikely, that these differences would affect the bees' solar ephemeris learning.

A second possible explanation for the different orientation we observed in Swarms 2 and 3 is that the bees in the two

colonies may have had different experience with celestial cues in the hours immediately preceding the afternoon dance recordings. There were certainly celestial cues available earlier in the day, because a large patch of blue sky had become visible by the time we stopped recording dances at 8:40 h LST in the morning. Also, 4 of the bees that danced by memory of their natal site in the afternoon, indicating that they had not re-learned the solar ephemeris function, had nonetheless danced correctly (3 bees) or bimodally (1 bee) in the morning. We do not have detailed records of the sky conditions throughout the period between the two recording sessions, but it seems likely that some of the bees that danced during the afternoon session had flown to the (empty) feeder under an incomplete cloud cover between the sessions. If the Swarm 3 bees, transplanted more recently, flew out more often than the Swarm 2 bees during this time, then this might account for the fact that some of the Swarm 3 bees knew the sun's actual location during the afternoon session.

A third difference between the Swarm 2 and Swarm 3 colonies is that the colonies spent different amounts of time at the recipient site before the first cloudy day occurred: Swarm 2 had been there for 15 days, while Swarm 3 had been there for only 4 days. As unlikely as it may seem, our results overall are consistent with the idea that bees that have been at a recipient site for short periods may be more likely to act on weak celestial cues penetrating the clouds than are bees that have spent many days at the recipient site (see all of the transplantees in Fig. 4 and the control bees in Fig. 6, for example). It is not clear why bees would do this, but it is suggested by our observations. Again, there is much to learn about how bees integrate old and new memories in selecting dance directions.

Overall, it is clear that the bees in Swarms 1 and 2 and about half of the bees in Swarm 3 failed to update their solar ephemerides at the recipient site. We cannot rule out the possibility that some of the Swarm 3 bees re-learned, although it seems unlikely given the results from the other swarmed bees and the other possible explanations for the orientation of the Swarm 3 bees.

Discussion

The landscape surrounding the nest is the fixed frame of reference against which bees initially learn the sun's daily pattern of movement. Dyer and colleagues (Dyer and Gould, 1981; Dyer, 1987; Dyer and Dickinson, 1994, 1996) have shown that the resultant solar ephemeris function becomes linked in each bee's memory to the bee's knowledge of the landscape around the nest, so that experienced bees can determine the sun's location under overcast skies using only earthbound cues. Towne and Kirchner (1998) have shown, and we have confirmed here (Figs 2–4), that this link between the solar ephemeris function and the landscape is surprisingly resistant to revision. When bees are passively transplanted from their natal landscape to a panoramically similar but differently oriented landscape, the bees fail to realign their solar ephemerides to the new landscape. This is especially

striking because the bees certainly attend carefully to the sun's location in their daily activities; they simply fail to use this information to update the relationship between their solar ephemerides and the landscape.

The failure of our bees to update their solar ephemerides when transplanted passively is less surprising when we consider that bees are not carried to new landscapes under natural conditions, let alone to landscapes that closely resemble their natal ones. Bees normally do displace themselves in swarming, however, so we initially expected bees put through a swarming process as they were transplanted to quickly realign their ephemerides to the new site. Even our simplest swarming process, in which the bees were re-hived 7 h after the swarm was created (Swarm 1, Fig. 6B,C), would seem likely to cause realignment of the solar ephemeris to the new landscape if such realignment normally occurs: bees put through a swarming process like the one we used quickly start searching for new nest sites, and our bees did extensive re-orientation flights as they departed their new hive for the first time (Fig. 5). Such bees readily adopt their new nest site, choosing the new site over their natal nest a short distance away (Robinson and Dyer, 1993). Nonetheless, most of our swarmed bees failed to realign their ephemerides to the recipient site. It remains possible that our swarming processes simply omitted essential stimuli needed to trigger re-learning in natural swarms, especially cues that may occur inside the nest starting days or even weeks before a swarm departs (Winston, 1987, pp. 181–186) or as a swarm moves into its new nest, although this seems unlikely given that such cues are not needed to trigger reorientation to the nest itself.

The cost of the bees' failure to update their ephemerides after swarming might be minimized by the rapid turnover of workers that normally occurs in colonies. Visscher and Dukas (1997), for example, found that the mean lifespan of field bees under natural conditions was just 7.7 days. Our own (very limited) observations on this issue suggest, however, that this rapid turnover of workers may not occur in colonies newly founded by swarms: the foragers in our Swarm 1 colony showed greater longevity than the bees in the non-swarmed control colony transplanted at about the same time. Such increased longevity in swarmed bees, whatever its mechanism, is probably necessary because newly-founded colonies need at least 3 weeks to produce a new generation of workers. It would certainly seem advantageous for the colony founders to update their solar ephemerides in such circumstances. This may be why younger bees tend to depart with swarms (Winston 1987, p. 186); perhaps many of the bees in natural swarms learn the solar ephemeris for the first time at their new nest site.

Taken together, our observations seem consistent with Lindauer's hypothesis that bees imprint on the sun's course (Lindauer, 1971), but the observations resonate even more with the view that sun learning in bees is accomplished by a purpose-built, adaptively specialized cognitive 'module' (reviewed by Gallistel, 1990; Shettleworth, 2000). Such modules often fail to be affected by information manifestly important to the animals in other contexts, a property called

impenetrability or encapsulation (Fodor, 1983), which can leave the animals seeming almost incredibly obtuse, like our long-term transplantees dancing as if they had never seen the sun at the recipient site.

This constrained, modular view of sun-learning is consistent with our understanding of how bees and ants learn the solar ephemeris function in the first place. These insects enter the world with an innate expectation that the sun's azimuth in the morning is opposite its azimuth in the afternoon, an expectation that is reasonably accurate, at least in tropical latitudes (Wehner and Müller, 1993; Dyer and Dickinson, 1994). The insects need only learn the relationship between their innate ephemerides and the local landscape and then revise the shapes of their ephemerides (more or less depending on the latitude and season) to match the local one, using the fixed landscape as a reference (Dyer and Dickinson, 1994; Dyer, 1996, 1998). Thus bees learn the solar ephemeris function with much innate guidance and then seem to store the memory in an encapsulated form resistant to, perhaps even incapable of, revision.

Then again, a compelling question that remains is whether the bees' failure to re-learn in our experiments is attributable to the similarity of the landscapes we used. Our results suggest that the bees' solar ephemerides may be inextricably linked to the bees' representations of the landscape around the nest – the direction of the sun's movement and the detailed shape of the ephemeris are first learned, after all, using the landscape as a fixed reference – and that the system linking the ephemeris to the landscape, once formed, may represent an impenetrable module. It remains possible, however, that the ephemeris could be re-learned when bees are forced to learn a new landscape. If this were true, then the failure of swarming alone to trigger realignment of the ephemeris may not be a problem under natural conditions, as most swarms will situate themselves in novel terrains.

Bees, then, link the landscape panorama around their nest to their celestial compass, as do ants (Åkesson and Wehner, 2002). Bees can also link local landmarks around a feeder to celestial cues (Dickinson, 1994) and to other external directional cues (Collett and Baron, 1994; Fry and Wehner, 2002). But do bees normally link panoramic landmarks more distant from the nest to their celestial compass? Our results are consistent with Dyer's conclusion that they do not (Dyer, 1996). On cloudy days, our long-term transplantees took the treeline at the recipient site to be their natal treeline, and the bees inferred the sun's direction accordingly. But the recipient site corresponded closely to the natal site for only several hundred meters from the hive (or less, depending on the direction), and bees routinely fly much farther than this. Despite ample experience at the recipient site, our bees continued to mistake the recipient site for their natal site for the purposes of inferring the sun's location, suggesting that the solar ephemeris is linked to panoramic landmarks only in the vicinity of the nest. The question deserves further work, however.

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References

- Åkesson, S. and Wehner, R. (2002). Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial frame of reference? *J. Exp. Biol.* **205**, 1971-1978.
- Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- Capaldi, E. A. and Dyer, F. C. (1999). The role of orientation flights on homing performance in honeybees. *J. Exp. Biol.* **202**, 1655-1666.
- Capaldi, E. A., Smith, A. D., Osborne, J. L., Fahrbach, S. E., Farris, S. M., Reynolds, D. R., Edwards, A. M., Martin, A., Robinson, G. E., Poppy, G. M. et al. (2000). Ontogeny of orientation flight in the honeybee revealed by harmonic radar. *Nature* **403**, 537-540.
- Collett, T. S. and Baron, J. (1994). Biological compasses and the coordinate frame of landmark memories in honeybees. *Nature* **368**, 137-140.
- Collett, T. S. and Zeil, J. (1997). The selection and use of landmarks by insects. In *Orientation and Communication in Arthropods* (ed. M. Lehrer), pp. 41-65. Basel, Boston, Berlin: Birkhäuser Verlag.
- Collett, T. S. and Zeil, J. (1998). Places and landmarks: an arthropod perspective. In *Spatial Representation in Animals* (ed. S. Healy), pp. 18-53. Oxford, New York, Tokyo: Oxford University Press.
- Combs, G. F. (1972). The engagement of swarming worker honeybees. *J. Apic. Res.* **11**, 121-128.
- Conover, W. J. (1999). *Practical Nonparametric Statistics* (3rd edn), pp. 218-224, 291-292. New York: John Wiley and Sons.
- Dickinson, J. A. (1994). Bees link local landmarks with celestial compass cues. *Naturwissenschaften* **81**, 465-467.
- Donahoe, K., Lewis, L. A. and Schneider, S. S. (2003). The role of the vibration signal in the house-hunting process of honey bee (*Apis mellifera*) swarms. *Behav. Ecol. Sociobiol.* **54**, 593-600.
- Dyer, F. C. (1987). Memory and sun compensation in honey bees. *J. Comp. Physiol. A* **160**, 621-633.
- Dyer, F. C. (1996). Spatial memory and navigation by honeybees on the scale of the foraging range. *J. Exp. Biol.* **199**, 147-154.
- Dyer, F. C. (1997). Spatial cognition: lessons from central-place foraging insects. In *Animal Cognition in Nature* (ed. R. P. Balda, I. M. Pepperberg and A. C. Kamil), pp. 119-154. New York: Academic Press.
- Dyer, F. C. (1998). Cognitive ecology of navigation. In *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making* (ed. R. Dukas), pp. 201-260. Chicago: University of Chicago Press.
- Dyer, F. C. and Dickinson, J. A. (1994). Development of sun compensation by honeybees: how partially experienced bees estimate the sun's course. *Proc. Natl. Acad. Sci. USA* **91**, 4471-4474.
- Dyer, F. C. and Dickinson, J. A. (1996). Sun-compass learning in insects: representation in a simple mind. *Curr. Dir. Psychol. Sci.* **5**, 67-72.
- Dyer, F. C. and Gould, J. L. (1981). Honey bee orientation: a backup system for cloudy days. *Science* **214**, 1041-1042.
- Esch, H. (1967). The sounds produced by swarming honey bees. *Z. Vergl. Physiol.* **56**, 408-411.
- Fodor, J. A. (1983). *The Modularity of Mind*. Cambridge, Massachusetts: MIT Press.
- Fry, S. N. and Wehner, R. (2002). Honey bees store landmarks in an egocentric frame of reference. *J. Comp. Physiol. A* **187**, 1009-1016.
- Gallistel, C. R. (1990). *The Organization of Learning*. Cambridge, Massachusetts: MIT Press.
- Gallistel, C. R. (2000). The replacement of general-purpose learning modules with adaptively specialized learning modules. In *The New Cognitive Neurosciences*, 2nd edn (ed. M. S. Gazzaniga), pp. 1179-1191. Cambridge, MA: MIT Press.
- Gould, J. L. (1980). Sun compensation by bees. *Science* **207**, 545-547.
- Gould, J. L. (1984). Processing of sun-azimuth information by honey bees. *Anim. Behav.* **32**, 149-152.
- Labhart, T. (1999). How polarization-sensitive interneurons of crickets see the polarization pattern of the sky: a field study with an opto-electronic model neurone. *J. Exp. Biol.* **202**, 757-770.
- Lehrer, M. (1993). Why do bees turn back and look? *J. Comp. Physiol. A* **172**, 549-563.
- Lindauer, M. (1955). Schwarmbienen auf Wohnungssuche. *Z. Vergl. Physiol.* **37**, 263-324.
- Lindauer, M. (1957). Sonnenorientierung der Bienen unter der Äquatorsonne und zur Nachtzeit. *Naturwissenschaften* **44**, 1-6.
- Lindauer, M. (1959). Angeborene und erlernte Komponenten in der Sonnenorientierung der Bienen. *Z. Vergl. Physiol.* **42**, 43-62.
- Lindauer, M. (1963). Kompassorientierung. *Ergebn. Biol.* **26**, 158-181.
- Lindauer, M. (1971). *Communication Among Social Bees*. 2nd edn. Cambridge, MA: Harvard University Press.
- Robinson, G. E. and Dyer, F. C. (1993). Plasticity of spatial memory in honey bees: reorientation following colony fission. *Anim. Behav.* **46**, 311-320.
- Rossel, S. and Wehner, R. (1984). How bees (*Apis mellifera mellifera*) analyze the polarization pattern in the sky: experiments and model. *J. Comp. Physiol. A* **154**, 607-615.
- Seeley, T. D. (1977). Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**, 201-227.
- Seeley, T. D. (1995). *The Wisdom of the Hive*. Cambridge, MA: Harvard University Press.
- Seeley, T. D. and Tautz, J. (2001). Worker piping in honey bee swarms and its role in preparing for liftoff. *J. Comp. Physiol. A* **187**, 667-676.
- Seeley, T. D., Kleinhenz, M., Bujok, B. and Tautz, J. (2003). Thorough warm-up before take-off in honey bee swarms. *Naturwissenschaften* **90**, 256-260.
- Shettleworth, S. J. (1998). *Cognition, Evolution, and Behavior*. New York: Oxford University Press.
- Shettleworth, S. J. (2000). Modularity and the evolution of cognition. In *The Evolution of Cognition* (ed. C. Heyes and L. Huber), pp. 43-60. Cambridge, Massachusetts: MIT Press.
- Siegel, S. and Castellan, N. J., Jr (1988). *Nonparametric Statistics for the Behavioural Sciences*. New York: McGraw-Hill.
- Towne, W. F. and Gould, J. L. (1988). Spatial precision of the honey bees' dance communication. *J. Insect. Behav.* **1**, 129-155.
- Towne, W. F. and Kirchner, W. H. (1998). Honey bees fail to update their solar ephemerides after a displacement. *Naturwissenschaften* **85**, 459-463.
- Visscher, P. K. and Dukas, R. (1997). Survivorship of foraging honey bees. *Insectes Soc.* **44**, 1-5.
- Visscher, P. K. and Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* **63**, 1790-1801.
- von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Belknap Press of Harvard University Press.
- Wehner, R. (1981). Spatial vision in arthropods. In *Handbook of Sensory Physiology*, vol. VII/6c (ed. H. Autrum), pp. 287-616. Berlin, Heidelberg, New York: Springer.
- Wehner, R. (1994). The polarization-vision project: championing organismic biology. In *Neural Basis of Behavioral Adaptation* (ed. K. Schildberger and N. Elsner), pp. 103-143. Stuttgart, New York: G. Fischer.
- Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Physiol. A* **189**, 579-588.
- Wehner, R. and Lanfranconi, B. (1981). What do ants know about the rotation of the sky? *Nature* **293**, 731-733.
- Wehner, R. and Müller, M. (1993). How do ants acquire their celestial ephemeris function? *Naturwissenschaften* **80**, 331-333.
- Wehner, R. and Rossel, S. (1985). The bee's celestial compass – a case study in behavioural neurobiology. *Fortschr. Zool.* **31**, 11-53.
- Wehner, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.
- Wei, C. A., Rafalko, S. L. and Dyer, F. C. (2002). Deciding to learn: modulation of learning flights in honeybees, *Apis mellifera*. *J. Comp. Physiol. A* **188**, 725-737.
- Weidenmüller, A. and Seeley, T. D. (1999). Imprecision in waggle dances of the honeybee (*Apis mellifera*) for nearby food sources: error or adaptation? *Behav. Ecol. Sociobiol.* **46**, 190-199.
- Winston, M. L. (1987). *The Biology of the Honey Bee*. Cambridge, Massachusetts: Harvard University Press.
- Zeil, J. (1993a). Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera): I. Description of flight. *J. Comp. Physiol. A* **172**, 189-205.
- Zeil, J. (1993b). Orientation flights of solitary wasps (*Cerceris*; Sphecidae; Hymenoptera): II. Similarities between orientation and return flights and the use of motion parallax. *J. Comp. Physiol. A* **172**, 207-222.
- Zeil, J., Kelber, A. and Voss, R. (1996). The structure and function of learning flights in bees and wasps. *J. Exp. Biol.* **199**, 245-252.