Honey Bees Extract Map Coordinates from the Dance

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Article

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Abstract

Honeybees communicate locations by the waggle dance, a symbolic form of information transfer. Here we ask whether the recruited bee uses only the indicated course vector or translates it into a location vector on a cognitive map. Recruits were captured on exiting the hive and displaced to distant release sites. Their flights were tracked by radar. Both the vector portions of their flights and the ensuing tortuous search portions were strongly and differentially affected by release site. Search patterns were biased toward the true location of the food and away from the location given by adding release-site displacement to the danced vector. The results imply that the bees recruited by the dance access the indicated location of the food on a shared spatial representation. Thus, the bee dance communicates two messages, a flying instruction and a map location.

Introduction

Honeybees are the only non-human animals known to communicate locations by a symbolic form of information transfer, the waggle dance\(^1,\ 2\). They also use the knowledge about the environment to navigate highly efficiently and adaptively between multiple locations\(^3\). The sources of information used for navigation and waggle dance communication are innate and acquired. The learned components consist of a memory of the outbound rhumb line between nest and food source, the picture like memory of the immediate surrounding of the nest and selected places and their visual, olfactory and gustatory features\(^4,\ 5,\ 6,\ 7\). In addition, multiple features of the landscape are stored in a spatial memory whose structure is either conceptualized as multiple independent snapshots used for navigation\(^8,\ 9,\ 10\), or as a cognitive map storing a multitude of environmental features in their geometric relation\(^11,\ 12,\ 13\). Here we ask how navigation and dance communication systems are linked.

The vector information of the waggle run codes a rhumb line to the indicated food— an instruction on how to get to a destination from a starting location. To a navigator with a map, a rhumb line may also be construed as specifying the location of the destination. If so construed by recruits, the dance could give access to information on their map of the foraging terrain. It could give them map-derived expectations as to the terrain they should see during the vector portion of their foraging flights, when they are on route to the indicated food-location. Map coordinates would also enable them to move toward it when they terminate their vector flight.

We address these questions by applying flight tracking with harmonic radar. This technique has been successfully used to prove symbolic information transfer in the waggle dance\(^14\). The recruits started not only at the hive entrance, but in a catch-and-release design in which recruits were captured while emerging from the hive and released at different sites in different compass directions hundreds of meters distant from the hive (Fig 1a). Our data support the conclusion that dance recruited bees use also their map of the foraging area to search for the communicated location.

Results
Experimental design and flight trajectories

Recruited bees were observed while they attended dancers that advertised for an artificial feeder at a location within the hive's foraging territory (F, in Fig. 1). When the recruit appeared at the hive entrance a radar transponder was glued to its thorax, and her flight trajectory was followed by harmonic radar with radar fixes every 3 s. Generally, recruits first performed a straight flight after departing from the hive entrance (vector flight), then a tortuous search in the area of the dance communicated feeding place, before a final vector flight back to the hive (Fig. 1b). By design, the danced location had no features indicative of food; most recruits released at the hive failed to find it. The transition from the vector to the search flight and from the search flight to the homing flight was identified by a sudden turn between two consecutive radar fixes of > 60° (see Methods).

Release-Site Dependent Perturbations of the Vector Flights

We parameterized the outbound vector by the compass bearing of the line from the first \( f_1 \) to the terminal \( f_t \) fix in the vector, the length of this line, the speed with which the outbound vector was completed \( [\text{length}/(t_{f_t} - t_{f_1})] \), and its straightness \( [\text{length}/(\text{sum over inter-fix segment lengths})] \). Releases from sites other than the hive greatly altered these parameters (Fig. 2). The patterns of alternation differed dramatically depending on the release site, hence, on the terrain the recruit observed during the vector flight. Therefore, these effects cannot be attributed to a factor that would be the same for any displaced release site, such as a failure to observe an expected horizon profile on setting out. Control recruits from another far distant hive released at R2 and R5 mostly flew around in the immediate vicinity of the release site and then disappeared. Their "outbound" vector flights were few and short (Supplementary information: Control experiment).

The site-dependent disruptions of the outbound vector flights and their dependence on the familiarity with the test area imply that a recruit's construal of the dance gives it access to information about terrain it should and should not see while flying the rhumb line.

Search Phase Statistics

The closest approach a recruit made during the course of its tortuous search for the food source indicated by the dance is the simplest indication of what if anything directed its search. There is an extensive experimental and theoretical literature indicating that searches efficiently survey terrain centered on an initial estimate of where the sought-for goal (e.g., the nest) should be\(^{15-17}\). Thus, we assumed that models of our recruits' search phases would posit Levy flights centered on the terminus of the danced rhumb line when drawn from an origin at the release site. We call these displaced rhumb-line termini the virtual locations of the food, denoted \( vF \) to contrast them with \( F \), the true location (Fig. 1c). If the only thing a recruit gets from a dance are flying instructions—fly this far in this direction and begin the search—then their closest approaches to the \( vF \)'s should be similar to the closest approaches of the hive-released recruits to \( F \)—and so should the centroids of their search fixes.
On the cognitive map hypothesis, on the other hand, a recruit has the map coordinates of F as well as the rhumb-line flying instructions. Assuming it can get its bearings when it aborts the outbound vector, either from the terrain it observes at termination or from terrain it observes in an initially Levy-like search, then it should direct its search toward F. How accurately it does so will depend on the accuracy of the map coordinates for F that it obtained from observing the dance and on how accurately it estimates its current location. The latter may be expected to vary in the course of its search, because initial portions of the search may bring it within range of familiar landmarks, from which it may improve its estimate of its current location. On that model, many recruits would be expected to approach F more closely than vF, and that is what we find (Figure 3a). Moreover, many of these approaches to F by displaced bees should fall within the range of closest approaches made by the hive-released recruits. We find that many displaced recruits do get within this range even though their search for F begins at an unexpected and often distant remove from F (Figure 3b).

In Figure 3a, the closest approaches to F and vF in each group displaced within the frame of reference of their cognitive map are compared by subtracting the latter from the former. When this difference is negative, a recruit got closer to F than to vF. Substantial fractions of the bees in groups R1, R2, R5, R6 and R7 did get closer to F than to vF: 17%, 28% 45%, 69% and 94%, respectively. In the groups released at R6 & R7, 24% and 38% of the bees got more than 200 meters closer to F than to their vF. Many of these closest approaches to F fell within the range of closest approaches made by recruits released at the hive. By contrast, very few control bees got within this range (purple plot in Fig 3b.)

It must not be thought that displaced bees never approached their vF. Many did at one point or another in their search, sometimes more than once. Many recruits released to the east of F, hence far to the east of the hive (at R5, R6 and R7, see Fig. 1a), also clearly went back to their release site at one point or another in their search, sometimes more than once. For these recruits, the release site lay in the same compass sector as the food. By contrast, recruits whose release site did not lie in the compass sector of F (R1 & R2) rarely returned to near their release site.

The differences in the searches of bees released either far to the west of F versus somewhat to the east of F are evident in the general tendencies of the searches, as measured by search centroids (the mean longitude and mean latitude of the xes in a search). The centroids of bees released at the hive or only slightly west of it lie far to the east of the release sites (Fig. S1a, Supplementary Material). They straddle the longitude lines for F and the vFs. By contrast, the centroids of the searches of recruits released to the east of F (R5, R6 & R7), do not straddle the longitude lines of the vFs; they lie hundreds of meters to the west of them in the compass sector of the release site and F (Fig. S1a).

The contrasting distributions of the longitudes of the centroid distributions are explained by the fact that recruits generally directed their search into the compass sector of F from the terminations of their east-bound vectors flights. Any hypothesis about what recruits get from a dance must explain the strong effect of release site on the compass sector of the subsequent search. The searches concentrate in
opposing compass sectors relative to vector termini, depending on the compass sector of F relative to the release site.

Movies giving fix-by-fix plots of every recruit's search-phase are publicly available (OSF)

They show that: 1) Different recruits within the same release group made very different searches: Some recruits in each group made a run toward the food, some toward the vF, and some to the RS. 2) Many searched systematically toward more than one target during different phases of their search. To capture this aspect of the data, we devised a measure of the strength with which segments of a search gravitated to a target location (Fig. 4).

With reference to Fig. 4, the efficiency with which the course segment defined by two successive fixes moves the bee closer to g is \( \cos(b_i) \cdot r_i \). The sum of successive efficiencies is proportional to their average efficiency. The overall progress toward g may be measured by the ratio between the initial distance to the goal \( (d_1) \) and the distance as of the most recent fix \( (d_3) \). \( G \) is the product of these two measures of goal progression: \( G_i = (d_1/d_i) \cdot \text{cumsum}(\cos(b) \cdot r) \), where \( i \) indexes over successive fixes in the search phase, \( b_i \) and \( r_i \) denote the bee's and \( r \)'s in Fig. 4 (inter-fix bearing errors and inter-fix distances), and \( d_1 \) is the distance to F from the first fix in the search phase.

The gravitation analysis was first applied to the search flights of hive released recruits and affirms that the searches of hive-released recruits gravitate toward F (Fig. S2).

Fig. 5 shows illustrative search fixes from displaced bees and the corresponding plots of gravitations toward F (red curves), vF (blue curves) and RS (green curves). Because the range of \( G \) is huge (note the differences in y-axis ranges in Fig. S2), the \( G \)'s have been logged—after converting their negative elements to the reciprocals of their absolute values. The reciprocals of the absolute values of the negative elements are <1; thus, their logarithms are negative. Only the positive values of \( G \) indicate the strengths and durations of the runs toward the different targets.

The \( G \) measure enables us to parse fix sequences algorithmically into runs directed at different plausible targets (F,vF and Rs). A sequence of fixes was scored as a gravitation toward one of the three plausible goals when the \( G \) score was >50 over the fixes in that segment and greater than the \( G \) scores of the two alternative goals.

More than half the bees in every group gravitated strongly one or more times toward the true location of the food during some portion of their search (blue bars in Fig. 6). This fraction was significantly greater than the equivalent fraction for the vF and RS goal locations (red and orange bars). It was 0 for one of the control groups taken from a distant hive (R5c); for the other (R2c), it was 0.38. The fraction of hive-released bees showing strong gravitation to F was 0.82. This value was approached or exceeded by three of the groups released at displaced sites in familiar territory (R1, R5 and R6). In short, displaced recruits released in familiar territory were about as likely to make a run toward F in the course of their search as
were recruits released at the hive. By contrast, recruits unfamiliar with the release terrain made such runs rarely or never.

Fig. 7 shows the two or three most unequivocal runs toward F in each displaced release group from the local hive, as measured by G. In several of these examples, the same recruit visited both F and vF, indicating knowledge of the location at the terminus of the displaced rhumb line (vF), the true location of the food (F), and the course between the two locations. Neither F nor vF had previously been a goal location for any recruit (see also Figure 1c).

In Panels a-d of Figure 7, the bees were going to F from the vicinity of vF on courses orthogonal to lines radiating from the hive. These sequences are not explicable by any combination of dispositions to move relative to local landmarks along lines radiating from or toward H. (In the Discussion we explain why this is important.) The single most striking performance was from Bee 116 in Panel C of Figure 7. The complete set of search fixes for this bee are shown in Panel B1 of Figure 5. It was released at R2 and began its search close to vF; it soon flew directly over the vF location and straight to the F location. When within a few meters of F, it turned around and flew directly back to vF; it then circled to the east of vF returned to vF and again flew directly south to within a few meters of F, from which it looped about 50 m to the west before beginning its hive-bound vector.

Search sequences like those in Fig. 7 are evidence that recruits extract two messages from a dance: the rhumb line to F—and F's map coordinates. These recruits had never found food at F; they had no pre-existing disposition to fly toward it; nor could the dispositions elicited by familiar landmarks they passed have directed them there, because such dispositions only move navigators along lines radiating from the hive.

Additional evidence for F-directed search flights comes from an analysis of the directional components during search flights (Supplementary Fig. 3 and 4). Recruits directed their search flights in either unimodal (toward vF or F) or bimodal distributions (both vF and F). Overall, these results indicate that recruits searched both in the direction of the dance-indicated vector (direction towards vF), and towards the location of the real feeder F.

The complete set of animated fix-by-fix sequences may be viewed [here](#). In them, one sees recruits approach F from diverse and distant locations in every compass direction. These approaches are examples of the distinguishing feature of map-based navigation—the ability to set a course to any location within the map's frame of reference from any other location within that frame, whether or not the navigator has pre-existing locale information (images) for either the origin or the terminus of the course.

**Discussion**

Our results strengthen the case for a Cartesian map in honeybees: 1) The rhumb-line vector portions of the displaced recruits' dance-directed foraging were perturbed and mostly aborted prematurely, suggesting that recruits had expectations about what they would and would not see during this portion of
their search for the danced source. 2) The perturbations were release-site specific, implying that the sight of terrain specific to each release site was what perturbed the vector flights. 3) The search pattern that followed the vector portion was directed away from the rhumb-line terminus (vF) in the majority of cases and toward F, the danced location of the food. 4) Its search often brought a displaced recruit within the range of closest approaches achieved by recruits released at the hive. 5) In not a few cases, their search brought them within a few tens of meters of the danced location, starting from locations unexpectedly arrived at and hundreds of meters distant. 6) Close approaches to the danced location culminated sustained flight segments with compass bearings orthogonal to lines radiating from the hive. 7) Close approaches to the true location of the food in displaced recruits were seen only in those recruits released in familiar territory, that is, within the frame of reference of a hypothesized cognitive map.

For decades, Tolman's hypothesis that rodents form a map of their environment on which they base their navigation\textsuperscript{18} was widely disdained\textsuperscript{19}. In recent decades, however, partly in the light of extensive neurobiological evidence\textsuperscript{20}, and partly from an appreciation of the importance of path integration in animal navigation\textsuperscript{21}, the hypothesis has been widely embraced by cognitive scientists and vertebrate neuroscientists\textsuperscript{22-25}—but not by the insect navigation community\textsuperscript{26-29}, despite the fact that neuronal activity signals similar to that found in mammals have now been obtained in Drosophila\textsuperscript{30-32}.

One source of resistance to the cognitive map hypothesis is that it is not always clear what proponents understand by it. We understand a cognitive map to be a metric vector space realized in neural tissue and anchored to the familiar terrain around a nest or hive that constitutes the map's frame of reference. Navigational computations—vector addition, vector inversion, Cartesian-to-polar and polar-to-Cartesian conversion—operate on vectors in this space. Among those vectors is one that marks the animal's current location; it is updated by path integration. Thus, the navigator knows where it is on its map.

Location vectors in this space specify the locations of landmarks and locations whose properties may prove useful in the future. They also give access to information such as the color, odor and shape of the flowers the foraging bee has visited\textsuperscript{21 Chaps 14 & 15, 33, 34, 4, 6}. In mammals, non-spatial information accessed by way of location vectors is represented in other vector spaces\textsuperscript{35-37}, and this appears to also be true in insects\textsuperscript{38, 39, 40}.

Crucially, the vector space representation of locations makes possible the setting of a course between any two locations within the frame of reference. The navigator need not have previously visited either location, because locations are represented by their coordinates, not (only) by images of surrounding terrain.

Location vectors do, however, give access to imagistic information when a location has been visited. Given map coordinates, the navigator may use them to access images of the terrain surrounding that location—if it has location-relevant snapshots in its database—and also images of the terrain it should expect to encounter on route there from the hive or from any other location within the frame of reference.
Several influential researchers prefer a dispositional account of insect navigation. Hoinville and Wehner put this view succinctly in a recent theoretical paper: “At any one time, the animal knows where to go rather than where it is on some kind of cognitive map.” 27, p. 5. The Hoinville and Wehner model posits that the way to go at any moment is the certainty-weighted resultant of two polar vectors—the global home vector and the currently operative local guidance vector 27. These resultant vectors are dispositions to move in some direction. They may be conceptualized as directed forces acting on a particle (the navigator) to determine its velocity (the direction and speed of its motion). The force-field metaphor captures the idea that the particle does not know where it is; it simply moves in accord with the forces/dispositions acting on it/within it.

An insect's currently operative dispositions depend on its motivational state. When outward bound, the home-vector disposition is suppressed, as are hive-oriented reactions to familiar landmarks. The recruits in our experiment were outbound and then executing a search pattern. Therefore, the home vector and hive-directed reactions to landmarks were suppressed. They had never found food at F. Whatever snapshots they may or may not have had of terrain near F, they would not have elicited approach. In the absence of a map, there are no map coordinates; thus, no means for the dance to single out any remembered landmarks for special treatment.

In a recruit engaged in the search for a danced location, movement dispositions evoked by familiar landmarks must be directed along lines that radiate from the hive toward whatever food sources it may have previously visited. Dispositions to move along lines radiating out from the hive to and past familiar landmarks cannot explain why many displaced recruits moved toward the food, from all points of the compass, for sustained portions of their search, on trajectories perpendicular to lines radiating from the hive.

The polar vector danced by a successful returned forager is the inverse of the home vector it has just flown—its most recent active disposition. Moreover, the bearing element in the danced vector must be converted by recruits from a solar to a compass bearing—by reference to the learned solar ephemeris—to compensate for the azimuthal movement of the sun. Thus, dispositional and map-based models of insect navigation both posit computations on vectors. However, only a map model enables the navigator to set a course from any location within the map's frame of reference to any other. And, only a map model enables the conversion of a rhumb line to map coordinates. The behavior of our displaced recruits implies that they made this conversion before flying the rhumb line. That explains the site-specific perturbations of their outbound vectors. It explains the strong effect of release site on the compass direction of the centroids of their searches relative to their vF. Finally, it explains why more often than not their search contained segments strongly directed toward F from the unexpected locations in which they found themselves after aborting their vector flight. They flew toward F despite the fact that they had never found food at F and had no rhumb to F from where they found themselves.

Methods
Experimental site, honeybee colony, experimental design

The experimental site was a highly structured flat agricultural landscape with grass fields stretching to the east of the area scanned by a radar (located at: 50°48'50.11"N, 8°52'21.32"E) with trees and bushes, pathways, and creeks close to the Großseelheim village (Germany). A group of bees from the hive at the radar cabin (R/H) were trained to F (distance: 397 m, direction: 71°). The trained bees were marked individually and with a white dot on the abdomen. These bees served as the dancers. Recruits were released only one at a time and then removed from then colony. They were released either at the hive (R/H) or at one of the five additional release sites (R1, R2, R5, R6, R7, Fig. 1 a).

Tracking by harmonic radar and segmentation of flight trajectories

We used a system with a sending unit consisting of a 9.4 GHz radar transceiver (Raytheon Marine GmbH, Kiel, NSC 2525/7 XU) combined with a parabolic antenna providing approximately 44 dBi. The transponder fixed to the thorax of the bee consisted of a dipole antenna with a low barrier Schottky diode HSCH-5340 of centered inductivity. The second harmonic component of the signal (18.8 GHz) was the target for the radar. The receiving unit consisted of an 18.8 GHz parabolic antenna, with a low-noise pre-amplifier directly coupled to a mixer (18.8 GHz oscillator) and a downstream amplifier with a 90 MHz ZF-filter. A 60 MHz ZF-signal was used for signal recognition, leading to a fixing of the bee carrying the transponder. The transponder had a weight of 10.5 mg and a length of 11 mm. We used a silver or gold wire with a diameter of 0.33 mm and a loop inductance of 1.3 nH. The range of the harmonic radar was set to 0.5 nautical miles. The frequency of radar fixes was every 3 s. The raw radar output was captured from the screen at a frequency of 1 Hz, stored as bitmap files, further analyzed offline by a custom-made program that detected and tracked radar signals (fixes), and converted circular coordinates into Cartesian coordinates taking into account multiple calibration posts in the environment. Finally, the fixes were displayed in a calibrated geographic map created with the software Pix4D from aerial images taken with a commercial drone (DYI Inspire). In the rare cases when no fixes were received from a bee for more than 30 s, the flight trajectory was interrupted, and the last, as well as the first, fix before and after interruption were marked.

Analyses of flight trajectories

Segmentation of flight trajectories: A total of 369 recruits were tested. Typically, recruits performed a sequence of three sequential flight segments: the outbound vector flight; the search flight; and the inbound homing flight (Fig. 1 a). Homing flights were not further considered here because all bees returned home on fast and straight flights. The transitions from the rather straight vector flight to the search flight and the search flight to the homing flight were characterized by a sharp turn of ≥60° with straight stretches before and after the turn with at least three fixes each.

Statistics
Statistical analyses were run by scripts in R or in Matlab™. The code that implements the G computation has been uploaded here, along with the raw data, the results of our analyses, and the code that produced those results. The Man-Whitney U-test was used to compare flight parameters between the control animals and the respective animals of the main experiment.

Circular statistics: Distributions of angles were tested for deviation from random by applying the Rayleigh-test. Comparisons between angular distributions were analyzed with the Watson- U^2 test in the cases of uni-modal distributions. The R package CircMLE \textsuperscript{42} was used to fit uniform, unimodal, and bimodal models of orientation to the directions $\beta$ between release sites R5, R6 or R7 and the respective search fixes (see Supplementary Fig. 2 and 3).

**Declarations**

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**Data and materials availability:** OSF | Bee Navigation with Randolf Menzel Files

**Related manuscripts:** none

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**Figures**

![Figure 1](image.png)

**Figure 1**

Experimental design and flight trajectories. a: Experimental area. R/H: radar and hive location; F: the real feeder for the dancing bees; release sites: R/H (hive release), R1, R2, R5, R6, R7. The dotted line gives the polar vector (rhumb line) to F communicated by the dancer (range: 388 m, compass bearing: 71°). b: Two flight trajectories of recruits released at the hive. The triangle marks the beginning of the flight and the square the end of the flight. The black uppointing arrow heads indicate the transition from the outbound...
vector flight to the search flight, and the red down pointing arrow heads the transition from the search flight to the straight homing flight. c: Flight trajectories of four recruits released at the release site R5. Notice the initial vector flights towards the virtual feeder location vF, the return flights to the release site, the flight component toward the real feeder F and the homing flights. The arrow from R5 to F marks the shortcut to the real feeder.

**Figure 2**

Effects of release site on parameters of the outbound vector portions of recruits' flights (box plots from one-way ANOVAs). Dashed horizontal lines are at medians for hive-released bees. p = p returned by ANOVA. \( \eta^2 \) = effect size (fraction of the variance accounted for by the variation in release site).
Figure 3

Cumulative distributions (CDFs) of approaches. a: CDFs of the difference between a bee’s closest approach (CA) to F and its closest approach to vF (CAF – CA_vF); one plot for each displaced release group. The portion of a CDF to the left of 0 is the proportion of bees in a release group that came closer to F than to vF. b: The CDFs of the closest approaches to F in hive-released recruits (HR, blue), in displaced bees released in familiar territory (red), to vF by displaced bees released in familiar territory (yellow) and by control recruits from another far distant hive released at the same sites (R2 & R5) as two of the recruits from R/H (R2c&R5c, purple).
Figure 4

The quantities in the computation of $G$, the tendency to gravitate toward a target location, $g$: $b_e$ is the circular distance of the bearing of the line between the two fixes from the bearing of $g$ from the second fix (the bearing error); $r$ is the fix-fix distance; $d$ is the distance to $g$ from the second fix.
Figure 5

Three illustrative search-fix sequences (panels on left) and the fix-by-fix plots of GF (red), GvF (blue) and GRS (cyan) in the panels on the right. The gravitations are plotted as a function of the successive fixes in the search phase a: Released at R1. b: Released at R2. Arrows indicate F and vF, which are mostly obscured by fix marks. Recruit flew twice directly from vF to F. c: Released at R5. Arrow indicates F.
Recruit went first to vF, then back to NW of R5, then due north toward F, then back to NW of R5, then due north directly over F.

**Figure 6**

The fraction of the searches in each release group that included at least one strong gravitation toward the goal that is indicated by the color of the bar (blue for F, red for vF, orange for RS). X² tests for differences in the F:vF (blue: red) proportions and F:RS (blue: yellow) proportions across groups R1,R2,R5,R6&R7 yield p's<.0001. R2c and R5c give the results for the two control groups (Supplementary information: Control experiment).
Figure 7

Sequence of fixes showing a strong tendency to gravitate to F from recruits released at each of the 5 release sites. H, RS, vF and F are marked on each panel. Arrows indicate the beginnings of the sequences. In Panels b-e, the terminations of the sequences obscure partly or completely the F that marks the true location of the food.
Figure 8

Parsing of a recruit's radar fixes into an outward-bound vector, a search component, and a hive-bound vector was done by an algorithm: magenta = vector portion; yellow = search portion; cross-ticks on search portion indicate fixes at 3s intervals; triangle marks beginning of hive-return vector. Bearing ($\alpha$: bearing of terminal vector fix in degrees clockwise from north). Length: line between release site and terminal of vector flight (dotted line). Speed: interval between start and end of vector flight and the real distance flown (AVL: accumulated distances of fix-fix segments). Straightness: proportion of LVL and AVL. F = food location (333m east and 191m north of the hive). F: feeding site of the dancers, N: north.

**Supplementary Files**

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- SupplementaryInformation.docx