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The wrong version of Fig. 10 was published. The correct version is printed below.

We apologise to authors and readers for this error.

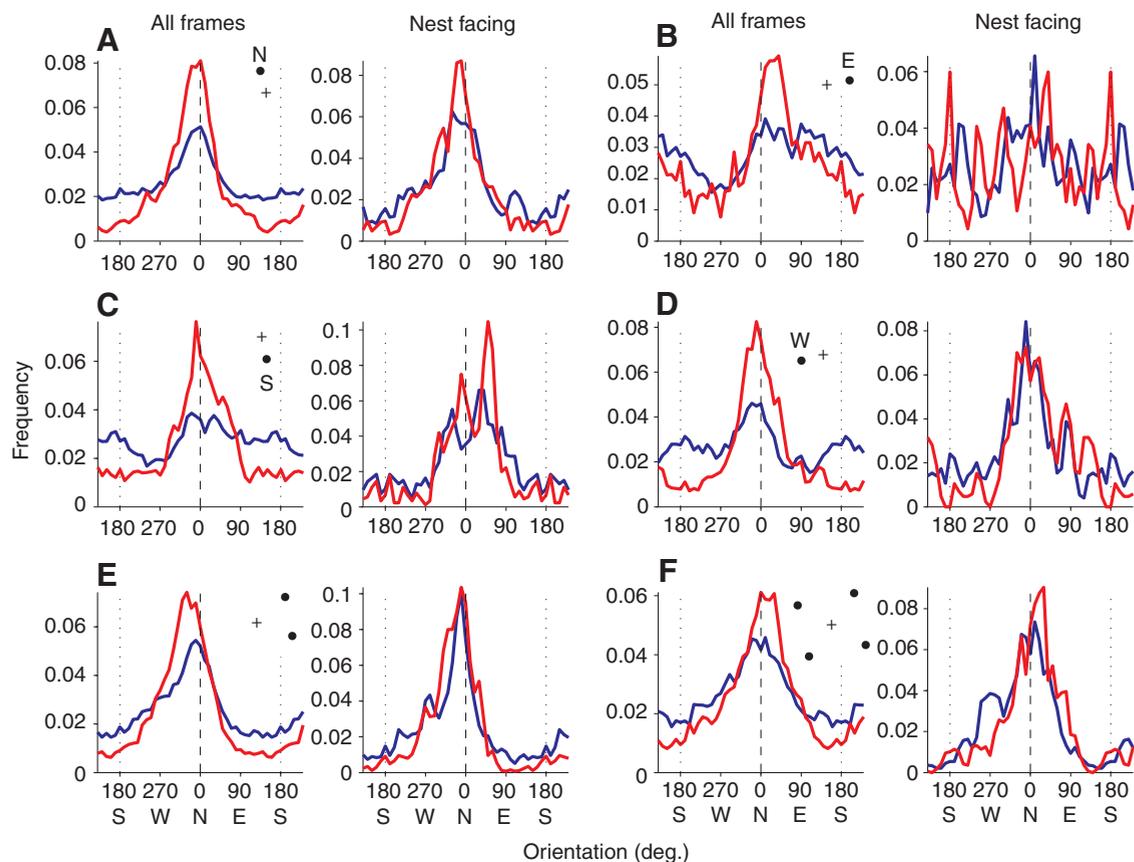


Fig. 10. Bumblebees' facing orientation in the garden with different arrangements of cylinders. (A–D) One cylinder is placed 8 cm and just west of north or east or south or west. (E,F) Two or four cylinders placed 20 cm from the nest. Left panel of each column: distribution of body orientations pooled over all frames of learning and return flights. Right panel: distribution of frames in which the bee faced within 10 deg. of the nest hole. Numbers of flights are given in Tables 1 and 2. See Fig. 4 for further details. Bees' peak facing orientation in both learning and return flights is by-and-large to the north for all the landmark configurations shown in this figure.

Preferred viewing directions of bumblebees (*Bombus terrestris* L.) when learning and approaching their nest site

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SUMMARY

Many bees and wasps learn about the immediate surroundings of their nest during learning flights, in which they look back towards the nest and acquire visual information that guides their subsequent returns. Visual guidance to the nest is simplified by the insects' tendency to adopt similar viewing directions during learning and return flights. To understand better the factors determining the particular viewing directions that insects choose, we have recorded the learning and return flights of a ground-nesting bumblebee in two visual environments – an enclosed garden with a partly open view between north and west, and a flat roof with a more open panorama. In both places, bees left and returned to an inconspicuous nest hole in the centre of a tabletop, with the hole marked by one or more nearby cylinders. In all experiments, bees adopted similar preferred orientations on their learning and return flights. Bees faced predominantly either north or south, suggesting the existence of two attractors. The bees' selection between attractors seems to be influenced both by the distribution of light, as determined by the shape of the skyline, and by the direction of wind. In the partly enclosed garden with little or no wind, bees tended to face north throughout the day, i.e. towards the pole in the brighter half of their surroundings. When white curtains, which distributed skylight more evenly, were placed around the table, bees faced both north and south. The bees on the roof tended to face south or north when the wind came from a wide arc of directions from the south or north, respectively. We suggest that bees switch facing orientation between north and south as a compromise between maintaining a single viewing direction for efficient view-based navigation and responding to the distribution of light for the easier detection of landmarks seen against the ground or to the direction of the wind for exploiting olfactory cues.

Key words: bumblebees, navigation, landmark detection, orientation flights, biological compasses, olfaction.

INTRODUCTION

Many bees and wasps learn the relationship between visual landmarks and a nest or feeding site during elaborate learning flights that they perform on their first few departures from the site (Bates, 1863; Wagner, 1907; Wolf, 1926; Wolf, 1927; Opfinger, 1931; Tinbergen 1932; Becker, 1958; van Iersel and van der Assem, 1964; Lehrer, 1991; Collett and Lehrer, 1993; Zeil, 1993a; Zeil, 1993b). The general interest of these flights is that they present a rare example of a relatively stereotyped manoeuvre that has evolved for acquiring information about visual landmarks. In the bees and wasps that have been studied, the stored information is likely to be used primarily for the task of guiding the insect's returns to the site that it is leaving. The functions of many details of learning flights still need decoding, but two features of the flights play an obvious role in simplifying visually guided homing. First, over much of the flight, the insect is oriented so that it faces in the rough direction of the site that it is leaving (reviewed by Wehner, 1981). Second, insects have a preferred facing orientation when close to the site that is similar across multiple learning and return flights (Zeil, 1993a; Zeil, 1993b; Collett, 1995).

The preferred facing orientation seems to differ between species. When the solitary ground-nesting wasp, *Cerceris* sp., emerges from a nest hole with a small cylinder close by, the wasp backs away so that the cylinder is always seen beyond the nest (Zeil, 1993a). The wasp's mean facing orientation is roughly parallel to the vector from the nest to landmark and so is set by that landmark. On its return

to the nest hole, the wasp approaches the nest, facing in the same orientation as it did on departure (Zeil, 1993b). The cylinder is again seen on the far side of the nest and can be used as a guiding beacon throughout the approach trajectory. Social wasps and honeybees learning about a food site on departure also have a preferred body orientation that is common to their departing and return flights. But the orientation of these wasps (Collett, 1995; Collett and Rees, 1997) and bees (Collett and Baron, 1994) is influenced less strongly by the position of a nearby landmark and perhaps more by compass information. In an insect's final approach to the nest, the landmark is often viewed with lateral retina. The distant panorama is reported to be an important determinant of viewing direction in the ground nesting bees, *Dasyglossa* and *Lasioglossum* (Zeil et al., 1996), and it is possible that differences in the panorama in which the various studies were conducted account for some of the reported differences between *Cerceris* and social wasps and bees.

We ask here what factors might determine the compass orientation in which the bumblebee, *Bombus terrestris* L., faces when learning and finding its nest site and whether these might be related to the visual environment of its nest. Even though little is known about landmark guidance in this species, *B. terrestris* is a good subject for such a study because it is relatively easy to record flights from many bees in similar conditions. Also, because this species nests in holes in the ground and normally emerges onto a horizontal surface, it is straightforward to examine how compass cues and local

landmarks influence the bee's facing orientation immediately after it leaves the nest.

The entrance to a bumblebee's nest is often hidden in ground cover. On approaching its nest, a bee gradually loses height so that small, upright landmarks close to the entrance, like plants or stones, are first seen against ground cover. If the bee is sufficiently low for landmarks to be seen against the sky, the edges of the landmark have high contrast and the shadows that they cast should not interfere with landmark recognition. But, if the bee is higher, landmarks may be easy or difficult to detect, depending on the bee's direction of approach. An example is given in Fig. 1, in which an upright branch is pictured against grass with the sun at different angles of azimuth relative to the viewing direction of the camera. With the camera facing the sun, the vertical branch contrasts darkly against grass, and the shadow of the branch is at a lower elevation than the branch itself. With the sun behind the camera, the contrast difference between the branch and grass is much smaller. The shadow is dark and lies at a similar elevation to the branch and could easily be mistaken for it. Thus, the branch will be most visible against the background and also most easily distinguished from cast shadows when the bee faces the sun. The branch has high contrast over at least 60 deg. either side of the sun's azimuth (Fig. 1), so that viewing angle is not critical.

It could therefore be helpful in detecting landmarks for bees to face towards the sun during learning and return flights. But other competing constraints are also likely to influence viewing direction. First, as bumblebees have a blind area behind them, the selected orientation may be chosen according to the arrangement of landmarks near the nest to give an approaching bee guidance cues within its frontal visual field, as occurs in *Cerceris*. Second, because landmark guidance may be view-based and dependent on retinotopic memories, there is an advantage in terms of memory load to sticking to one direction of flight and a single viewing orientation. Moreover, a foraging trip can take as long as two hours so that adjacent learning and return flights can occur with the sun in distinctly different positions. For such reasons, it might be disadvantageous for the bee to change its orientation continuously to track the sun. Nonetheless, it may help in detecting landmarks to keep the sun roughly in the frontal hemisphere of the eye, by means of occasional switches of body orientation over the day.

We have recorded learning and return flights in two different visual environments using a variety of landmark arrangements. Most data were obtained from bees tested in a domestic garden in Lewes, East Sussex, UK. The garden is partway up the south side of a valley with steep southern flanks that for much of the morning occlude the sun. The house is built into the hill, which obscures afternoon sun from the southwest. The horizon is lowest in a roughly 80 deg. sector between north and west (Fig. 2A). The second set of recordings was made on a more open site on the flat roof of a building at the University of Exeter. The view from the roof is clear and the skyline is lowest to the south but a little broken by trees to the west and buildings to the north (Fig. 2B).

To see whether bumblebees behave like *Cerceris* and orient towards single landmarks, we placed a single cylinder roughly north or east or south or west of the nest hole. To reduce the possibility that landmarks might induce a directional bias, in other experiments we placed four cylinders symmetrically about the nest hole. Out of curiosity, we also used two cylinders to the west or to the east of the nest hole.

In the present study we report the regularities in facing orientation that we found and discuss their possible relation to landmark

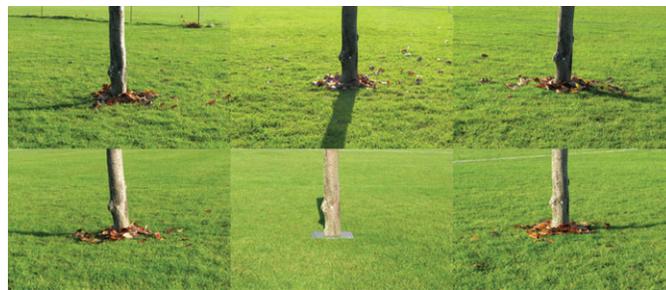


Fig. 1. Landmarks against a horizontal background are most detectable when viewed in the direction of the sun. An upright branch against grass viewed from different directions relative to the sun's azimuth. Top row: camera faces towards the sun and 60 deg. either side. Bottom row: camera faces away from the sun and 60 deg. either side. Photographs were taken at about 11:30 h in mid-November at a latitude of 50.87°.

detection and view-based homing. At least two factors turned out to be involved in setting the bees' facing orientation. The first is the distribution of light, as shaped by the skyline. The second factor is the direction of the wind, suggesting that the use of olfactory cues in nest location may also have played a role in the design of the bees' learning flights.

MATERIALS AND METHODS

Flights from and to a small artificial nest hole in the centre of a tabletop (180 cm by 150 cm in the garden and 150 cm by 150 cm on the roof) were recorded between late June and late August in 2007 in the garden and between late May and early June in 2008 on the roof. During the latter period, the sky was often clouded over. The tabletop was covered with white bath mats, which provided contrast against which the bee could be viewed. The pile of the mat gave visual texture that was essential for bees to stabilise their flight when flying low over the substrate. Varying numbers of black cylinders, 20 cm high by 2.3 cm wide in the garden and 20 cm by 2.3 cm or 9 cm by 2.6 cm on the roof were used as landmarks.

In the garden, a camcorder (Sony HDR HC7E, Tokyo, Japan) was suspended from scaffolding oriented along a west-southwest and east-northeast axis 2 m above the table. The orientation of the scaffolding turned out to be oblique to the bees' preferred viewing

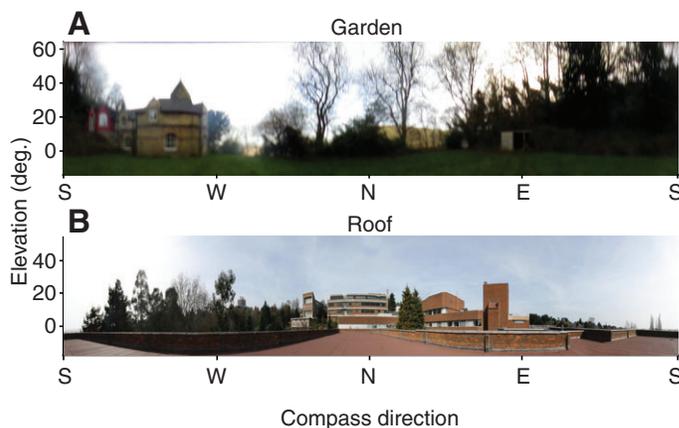


Fig. 2. Panoramic views from the nest site in the garden (A) and on the roof (B). Zero on the vertical scale indicates the elevation at the height of the nest entrance. The skyline is lowest in the northwest quadrant in the garden and to the south on the roof.

orientation so we doubt it is an important determinant of their orientation. On the roof, a vertical strut at each north, east, south or west corner of the table supported a thin cross 150 cm above the table, to which the camera was fixed. To avoid complications that might be caused by the shadows cast by this framework, we only analysed those flights of the 2008 roof data set in which shadows were absent. A separate tape-deck or second camcorder fed by the camcorder above the nest hole served as a data recorder. The camcorder recorded at 25 frames per second. Frames were split to avoid interlacing and to give a temporal resolution of 20 ms.

For one experiment in the garden, the scene beyond the table was completely masked by encircling the table with two layers of 2 m-long, white curtains hung from the scaffolding and attached to the edge of the table.

Commercially reared colonies of *B. terrestris* came from Koppert, UK. During experiments, a colony nest-box was fixed below the table and its entrance hole was attached *via* a series of tubes, gates and blind alleys to the hole in the centre of the tabletop through which the bees left their nest and later returned to it. Bees were only allowed to leave and enter the hive while we were monitoring their behaviour. All bees were marked individually with colours and/or number plates, either before their first departure, or failing that, on their first return. Thus, we knew the number of foraging trips made by each bee. A clear distinction cannot be made between learning flights and foraging flights as many bees returned with pollen on their first trip from the nest (confirming observations of Juliet Osborne, personal communication). By manipulating gates, bees could usually be persuaded to leave singly. Flights to and from the nest were recorded from above over several days. Each group of about 10 bees experienced only one arrangement of landmarks.

We rarely obtained complete records of an individual bee's learning and return flights. Data from flights were discarded when returning bees coincided and interfered with departing ones, and sometimes bees returned when the recording device was turned off. Although the bees' height was not monitored, bees flew close to the table surface for much of each learning flight. They only gained height towards the end of the recorded flight segments.

The information from digital tapes was transferred to a hard drive using Adobe Premiere Pro (San Jose, CA, USA). Software written in MatLab extracted a bee's horizontal coordinates in terms of the centre of mass of the bee's image. The program also determined the compass orientation in which the bee faced. The orientation of the body axis is given by the major axis of the bee's image with the head-end identified from both the shape of the image and the direction of movement between frames. The program allowed the computed values to be checked and when necessary adjusted by hand. The program's most frequent error was in misidentifying the bee's head-end. In all, about 693 learning flights and 533 return flights were recorded. In addition to analysing whole flights, we also examined the bees' orientations when they faced within 10 deg. of the nest or landmarks (i.e. when a line from the centre of the nest hole or landmark made an angle of 10 deg. or less with the bee's longitudinal body axis) or when the bee was no more than 7 or 8 cm from the nest.

To determine whether body orientation gives a reasonable measure of gaze direction, we recorded some flights at 250 frames per second with a Phantom V5.1 high-speed digital camera (Vision Research Inc., Wayne, NJ, USA). The camera viewed an area of about 20 cm by 20 cm so that the magnification was high enough to measure both head and body orientation. Head orientation was obtained from the line connecting the bases of the antennae and

body orientation from the major axis of the image of the bee. Head and body orientation were encoded by positioning a cursor manually.

The wind on the roof was relatively strong on several recording days. The direction of the wind during successive 10 min periods was obtained from the archives of the University of Exeter weather station (IDEVONEX1; 50°44'17.9"N 3°31'18.9"), which was 750 m east-northeast of the recording site. Unfortunately, the archive did not have data for all the relevant dates.

To analyse statistical differences between the viewing orientations adopted in different experimental conditions, we need a single measure of orientation for each flight. This measure came from a frequency distribution of body orientations in 10 deg. bins that included either every frame of a single flight or selected frames of that flight. We determined the 'peak orientation' of a flight as the bin with the most counts. Means of these peak orientations, their standard errors and vector lengths were then computed for all flights grouped according to landmark arrangement or other factors. The statistical significance of differences in peak orientations between various conditions was assessed with Watson's non-parametric U^2 test. Statistical analysis of circular data was performed using the software package Oriana (Kovach Computing Services, Anglesey, Wales, UK).

RESULTS

We will describe the spatial pattern of the bees' learning and return flights elsewhere. Here we focus on the compass orientations in which bees faced and we show that bees tended to face mostly either north or south. The area surveyed by the camera varied somewhat between landmark arrangements but typically extended about 50 cm from the nest. Within this area, bees in the enclosed garden faced predominantly north but with south and northwest peaks in some experimental conditions. On the more open roof, the bees' predominant facing orientation was south, with a small component to the north. We start by comparing the bees' facing orientation during flights recorded in the garden and the roof for two arrangements of cylinders: one cylinder roughly to the north of the nest hole and four cylinders distributed symmetrically about the nest hole. In the second part of the results, we describe the bees' facing orientation for various landmark arrangements tested in the garden. Although a bee's direction of gaze depends on the orientation of its head rather than its body, high-speed and high-magnification recordings of head and body during learning flights show that body orientation does give a reasonable estimate of gaze direction. The distribution of the difference between head and body facing orientations (Fig. 3), measured during 209.5 s of learning flights, has

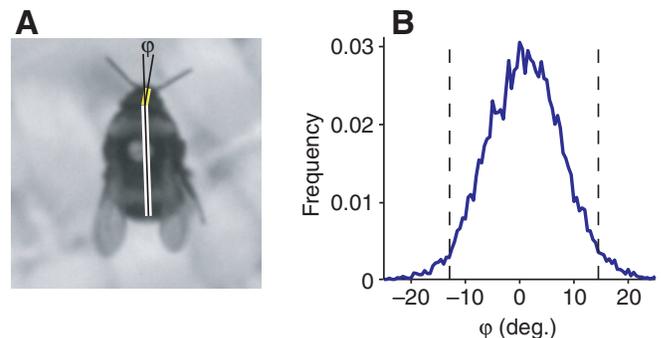


Fig. 3. Frequency distribution of angles between the facing orientations of head and body (ϕ). (A) Image of bee with head and body orientation superimposed. (B) Frequency distribution of ϕ . Broken lines enclose 95% of the data.

a mean of 0.78 ± 7.01 deg. (\pm s.d.). The mean of the absolute difference between head and body orientation is 5.58 ± 4.32 deg. (\pm s.d.).

Comparing flights in the garden and on the roof

One cylinder 8 cm north of the nest hole

The bees' facing orientation during learning and return flights in the garden is shown in Fig. 4. First, we wanted to know how consistent are the flights of all the bees, which were exposed to one cylinder to the north. The distribution of facing orientations accumulated over every frame of every flight shows a peak that in

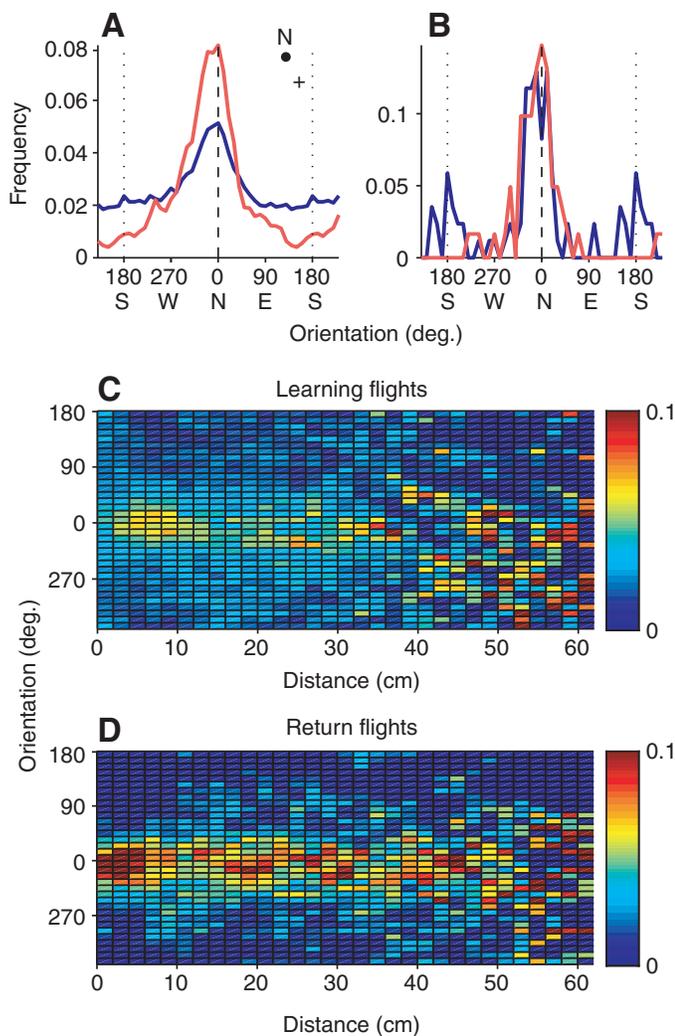


Fig. 4. Bumblebees' facing orientation in the garden during learning and return flights with a cylinder placed 8 cm from and 15 deg. west of north of the nest hole. (A) Frequency distribution of the horizontal-facing orientation on all frames of 85 learning flights and of 61 return flights. Bin width is 10 deg. Here and in other figures, frequency expresses the number of frames in each bin plotted as the proportion of the total number of frames. Throughout the paper, blue lines (dark) show learning flights and red lines (pale) return flights. The broken vertical line at 0 deg. indicates north and the dotted lines at 180 deg. indicate south. Distribution wraps around to avoid masking peaks to the south. + and ● show nest hole and cylinder, respectively, with N upwards. (B) Frequency distribution of the peak orientation of each learning and return flight. (C,D) Colour map of compass direction against distance from the nest. Data are normalised across each column for learning and return flights. Bin width is 2 cm. C, learning flights; D, return flights.

learning and return flights is just to the west of north (Fig. 4A). Second, to test whether this distribution might be biased by very long flights, we determined the peak orientation for each flight (see Materials and methods) and made a histogram of these values. The most prominent peak is again just west of north with a much smaller peak to the south (Fig. 4B). Third, to examine how the bees' facing orientation varies with distance from the nest, the distribution of orientations is pooled over concentric 2 cm-wide annuli centred on the nest and plotted as a false colour map of body orientation against distance (Fig. 4C,D). On learning flights, a broad north peak extends to about 40 cm from the nest. There appears to be two hot spots within this range. One is close to the nest at about 6 cm and the other is more than 30 cm from the nest, suggesting possibly that bees store views of their surroundings at these two distances. Interestingly, the bees seem to face into their preferred orientation further from the nest on return flights than they do on learning flights, so allowing themselves to be guided towards the site of an acquired view.

The distributions with a single cylinder to the north differ for flights recorded on the roof (Fig. 5). Here the north peak is much less prominent, and there is an additional large south peak, which is clearer for learning flights than for return flights (Fig. 5A,B). The distribution of orientations varies during the day (Fig. 5C–F). Bees faced south around midday and early afternoon and north later on. The time course of changes in facing orientation from south to north is shown in Fig. 5D,F. These panels display as a bar chart the number of peak orientations that lay within ± 45 deg. of north, east, south and west during successive two-hour intervals.

On the basis of this time course, we separated the learning and return flights into two groups. The mean vector of the peak orientations adopted within each learning flight before 15:30 h was 148 deg. ($N=38$, vector length=0.3). The mean vector after 15:30 h was 357 deg. ($N=29$, vector length=0.48). The two mean vectors differ significantly (Watson's U^2 test: $U^2=0.388$, $P<0.001$). A similar significant difference was found on return flights. The mean vector before 16:30 h was 196 deg. ($N=21$, vector length=0.4), and after 16:30 h it was 344 deg. ($N=21$, vector length=0.6), with $U^2=0.507$, $P<0.001$.

Four cylinders surrounding the nest hole

The pattern of the bees' orientation in Figs 4 and 5 might have been biased by the single landmark to the north. Any bias of this kind was avoided by using four cylinders distributed symmetrically about the nest hole. Each cylinder was placed 20 cm from the nest hole, one at each cardinal compass point. Despite the symmetrical arrangement of landmarks, bees continued to face north in the garden (Fig. 6A,B). The mean vector of peak orientations of learning flights is 354 deg. ($N=30$, vector length=0.81) and that of return flights is 355 deg. ($N=27$, vector length=0.59).

To test whether the north-facing peak might be induced by the panorama with its relatively low skyline to the northwest (Fig. 2A), we hung 2 m-long white curtains around the experimental table. The curtains both obscured the entire panorama and distributed the light more evenly within the enclosed area. A new group of bees, recorded with the curtain in place, exhibited a bimodal distribution of body orientations, with a prominent south peak in addition to the north peak (Fig. 6C,D). A statistical indication of bimodality is that the mean vector of the peak orientations of learning flights was longer when computed axially over 180 deg. (learning flights: mean vector=166 deg., vector length=0.52, $N=38$; return flights: mean vector=174 deg., vector length=0.55, $N=43$) than when computed normally over 360 deg. (learning flights: mean vector=252 deg.,

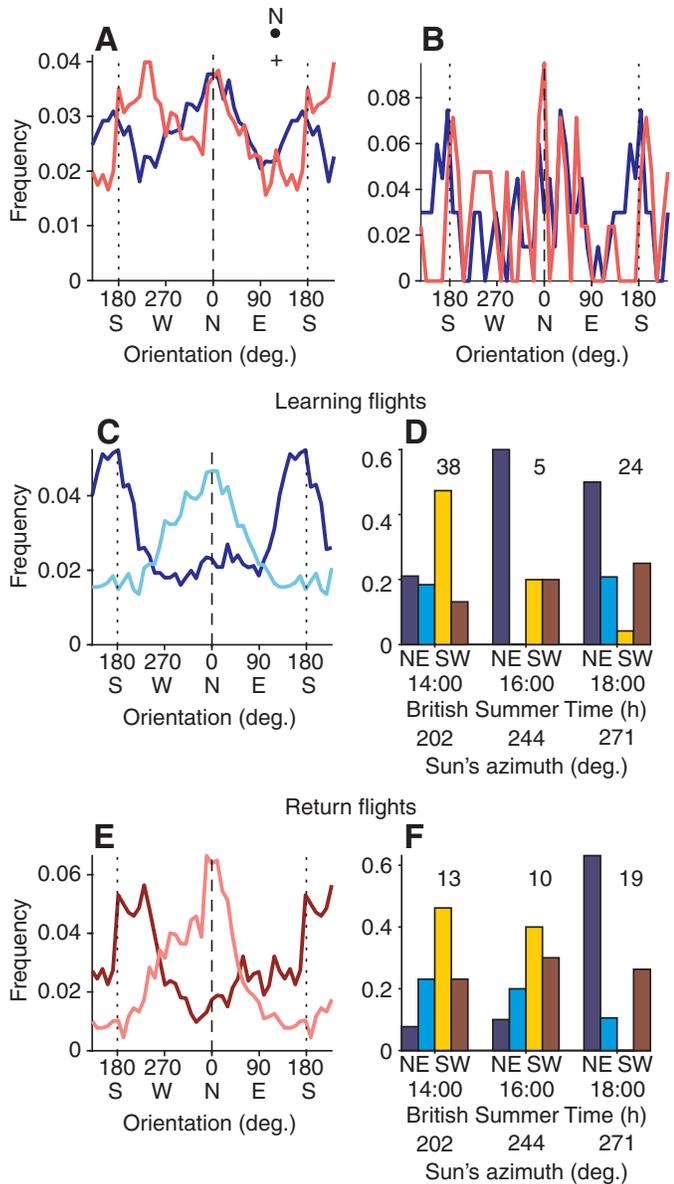


Fig. 5. Bumblebees' facing direction on the roof during learning and return flights with a 9 cm high cylinder placed 8 cm due north of the nest hole. (A) Frequency distribution of the horizontal orientation of the bee's long axis on all frames of 67 learning flights and of 42 return flights. (B) Frequency distribution of the peak orientation of each learning and return flight. (C–F) Data segregated according to time of day. (C) Dark blue shows frequency distribution as in A for learning flights recorded before 15:30 h; light blue for learning flights after 15:30 h. (D) Peak orientations of learning flights in successive 2 h bins categorised as north, east, south, west (± 45 deg.). Numbers at the top of the panel are total flights in each bin. Times below abscissa indicate the mid-point of each bin, and the sun's azimuth is given for each stated time. (E) Dark red shows frequency distribution of return flights recorded before 16:30 h; light red for return flights after 16:30 h. (F) As D but for return flights. See Fig. 4 for further details. Bees faced roughly south before mid to late afternoon and faced north in the late afternoon and early evening.

vector length=0.23, $N=38$; return flights: mean vector=147 deg., vector length=0.27, $N=43$).

This bimodal pattern of orientation also occurred at the start of learning flights when bees were less than 7 cm from the nest hole (Fig. 6E,F) (peak orientations of learning flights: axial mean

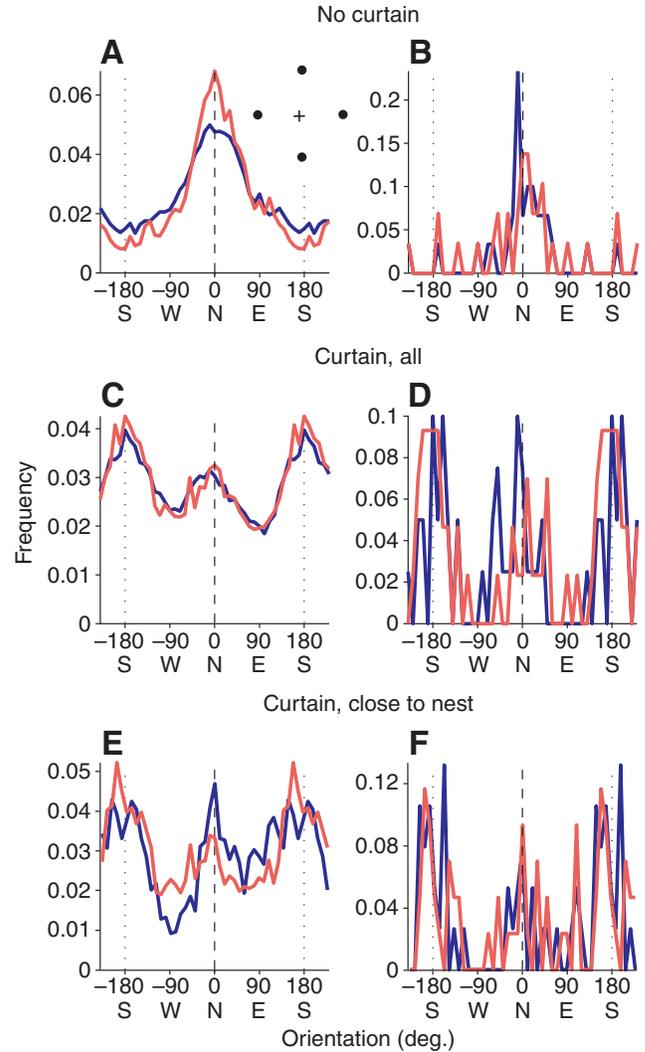


Fig. 6. Bumblebees' facing orientation in the garden during learning and return flights with four cylinders each placed 20 cm from and north, south, east or west of the nest hole. Left column: frequency distributions of body orientation pooled over all frames. Right column: frequency distributions of the peak orientation of each flight. (A,B) Recordings of 30 learning flights and 27 return flights with no curtain around table. (C–F) Recordings of 39 learning flights and 43 return flights with curtain. (C,D) All frames. (E,F) Only frames in which the bee was less than 7 cm from the nest hole. See Fig. 4 for further details. Bees face north with four landmarks arranged symmetrically about the nest. They face both north and south when the garden panorama is masked by the curtain.

vector=166 deg., vector length=0.51, $N=38$; peak values of return flights: axial mean vector=168 deg., vector length=0.36, $N=43$). For these statistics, return flights include all frames close to the nest hole whereas learning flights include only those frames in which the bee is both close to and facing the nest hole. Learning flights, unlike return flights, probably consist of several components. There are flight segments towards and facing the nest, in which bees may store views of the nest's surroundings (Collett and Lehrer, 1993) but also landmark-based manoeuvres and flight segments away from the nest. Consequently, orientation distributions tend to be narrower when bees face the nest, as we show in the next section. The fact that the distribution of facing orientations is bimodal close to the nest suggests that the bimodality is likely to be a direct effect of

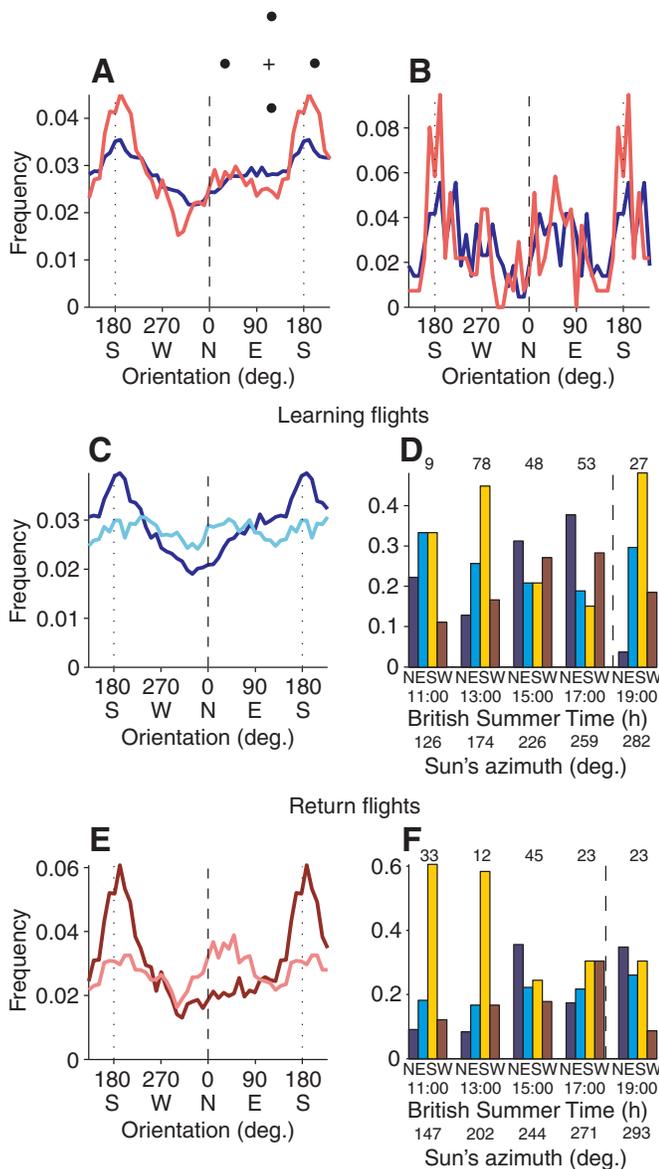


Fig. 7. Bumblebees' facing orientation on the roof during 208 learning and 137 return flights with four 20 cm high cylinders each placed 20 cm from and north, south, east or west of the nest hole. (A–F) Format as Fig. 5. Bees tended to face south from mid-morning to mid-afternoon, thereafter their orientation was more variable.

the appearance of the surroundings influencing the bees' orientation as soon as they emerge from the nest hole. It is less likely to be an indirect effect of the curtain at the edge of the table constraining and changing the pattern of the bees' flight.

The distribution of orientations for flights on the roof is much more variable and exhibits a small south peak (Fig. 7A,B). Again the distribution varies with time of day (Fig. 7C–F) with the relative frequency of south peaks greatest around midday. The mean vector of the peak orientations of learning flights was 154 deg. ($N=117$, vector length=0.25) before 15:30h. The mean vector of the peak orientations after 15:30h was not well directed (mean=334 deg., $N=99$, vector length=0.07). The two distributions differ significantly ($U^2=0.374$, $P<0.002$). Similar significant differences are found between return flights. The mean vector before 16:30h was 171 deg. ($N=72$, vector length=0.33), and after 16:30h it was 48 deg. ($N=65$,

vector length=0.16); $U^2=0.318$, $P<0.005$. From 15:00h onwards the pattern is unclear. North peaks were more frequent in the late afternoon but from 18:00h there is no clear preference. No significant differences were seen between learning and return flights in the earlier ($U^2=0.073$, $0.5>P>0.2$) or in the later samples ($U^2=0.083$, $0.5>P>0.2$). This similarity between learning and return flights suggests that the temporal pattern is more than a randomly noisy distribution.

To examine whether there may also be changes of orientation with time of day in the garden, we have pooled data from all the cylinder arrangements for which the mean vectors of the flights were within 40 deg. of north (i.e. all the conditions listed in Tables 1 and 2 except for the condition with two cylinders to the west of the feeder). In Fig. 8, we plot the number of peak orientations that were within ± 45 deg. of north, east, south or west for every hour during the day. Throughout the day, most peak orientations lay within the north category (learning flights: 142 out of 276; return flights: 178 out of 259). For learning flights, south is the next most populated category (55 out of 276 flights). The pattern differs for return flights. In this case, west is the second most occupied category (50 out of 259 flights), and the proportion of west peaks rises as the day progresses and the sun moves westward. Thus, in the garden north is preferred throughout the day.

What factors determine facing orientation?

The data recorded both in the garden and on the roof show that bees tend to face predominantly either north or south. The garden data indicate that the distribution of light is likely to be one determinant of whether bees face north or south. Although the lowest part of the skyline in the garden is in the northwest quadrant (Fig. 2A), bees tended to face more nearly north than northwest. With curtains distributing light more evenly, the bees' facing orientation became bimodal, facing either north or south.

We do not know whether the distribution of light influenced facing orientation on the roof. At Exeter's latitude in late May, the sun's azimuth moves from the northeast to the southeast quadrant at about 08:30h and from the southwest to the northwest quadrant at about 18:00h. Thus, over the recording period, the sun was mostly in the southern half of the sky and we might expect the bees to face south. The observed variation with time of day turns out to be, at least in part, related to the prevailing direction of wind (Fig. 9). The wind was stronger on the roof than in the enclosed garden, where the wind was mostly negligible or slight.

Wind directions were supplied by the weather station to an accuracy of 22.5 deg. Each learning and return flight for which we had a wind direction was placed in the corresponding 22.5 deg. wind-direction bin. Flights within each bin were categorised as north, east, south or west according to the flight's peak orientation and are shown as a bar chart in Fig. 9A. Data from bins with fewer than five flights are not displayed. Because of a lack of flight and/or wind data, not all wind directions are represented in Fig. 9A. Nonetheless, it is clear that there are more counts in the south facing ($N=48$) than in the north facing ($N=19$) category, when the wind came from a broad southerly sector, and more counts in the north facing ($N=21$) than in the south facing ($N=8$) category, when the wind was from a northerly sector (Fisher's exact test: $P<0.0001$).

Closer analysis indicates that bees do not fly directly up-wind. Instead, they tend to face north or south when the wind came from a broad swath of northern or southern directions, respectively. The evidence is given in Fig. 9B, in which are shown distributions of facing orientations pooled over all flights with the wind in a given direction. The peaks of the distributions are roughly north or south,

Table 1. Means and vector lengths of the peak orientation of learning and return flights with nest hole marked by a single cylinder

Frames included:	All	Nest facing	All	Nest facing	All	Nest facing	All	Nest facing
Landmark position relative to nest hole	North (345 deg.)	North	South (168 deg.)	South	East (77 deg.)	East	West (257 deg.)	West
Learning flight								
Mean vector	335 deg.	326 deg.	5 deg.	5 deg.	35 deg.	357 deg.	333 deg.	0 deg.
Vector length	0.53	0.48	0.44	0.46	0.24	0.30	0.27	0.60
Standard error	8 deg.	9 deg.	16 deg.	16 deg.	28 deg.	23 deg.	31 deg.	13 deg.
Number of flights	85	79	31	26	34	31	22	21
Return flight								
Mean vector	336 deg.	335 deg.	357 deg.	13 deg.	26 deg.	8 deg.	346 deg.	359 deg.
Vector length	0.82	0.55	0.77	0.57	0.66	0.25	0.80	0.54
Standard error	5 deg.	9 deg.	8 deg.	14 deg.	13 deg.	40 deg.	6 deg.	12 deg.
Number of flights	61	60	23	23	16	16	34	34

rather than related closely to the precise wind direction. These data suggest that the wind biases the bees' facing orientation towards a north or a south attractor, much as in the garden bees tended to face almost due north or south, depending on the distribution of light.

Landmark arrangements and facing orientation in the garden

We ask in this section whether the arrangement of local landmarks close to the nest hole influences the bees' facing orientation. For each landmark arrangement, we pool facing orientations over all frames of learning or return flights and also over frames in which bees faced the nest. 10% of the frames on learning flights are nest facing, and on return flights the proportion is slightly higher (13%). This difference is consistent across landmark arrangements and most probably reflects that more complex manoeuvres occur in learning flights than in return flights.

Landmark arrangements with little effect on orientation

We first examine the bees' orientation during learning and return flights in which a single cylinder was placed 8 cm from the nest hole and about 15 deg. clockwise of each of the four cardinal compass directions (Fig. 10; Table 1). With the cylinder to the 'north' of the nest hole, the peak of the distribution of orientations and the mean vectors of both learning and return flights were slightly to the west of compass north, both when all frames were included and for those frames in which the bees faced the nest (Fig. 4; Fig. 10A; Table 1). With the cylinder to the 'east' or 'west', the peak of the distribution of orientations (Fig. 10B,D) and the mean vector of the peak orientations (Table 1) of learning flights pointed approximately north for frames in which bees faced the nest. If all frames are

included, the mean vectors of the peak orientations of learning flights shift a little east when the cylinder was to the east and a little west when it was to the west (Table 1), suggesting the influence of landmark-based flight patterns. The peaks of the distributions of facing orientations also shifted slightly east or west matching the direction of the cylinder, and the flanks were higher on the side of the cylinder (Fig. 10B,D). We placed a white curtain behind the cylinder to the west to increase that cylinder's visibility but without an effect on the bees' orientation (comparisons not shown). The distribution for the 'south' cylinder is broader because the cylinder gets in the way of the bees tendency to leave to the south. Because learning flights comprise several distinct components, the major peaks of the distributions are mostly narrower for nest-facing frames than for distributions including all frames.

The pattern was much the same for return flights, except when the cylinder was to the 'south'. In this case, the prominent NE peak when the bees face the nest suggests that they avoided the cylinder by flying to its west. On return flights, the bee is primarily aiming for the nest, so that, with all frames included, the peaks are narrower on return than on learning flights.

To test whether single landmarks exert a stronger effect on the bees' facing orientation when the bee is close to that landmark, we restricted analysis to frames in which the bees were closer than 8 cm to the nest and facing it. We combine in Fig. 11A data from flights in which the cylinder was 'south' or 'east' or 'west' of the nest. The single peak to the north suggests that even when the landmark is close it fails to shift the bees' predominant orientation.

Might nearby landmarks have a more pronounced effect when they are viewed against the sky? To answer this question, we

Table 2. Means and vector lengths of the peak orientation of learning and return flights with nest hole marked by two or four cylinders

Frames included:	All	Nest facing	All	Nest facing	All	Nest facing	All	Nest facing	Facing NW cylinder (292 deg.)
Landmark arrangement	N,E,S,W (Fig. 6A)	N,E,S,W	4 square (Fig. 10F)	4 square	2 east (Fig. 10E)	2 east	2 west (Fig. 12)	2 west	2 west
Learning flight									
Mean vector	354 deg.	357 deg.	332 deg.	341 deg.	333 deg.	322 deg.	297 deg.	285 deg.	294 deg.
Vector length	0.81	0.68	0.44	0.74	0.72	0.58	0.61	0.64	0.89
Standard error	7 deg.	9 deg.	12 deg.	7 deg.	6 deg.	8 deg.	7 deg.	7 deg.	3 deg.
Number of flights	30	29	50	45	61	57	66	58	66
Return flight									
Mean vector	355 deg.	346 deg.	8 deg.	357 deg.	322 deg.	331 deg.	297 deg.	298 deg.	294 deg.
Vector length	0.59	0.31	0.56	0.60	0.83	0.78	0.66	0.62	0.86
Standard error	12 deg.	25 deg.	10 deg.	9 deg.	5 deg.	5 deg.	7 deg.	8 deg.	4 deg.
Number of flights	27	27	40	40	56	56	52	52	52

N, north; E, east; S, south; W, west.

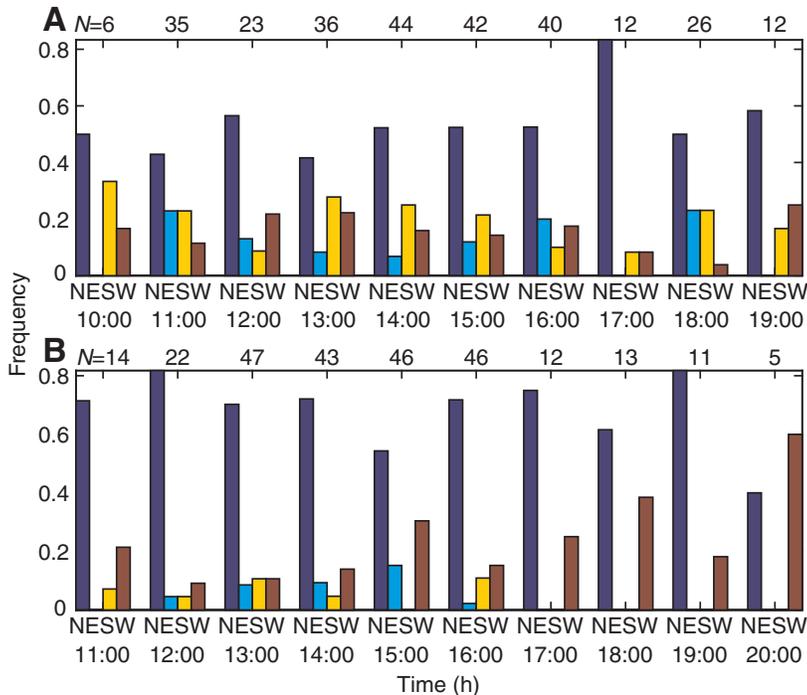


Fig. 8. Bumblebees' facing orientation plotted against time of day for learning and return flights recorded in the garden. The peak orientation of each flight in successive 1 h bins is categorised as north, east, south or west (± 45 deg.). Format as in Fig. 5D. See text for more detail. Bees in the garden exhibit only minor changes in facing orientation over the course of the day.

analysed flights on the roof recorded before 15:30 h in which bees had one cylinder 8 cm to the north of the nest hole. Close to the nest the 9 cm cylinder subtends about 45 deg. so that the upper half is viewed against the sky. Bees then tended to face southwards during learning flights (Fig. 5) and in Fig. 11B the same southward orientation is seen during learning flights when the bee is no more than 8 cm from the nest and facing it. As in Fig. 5, the pattern differs somewhat for return flights. The cylinder just to the north does not shift the bees' tendency to face south.

Bees in the garden also faced north with more complex arrangements of cylinders. They did so with two landmarks to the east of the nest hole, one placed 20 cm south-southeast and one 20 cm north-northeast of the nest hole (Fig. 10E; Table 2). They continued to face north when two cylinders were added to the west to make a square array (Fig. 10F; Table 2). With one exception, which we discuss below, the bees' preferred facing orientation was largely unaffected by the configurations of landmarks that we tried.

A landmark arrangement that influences the bees' facing orientation

With two cylinders placed to the west of the nest hole, the distribution of facing orientations in the garden differed strikingly from the habitual northward direction. The bees' facing orientation then matched the compass direction of the northwest cylinder from the nest (Fig. 12; Table 2). Bees faced northwest when all frames were included and when they faced the nest or the northwest cylinder but not when they faced the southwest cylinder (Fig. 12A). The northwest cylinder may be particularly salient because, when viewed from close to the nest, it lies within the dip in the skyline (Fig. 2A).

The plot of orientation against distance from the nest for frames in which the bee faced the northwest cylinder (Fig. 12C) has a similar pattern across learning and return flights. In both flights, the corridor of orientations within which bees tend to face the landmark becomes increasingly narrow, the closer the bees are to the nest. This pattern suggests that bees funnel into the nest from the southeast

and leave the nest towards the southeast. The plot for frames in which bees faced the nest (Fig. 12D) is less focused and more complex, both in learning and in return flights. The bees' predominant orientation was roughly northwest until they came within 6–10 cm of the nest hole. In this region, bees tended to face in a more westerly direction. Perhaps this shift allows a view stored near the nest to include both cylinders so that both can contribute to pinpointing the nest on returns. But the overall northwest-facing orientation suggests that in addition bees store a view close to the nest when facing the northwest cylinder (see Discussion).

The northwest-facing orientation is apparent in the bees' first departure from and return to the nest (Fig. 12B). The bees' mean facing orientation in these initial flights differs significantly from the facing orientation of the first flights for the seven landmark configurations in the garden (Figs 6 and 10) during which bees tended to face north. As expected, the mean vector of the peak orientations of the first flights with the combined landmark configurations is almost north (learning flights: $N=61$, mean vector=354 deg., vector length=0.46; return flights: $N=50$, mean vector=351 deg., vector length=0.77). The mean vectors of the peak orientations of flights with two cylinders to the west are directed significantly more westward (learning flights: $N=9$, mean vector=273 deg., vector length=0.52; return flights: $N=8$, mean vector=308 deg., vector length=0.70; U^2 for learning flights=0.287, $P<0.01$, U^2 for return flights=0.258, $P<0.02$). The northwest cylinder thus acts immediately to bias the bees' facing orientation towards it.

DISCUSSION

North-south attractors and the detection of landmarks

Our data show that under a variety of conditions bees tend to orient along a roughly north-south axis, suggesting the possible involvement of a celestial or magnetic compass in the control of their orientation. As with other insects tested (Zeil, 1993b; Collett, 1995), the bees' preferred orientations on return flights mostly matched those assumed on learning flights.

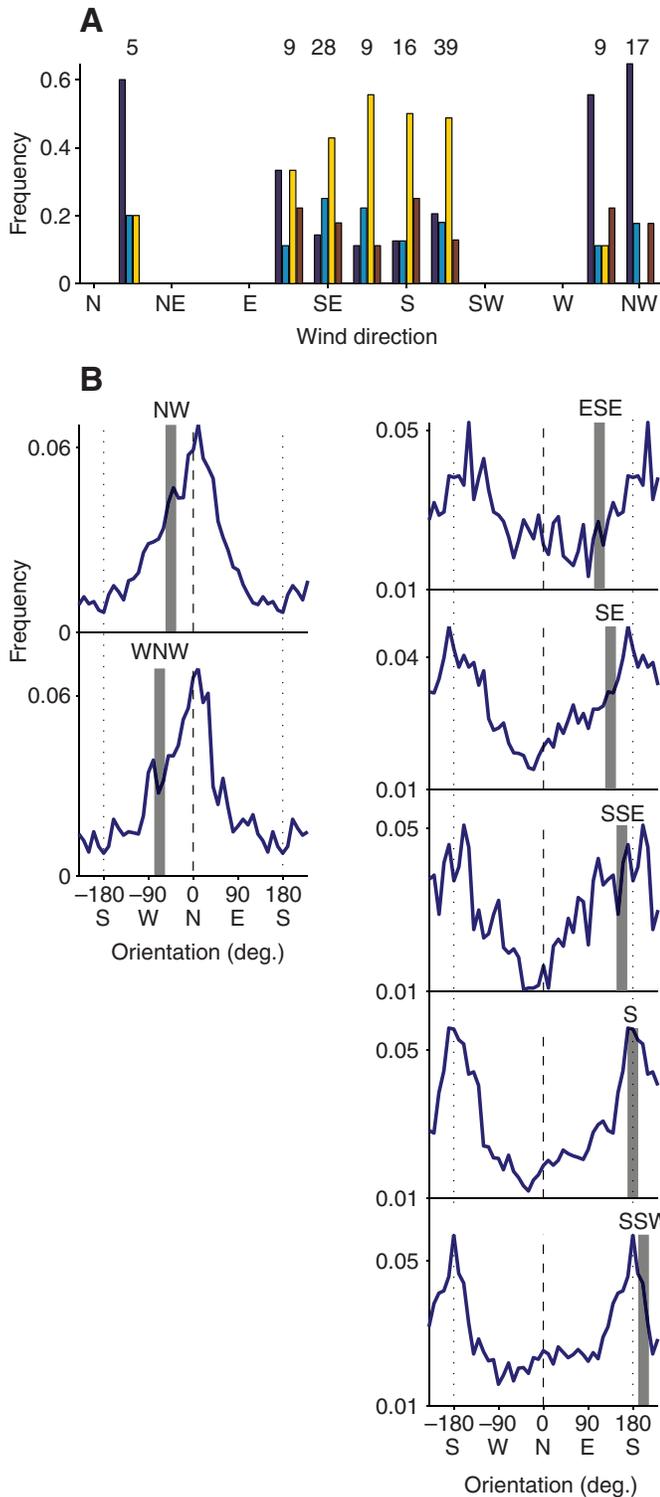


Fig. 9. Wind direction influences facing orientation on the roof. (A) Wind direction and peak orientations. The peak orientations of all learning and return flights are categorised as north (dark blue), east (light blue), south (yellow), west (brown) (± 45 deg.), as in Fig. 5D, and grouped according to the wind direction (in bands of 22.5 deg.). The total number of flights is shown above the relevant wind direction. Cases with fewer than five flights are excluded. Bees faced predominantly north or south, according to whether the wind was roughly from the north or south quadrant, respectively. (B) Distributions of facing orientations containing all frames of all flights associated with a particular wind direction, as indicated by the grey, vertical bar. Cases with fewer than nine flights are excluded. The peaks of the distributions do not track wind direction but are clustered around north or south.

curtains, the bees' facing orientation became bimodal – sometimes bees faced north and sometimes south.

In the Introduction we suggested that when a ground nesting bee descends to find its nest, small landmarks viewed against the ground are most detectable when the bee faces the sun. The selection of a north or south attractor according to which is in the brighter half of the sky is one way of implementing a compromise between maintaining a fixed orientation (to allow an efficient use of view-based memories) and keeping the sun broadly within the fronto-lateral visual field (to enhance the detectability of landmarks, as suggested by Fig. 1). The behaviour of bees in the garden is consistent with such a suggestion, but more work is needed to test the hypothesis properly. Two lines of approach would be informative: first, experimental manipulation of compass and panoramic cues to determine what controls the bees' north–south orientational axis; second, recordings taken in open surroundings over complete days, to see whether bees in northern latitudes do face north early and late in the day and south during the middle of the day.

There are two reported cases of insects that do not face the sun during learning flights. Vollbehr finds that honeybees, on their first learning and return flights from and to the hive, do just the opposite and fly with the sun directly behind them (Vollbehr, 1975). If the bees are kept captive for some hours after their outward flight, they still approach the nest with the sun behind them. Although perverse from the point of view of Fig. 1, this behaviour may be appropriate for the honeybees' normal nesting site, which is in tree-trunks well above the ground, where the background to the nest site is likely to be sky or neighbouring tree trunks.

The second example is the solitary wasp, *Cerceris*, which, like *B. terrestris*, is a ground nesting insect. Its orientation is controlled principally by landmarks rather than by compass cues (Zeil, 1993a). Why might these two ground nesting insects differ? One possible reason is that *Cerceris* catches insects and may have a more prominent zone of high acuity in their frontal retina for hunting (Land, 1997). In this case, *Cerceris* might gain more from keeping landmarks near to its frontal field than from choosing an orientation that enhances contrast. A second possible explanation of differences between the two species is that bumblebees may use olfactory cues for nest location (see below). The colonial nest holes of bumblebees are probably smellier than the nests of solitary wasps.

As pointed out elsewhere (e.g. Brännert et al., 1994; Jander, 1979) there are common features but also marked differences between the learning flights of different species. In general, the design of an insect's learning flights seems to be tuned to accommodate the particularities of its habitat, its behaviour and its sensory systems. Here we see that an insect's preferred facing orientation may also depend on a variety of factors.

The bees' choice between a north and a south attractor seems to be influenced both by the distribution of light and by the direction of wind (Fig. 9). The influence of the distribution of light in biasing orientation to the north was suggested by the bees' behaviour in the garden. Although the brightest part of the panorama was in the northwest quadrant where the skyline was lowest, bees generally faced north rather than northwest. If light was distributed more evenly by surrounding the table on which the bees flew with white

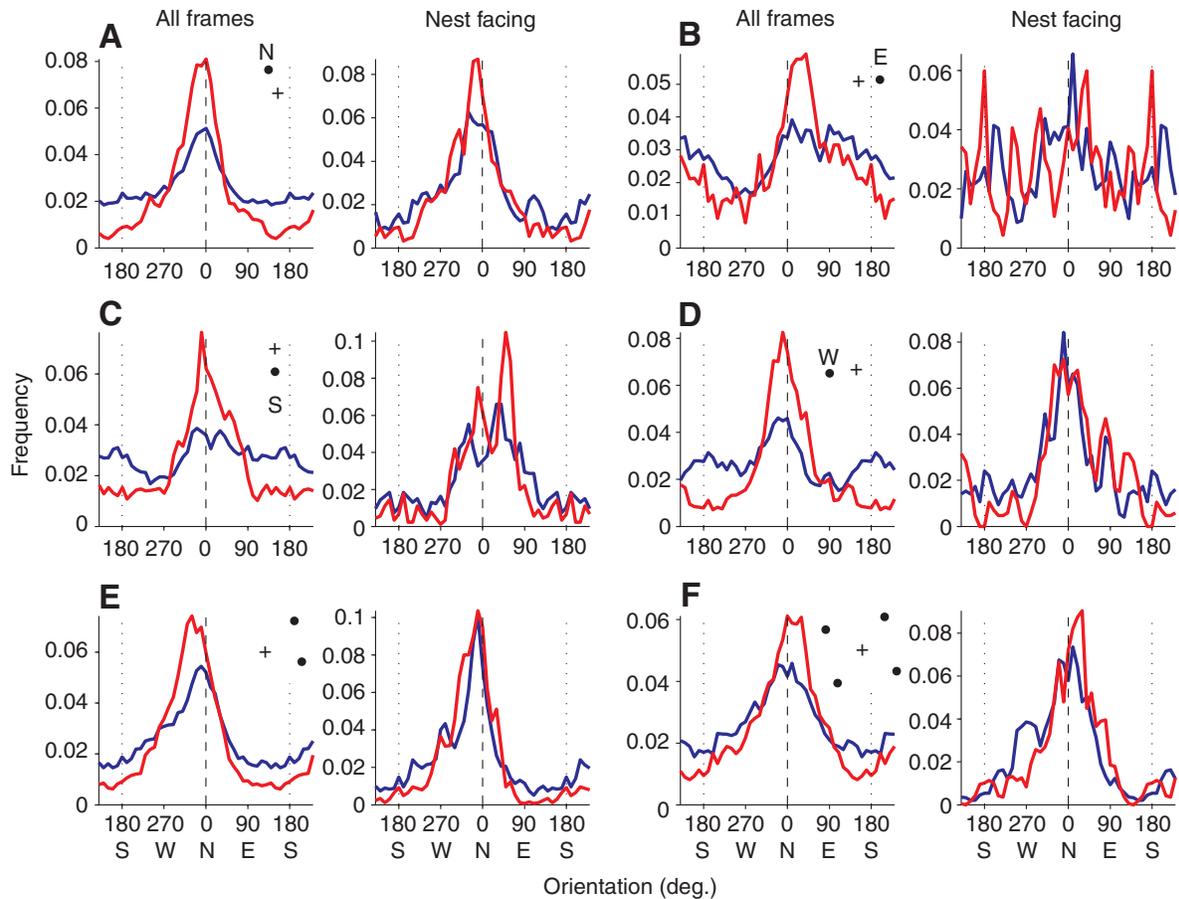


Fig. 10. Bumblebees' facing orientation in the garden with different arrangements of cylinders. (A–D) One cylinder is placed 8 cm and just west of north or east or south or west. (E,F) Two or four cylinders placed 20 cm from the nest. Left panel of each column: distribution of body orientations pooled over all frames of learning and return flights. Right panel: distribution of frames in which the bee faced within 10 deg. of the nest hole. Numbers of flights are given in Tables 1 and 2. See Fig. 4 for further details. Bees' peak facing orientation in both learning and return flights is by-and-large to the north for all the landmark configurations shown in this figure.

Under what circumstances do landmarks close to the nest influence facing orientation?

In the garden, the only clear example we found of a cylinder setting the bees' facing orientation was when it lay to the northwest of the nest hole. Facing orientation was then biased away from the postulated north attractor towards the landmark (Fig. 12). This cylinder position is special because the cylinder when viewed from close to the nest falls within the quadrant with a relatively low skyline and so is seen against the sky (Fig. 2A).

How in general might wasps (Zeil, 1993a; Zeil, 1993b) and bees learn a facing orientation that matches the compass direction of the vector from the nest to a landmark and then use it on their return flights? As the nest hole itself is inconspicuous, the heading direction from nest to landmark is most easily learnt in terms of compass or panoramic cues while the insect faces and stores a frontal view of the cylinder when it is still near the nest. The insect faces in this direction on its first flights from and to the nest (Fig. 12B), suggesting that it can learn this facing orientation when it is close to the nest on its first departure. This orientation can then be expressed on return flights, when the insect is relatively far from the nest and the nest hole is probably invisible to it.

Salience does not appear to be enough for a nearby landmark to control the bees' preferred facing orientation. The north landmark on the roof (Fig. 11B) was both close and salient but it did not pull the bees away from their chosen attractor. Similarly, the west

landmark in the garden (Fig. 10) did not bias the bees' facing orientation, even if a white curtain was hung behind it. But the northwest landmark was both salient and close to the north attractor.

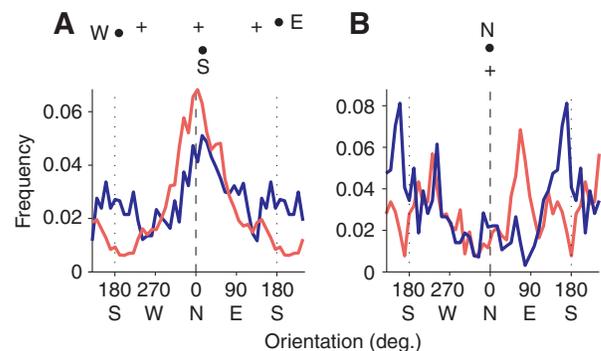


Fig. 11. Bumblebees' facing orientation when they are close to a landmark. (A) Learning and return flights in the garden with one cylinder placed roughly west, south or east of the nest hole. (B) Learning and return flights on the roof before 15:30 h with one cylinder placed north of the nest. See Fig. 4 for further details. Frequency distributions of facing orientations include only those frames in which bees were less than 8 cm from the nest. Learning flights include just those frames in which bees face the nest but return flights contain all frames. Bees do not preferentially look in the direction of the cylinder even when they are near to it.

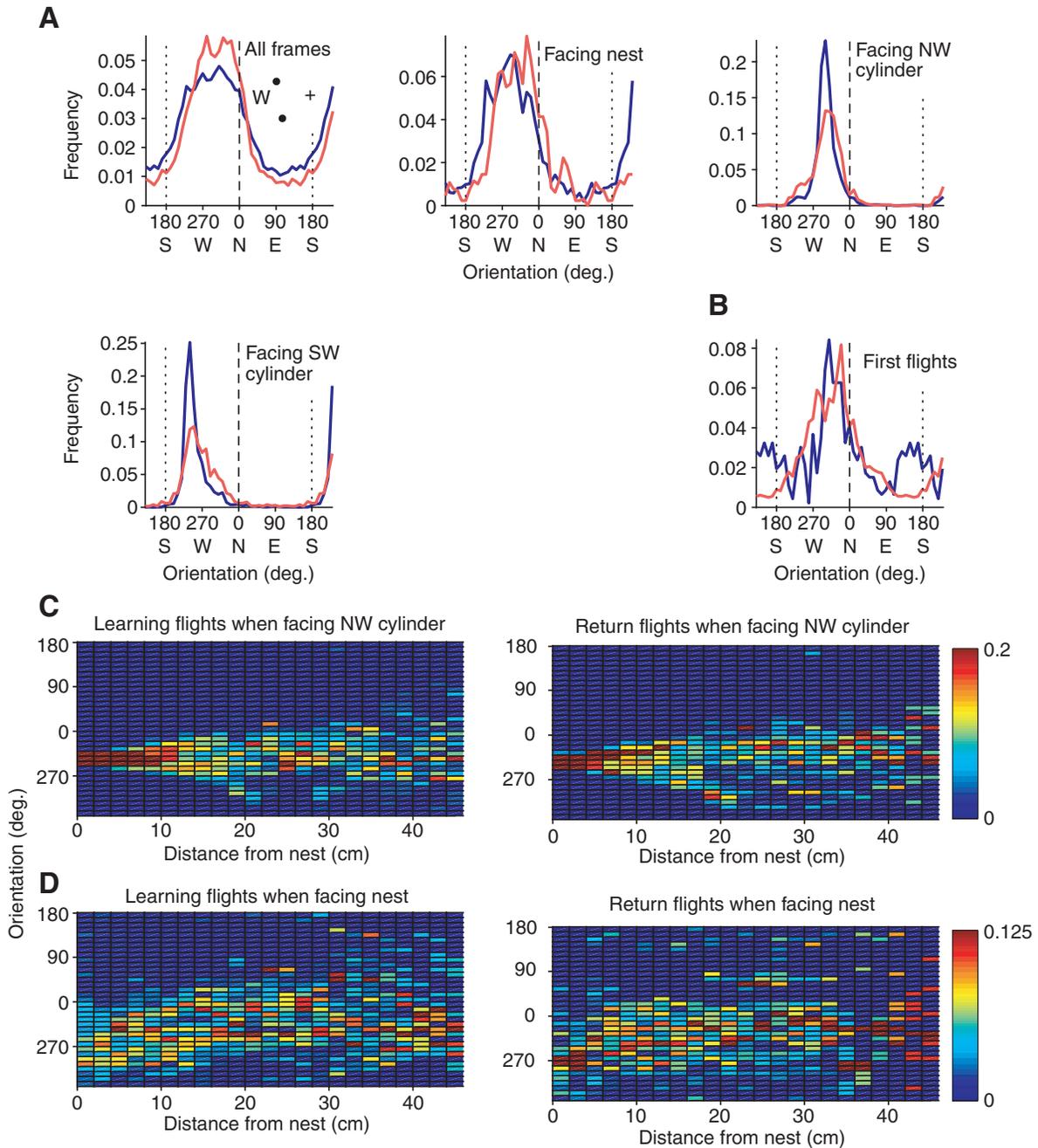


Fig. 12. Bumblebees' facing orientation during flights in the garden with cylinders 20 cm to the northwest and southwest of the nest hole. (A) Distribution of orientations during learning and return flights with all frames, frames in which bees faced the nest, and frames in which they faced the northwest or southwest cylinder. (B) Distribution of body orientations during the first learning and return flights. See Fig. 4 for further details. Learning flights include just those frames in which bees face the nest but return flights contain all frames. (C,D) Plots of body orientation against distance from the nest when bees faced the northwest cylinder or the nest, respectively. Bees presented with this configuration of cylinders tend to face along the vector from the nest to the northwest cylinder during learning and return flights.

Proximity to the chosen attractor and salience may both be needed for a landmark to be fully effective. Intriguingly, the effect of a salient landmark can be suppressed by landmarks which on their own do not strongly bias facing orientation. The north-northeast cylinder, although close to the north attractor, did not influence the bees facing orientation when combined with the south-southeast cylinder (Fig. 10E). Nonetheless, when this pair was added to the two cylinders to the west, the four landmarks together somehow suppressed the attractive effect of the northwest cylinder (Fig. 10F).

Bumblebee learning flights may be designed to exploit both visual and olfactory cues

The influence of the northwest cylinder (Fig. 12) on the bees' orientation leaves little doubt that vision helps to guide their returns. Bees also searched in the correct position relative to landmarks when the nest hole was covered up with another bathmat or when the landmarks were shifted (data not shown). But, in addition, bees on the roof showed a clear response to wind. They faced north if the wind came from the northeast or northwest quadrant and they faced

south when winds came from the southwest or southeast quadrant (Fig. 9). This effect suggests that the bees' flight pattern during learning and return flights may be designed to exploit olfactory as well as visual cues. In a subsequent paper, we will describe the bees' zigzag flight patterns (for a review of such patterns in other insects, see Cardé and Willis, 2008) that lend support to this suggestion. Honeybees rely on both vision and olfaction to guide their way to a food source (von Frisch, 1967). Similarly, the desert ant, *Cataglyphis fortis*, uses olfactory as well as visual cues to pinpoint the location of food (Wolf and Wehner, 2000) and its nest (Steck et al., 2009). The study of learning and return flights may prove useful in understanding what movement patterns help extract navigational information from these two modalities.

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