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CORRECTION

Correction: Evidence of trapline foraging in honeybees

Alexis Buatois and Mathieu Lihoreau

There were some errors in *J. Exp. Biol.* (2016) **219**, 2426-2429 (doi:10.1242/jeb.143214).

In Materials and Methods, the maximum distance between flowers was incorrect. This should read: ‘The same configuration was used at a small spatial scale (distance between flowers: 1.48–4.19 m) and at a larger spatial scale (distance between flowers: 14.8–41.9 m).’. The coordinates of each flower provided in the supplementary information (and from which these distances can be calculated) were correct.

In Results and Discussion, the percentage of honey bees was incorrectly given as 61%. The sentence should have read: ‘This sequence was increasingly used over time (Fig. 2C), and the majority of honeybees (56%) selected an optimal sequence (Fig. 1).’.

Additionally, in Fig.1A, last panel, the arrows incorrectly indicate a route H-F2-F3-F1-F4-H. This should be H-F3-F2-F1-F4-H; the sequence is correct in the supplementary information. Fig. 1B, first panel, showed an incorrect number (and percentage) of honey bees. This should be N=1 (12.5%). The corrected figure appears below.

These mistakes do not affect the results and conclusion of the paper. Both the online full-text and PDF versions of the article have been updated and the authors apologise to the readers for any inconvenience caused.

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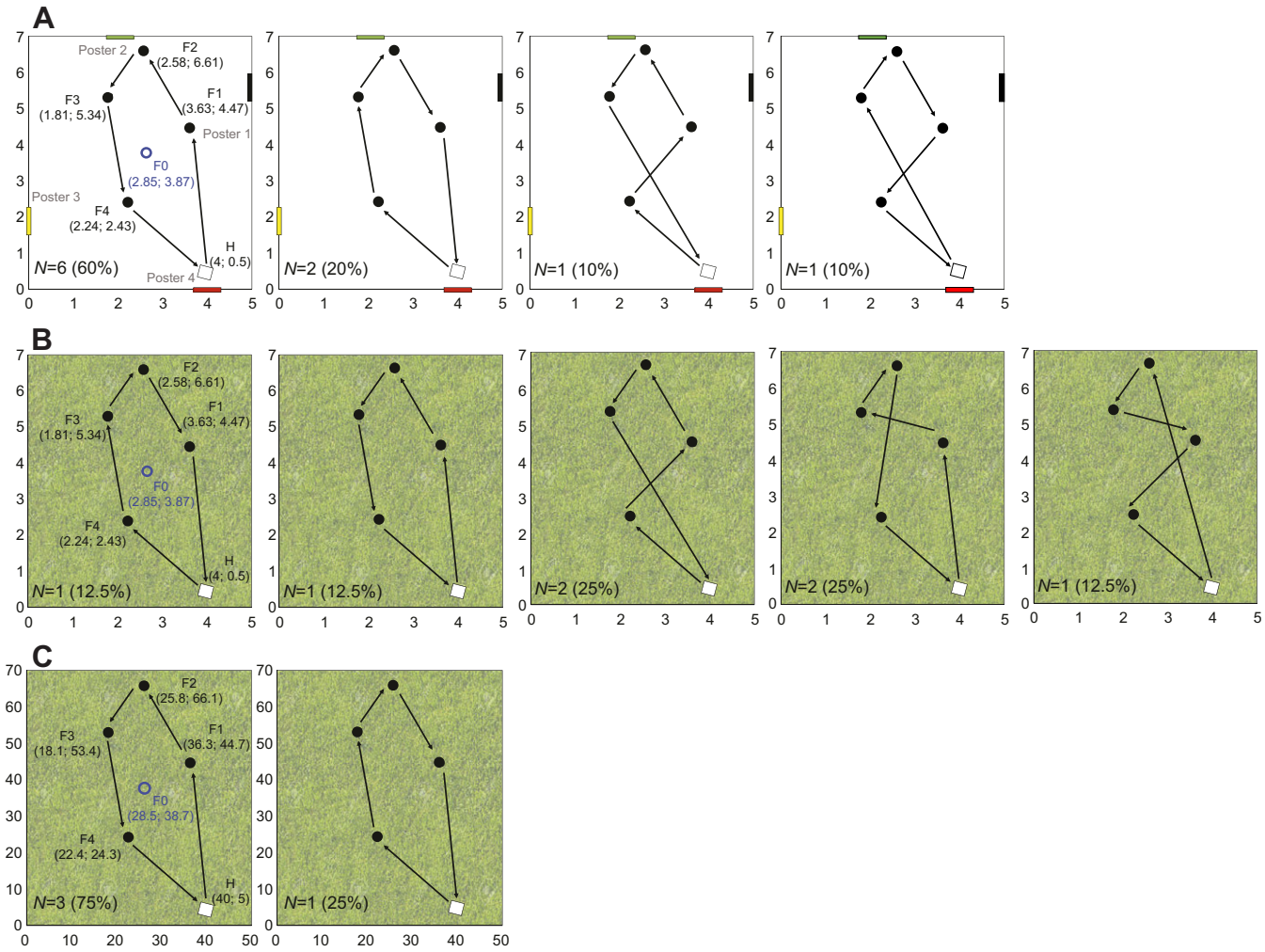

Fig. 1 (corrected). Arrays of flowers and geometry of favourite sequences. Data are shown for (A) experiment 1, small array of flowers in the laboratory; (B) experiment 2, small array of flowers in the field, and (C) experiment 3, large array of flowers in the field. H is the hive, F0 the pre-training flower, F1–F4 the experimental flowers, and posters 1–4 the landmarks. Numbers in parentheses are Cartesian coordinates (m). Arrows indicate the direction in which the honeybee moved. *N* is the number of honeybees that have selected the sequence. A bee moving between nearest-neighbour flowers (F4–F1–F2–F3) would fly 11.6% longer than a bee using an optimal sequence (F1–F2–F3–F4 or F4–F3–F2–F1).

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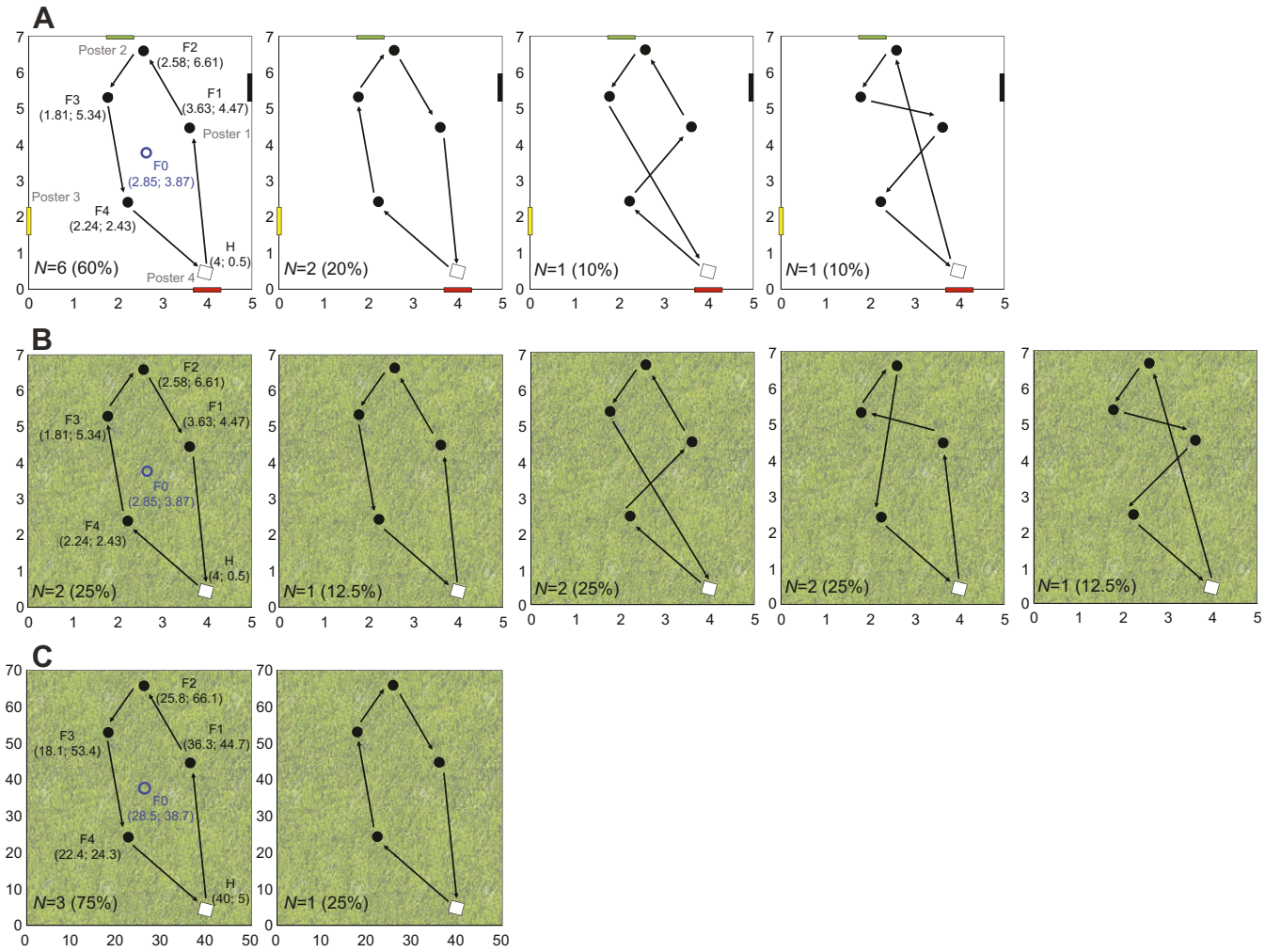

Fig. 1 (original). Arrays of flowers and geometry of favourite sequences. Data are shown for (A) experiment 1, small array of flowers in the laboratory; (B) experiment 2, small array of flowers in the field, and (C) experiment 3, large array of flowers in the field. H is the hive, F0 the pre-training flower, F1–F4 the experimental flowers, and posters 1–4 the landmarks. Numbers in parentheses are Cartesian coordinates (m). Arrows indicate the direction in which the honeybee moved. *N* is the number of honeybees that have selected the sequence. A bee moving between nearest-neighbour flowers (F4–F1–F2–F3) would fly 11.6% longer than a bee using an optimal sequence (F1–F2–F3–F4 or F4–F3–F2–F1).

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SHORT COMMUNICATION

Evidence of trapline foraging in honeybees

Alexis Buatois and Mathieu Lihoreau*

ABSTRACT

Central-place foragers exploiting floral resources often use multi-destination routes (traplines) to maximise their foraging efficiency. Recent studies on bumblebees have showed how solitary foragers can learn traplines, minimising travel costs between multiple replenishing feeding locations. Here we demonstrate a similar routing strategy in the honeybee (*Apis mellifera*), a major pollinator known to recruit nestmates to discovered food resources. Individual honeybees trained to collect sucrose solution from four artificial flowers arranged within 10 m of the hive location developed repeatable visitation sequences both in the laboratory and in the field. A 10-fold increase of between-flower distances considerably intensified this routing behaviour, with bees establishing more stable and more efficient routes at larger spatial scales. In these advanced social insects, trapline foraging may complement cooperative foraging for exploiting food resources near the hive (where dance recruitment is not used) or when resources are not large enough to sustain multiple foragers at once.

KEY WORDS: *Apis mellifera*, Honey bee, Navigation, Spatial cognition, Route learning

INTRODUCTION

Pollinators such as bees face complex foraging problems as they exploit ephemeral floral resources that are scattered in space and vary in quality. Manipulative experiments in bumblebees foraging on artificial flowers show how individual foragers can learn stable, repeatable traplines, minimising travel distances between feeding locations (Lihoreau et al., 2010, 2012; Ohashi et al., 2007), an optimisation task akin to the well-known travelling salesman problem in network theory (Cramer and Gallistel, 1997). Mathematical models indicate that this routing behaviour is particularly efficient for foragers exploiting patchily distributed resources from a central place, thus suggesting that traplining is taxonomically widespread among pollinators (Ohashi and Thomson, 2005; Possingham, 1989). Better understanding of the complex spatial strategies of pollinators is crucial to assessing patterns of pollen flow and their consequences on plant populations and communities (Fortuna et al., 2008).

Despite intensive research on the honeybee, a key pollinator worldwide and a model species in insect navigation, this question has never been explored. In contrast to bumblebees, honeybee foragers communicate using a symbolic language (the waggle dance) that conveys information about the location of resources discovered more than ca. 100 m away from the hive (von Frisch, 1967; Riley et al., 2005). Therefore, most studies on honeybee navigation have focused on how foragers learn to fly back and forth between the hive and one (or two) distant feeding locations and how they communicate this information (Collett et al., 2013). However, little is known about how foragers move between different feeding locations. In nature, honeybees may visit hundreds of flowers per foraging trip (von Frisch, 1967), thereby creating ample opportunities for foragers to simultaneously exploit multiple flower patches or plants. Early field observations suggest that individual honeybees confine their foraging activities to relatively stable groups of plants over many successive days (Ribbands, 1949). More recent studies indicate that foragers can learn flight sequences between multiple visual landmarks to resolve mazes (Collett et al., 1993; Zhang et al., 1996) and discriminate the direction of different feeding locations from a single starting point or hub (Najera et al., 2012).

Here we examined the ability of honeybees to establish traplines. We observed individually marked foragers exploiting four artificial flowers over 30 consecutive foraging bouts. We compared their routing performances in the laboratory and in the field at different spatial scales to identify how environmental factors affect this behaviour.

MATERIALS AND METHODS

Study sites

All experiments were conducted in spring 2015. Laboratory observations were made in a 7×5 m flight room (Fig. 1A) equipped with 12 wide-spectrum LED lights (6500K). A poster uniquely characterised by a bicolored pattern was placed on each wall to provide 2D landmarks (Fig. S1). Field observations were made in a 300×150 m flat ploughed land free of natural flowers, on sunny days with clear sky (Fig. S2).

Bees and artificial flowers

We used a small colony of *Apis mellifera* (Linnaeus 1758) (ca. 2000 workers) in an observation hive. The hive entrance was equipped with a transparent tube fitted with shutters to control honeybee traffic. The colony was fed with *ad libitum* defrosted pollen directly into the hive. Workers collected sucrose solution (40% w/w) from artificial flowers made of a blue landing platform sitting on a transparent cylinder attached to a 50 cm stand (Fig. S3). For large-scale field observations, a wi-fi camera (D-Link) was positioned above each flower (Fig. S3C). Live images of all flowers were displayed on a single computer screen.

Honeybees were tested in a four-flower array (24 possible sequences to visit all flowers once, starting and ending at the hive). The spatial configuration of flowers maximised the discrepancy between the two optimal sequences minimising path length to visit all flowers and the sequence linking unvisited nearest-neighbour flowers (Fig. 1). The same configuration was used at a small spatial scale (distance between flowers: 1.48–4.19 m) and at a larger spatial scale (distance between flowers: 14.8–41.9 m). In both cases, flowers were located less than 100 m away from the hive, thus

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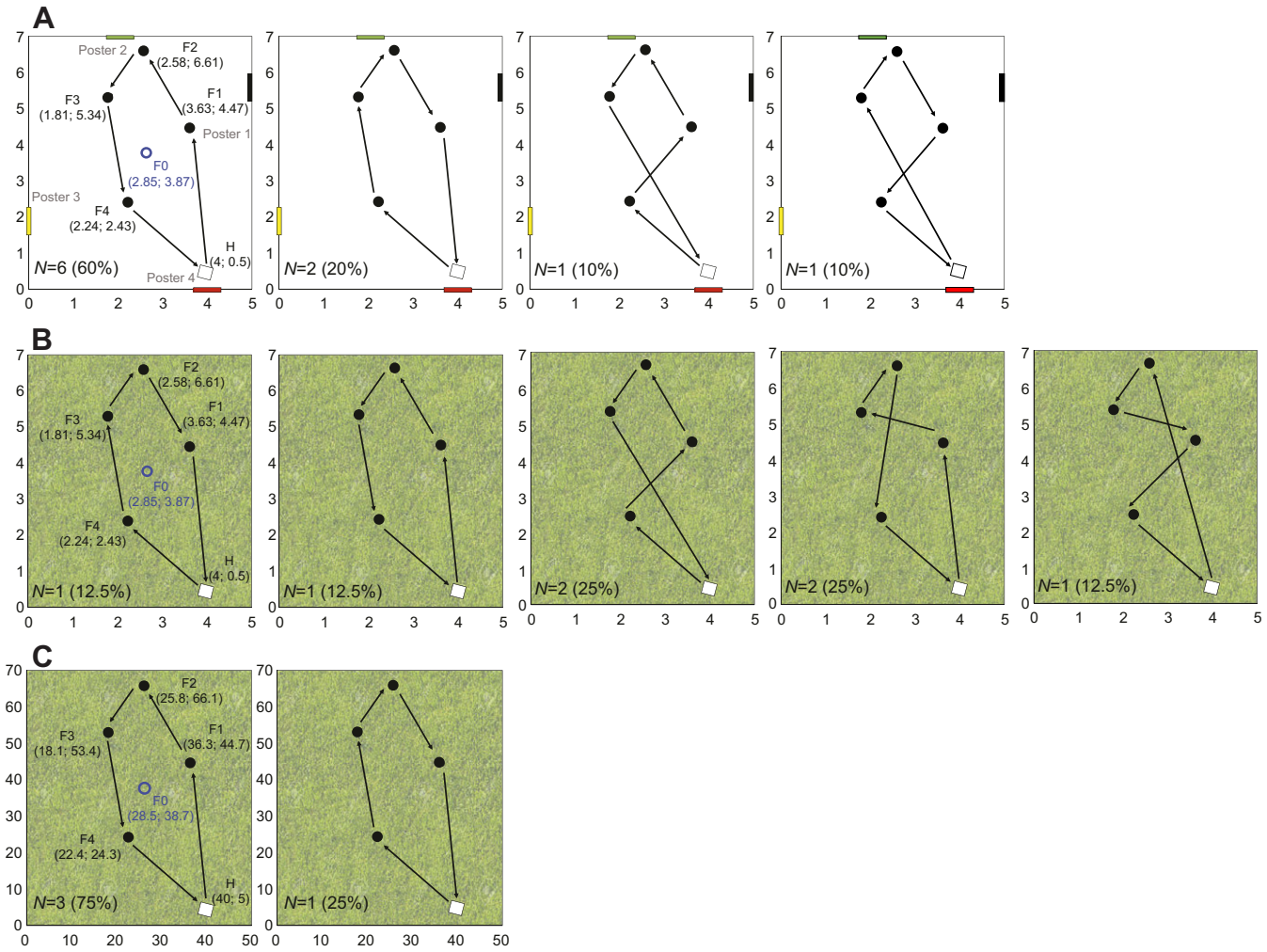

Fig. 1. Arrays of flowers and geometry of favourite sequences. Data are shown for (A) experiment 1, small array of flowers in the laboratory; (B) experiment 2, small array of flowers in the field, and (C) experiment 3, large array of flowers in the field. H is the hive, F0 the pre-training flower, F1-F4 the experimental flowers, and posters 1-4 the landmarks. Numbers in parentheses are Cartesian coordinates (m). Arrows indicate the direction in which the honeybee moved. *N* is the number of honeybees that have selected the sequence. A bee moving between nearest-neighbour flowers (F4-F1-F2-F3) would fly 11.6% longer than a bee using an optimal sequence (F1-F2-F3-F4 or F4-F3-F2-F1).

preventing dance communication (von Frisch, 1967). Because *A. mellifera* workers detect visual targets from a background subtending a visual angle of ∼5 deg (Giurfa et al., 1996), we assume that honeybees could see our 50 cm flowers at a maximum distance of 5.7 m. Thus honeybees could detect all flowers from any flower location in the small array but not in the large array.

Procedure

Honeybees were pre-trained on a flower providing *ad libitum* sucrose solution (Fig. S3A) and paint-marked for individual identification (von Frisch, 1967). Once a honeybee made regular foraging bouts (foraging trip starting and ending at the hive), its nectar crop capacity was measured (range: 32–54 µl, *N*=22). The honeybee was then tested for 30 successive bouts (ca. 6 h) with all experimental flowers in their final position (Fig. 1). At each foraging bout, each flower provided one-fourth of the honeybee's crop capacity. Sequences of flower visits were recorded, detailing the time of arrival to and departure from each flower. Between testing honeybees, flowers were cleaned with ethanol (70% w/w) to remove chemical cues that could influence the next foragers (Giurfa and Núñez, 1992). The same procedure was used in the small flower array in the laboratory (experiment 1, *N*=10) and in the field (experiment 2, *N*=8), and in the large array in the field (experiment 3, *N*=4). The lower sample size used in experiment 3 reflects the increased difficulty of pre-training bees and keeping them motivated to forage on artificial flowers at greater distances from the hive.

Sequence analyses

Foraging performances were analysed using generalised linear mixed models (GLMM) on bins of 10 foraging bouts (random factor: bouts within individual) in SPSS. Route repeatability was examined using determinism (DET), a metric for detecting repeating sequences in traplining data (Ayers et al., 2015). DET varies between 0 (the honeybee never repeats the same sequence) and 1 (the honeybee always repeats the same sequence). For each honeybee, a DET was calculated for bins of 10 bouts on sequences of four-flower visits. Observed DET were compared with 1500 simulated DET of randomly generated sequences, either including or excluding revisits (the R code to generate random sequences is available on request from the corresponding author). For analyses of route frequency, four-flower sequences (excluding revisits) were used (Fig. S4). Observed frequencies were compared with random

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using binomial test with a probability of 1/24 (Lihoreau et al., 2010). Sequences repeated at least four times over the 30 bouts were used more often than expected by chance (binomial test, $P<0.05$).

RESULTS AND DISCUSSION

First we tested the influence of environmental cues on route learning by comparing the foraging sequences of honeybees in the small array of flowers in the laboratory and in the field (experiment 1 versus experiment 2). In both settings, honeybees improved foraging performance as they gained experience. Honeybees made shorter foraging bouts (Gaussian GLMM, bout: $F_{1,48}=7.08$, $P=0.011$; experiment: $F_{2,48}=2.27$, $P=0.114$; bout×experiment: $F_{2,48}=1.87$, $P=0.165$), visited more flowers per bout (gamma GLMM, bout: $F_{2,48}=13.11$, $P<0.001$; experiment: $F_{1,48}=0.63$, $P=0.431$; bouts×experiment: $F_{2,32}=2.01$, $P=0.145$) and decreased their frequency of immediate revisits to flowers (gamma GLMM, bout: $F_{2,48}=42.59$, $P<0.001$; experiment: $F_{1,48}=9.31$, $P=0.004$; bouts×experiment: $F_{2,48}=1.07$, $P=0.351$; Fig. 2A) as the number of foraging bouts completed increased. Honeybees also used increasingly repeatable flower visitation sequences through time, reaching statistically indistinguishable, non-random DET in the last 10 bouts in the laboratory and in the field (Fig. 2B). All individuals used a favourite sequence (the most common four-flower visitation sequence excluding revisits) in 31.3±6.2% (mean±95%CI, $N=18$ honeybees) of their foraging bouts. This sequence was increasingly used over time (Fig. 2C), and the majority of honeybees (56%) selected an optimal sequence (Fig. 1). Only four individuals (22%) had stabilised the sequence (used more than five times in a row) by the end of the 30 bouts (Fig. S4), indicating that route fidelity is imperfect when foraging in close feeding locations, a situation replicating within-patch foraging. The similarity of the foraging performances of honeybees in the laboratory and in the field indicates that natural visual cues (sun, polarised light) are not essential for the establishment of a route in these insects.

Next we tested the influence of spatial scale on this routing behaviour by comparing the foraging sequences of honeybees in the small and large arrays of flowers in the field (experiment 2 versus experiment 3). When tested at larger spatial scales, honeybees also considerably improved foraging performance with experience by reducing the duration of their foraging bouts (Gaussian GLMM, bout: $F_{2,30}=15.51$, $P<0.001$; experiment: $F_{1,30}=1.4$, $P=0.263$; experiment×bout: $F_{2,20}=0.12$, $P=0.89$), visiting more flowers per bout (gamma GLMM, bout: $F_{2,30}=17.09$, $P<0.001$; experiment: $F_{1,30}=2.25$, $P=0.144$; experiment×bout: $F_{2,30}=6.13$, $P=0.006$) and making less immediate revisits to flowers (gamma GLMM, bout: $F_{2,30}=13.92$, $P<0.001$; experiment: $F_{1,30}=2.53$, $P=0.123$; experiment×bout: $F_{2,30}=0.24$, $P=0.787$; Fig. 2A). However, route following was considerably more pronounced in the large array than in the small array. The DET was two times higher in the last 10 foraging bouts (Fig. 2B), honeybees used their favourite sequence twice as often (Fig. 2B) and each individual selected an optimal favourite sequence that they stabilised (Fig. 2D, Fig. S4). Therefore, honeybees show much higher levels of route fidelity between distant feeding locations, a situation replicating between-patch foraging.

Historically, research on honeybee navigation has focused on the ability of foragers to learn routes between a few important locations, such as the hive and a feeder (Collett et al., 2013; von Frisch, 1967). Using arrays of feeders, we show that honeybees can learn more complex foraging circuits integrating at least five different locations. Although we used relatively low sample sizes, all foragers tested behaved in a similar way, indicating that this routing behaviour is not specific to only one individual.

Route following by honeybees meets several key features of trapline foraging previously described in bumblebees and some other nectar-feeding insects, birds and mammals (Janzen, 1971; Lihoreau et al., 2010, 2012; Ohashi et al., 2007; Tello-Ramos et al., 2015): (1) honeybees used flower visitation sequences that became increasingly similar with training, ultimately stabilising into a single route (Lihoreau et al., 2012); (2) route establishment was accompanied by a reduction of revisits to empty flowers (Ohashi et al., 2007) and overall travel distances (Lihoreau et al., 2010); and (3) route optimisation was more pronounced at larger spatial scales (Lihoreau et al., 2012). Presumably, the energetic costs of flying long (suboptimal) routes in the large-scale array increased the investment of foragers in route learning. However, it is also possible that route learning is facilitated when foragers navigate between discrete locations further apart. Future experiments manipulating the travel cost of visiting all flowers while keeping the distance between neighbour flowers constant are needed to disentangle these two hypotheses.

The development and validation of an experimental approach for studying trapline foraging by honeybees holds considerable promise for exploring the full complexity of spatial cognition in bees and addressing the major unresolved question of how features of the environment are memorised in their miniature brains (Collett et al., 2013; Degen et al., 2015). Simulation models already provide some empirically testable predictions. For instance, it has been suggested that trapline development can emerge using a simple route-based guidance system (a suite of vector flights joining different locations) supported by path integration and visual memories of landmarks,

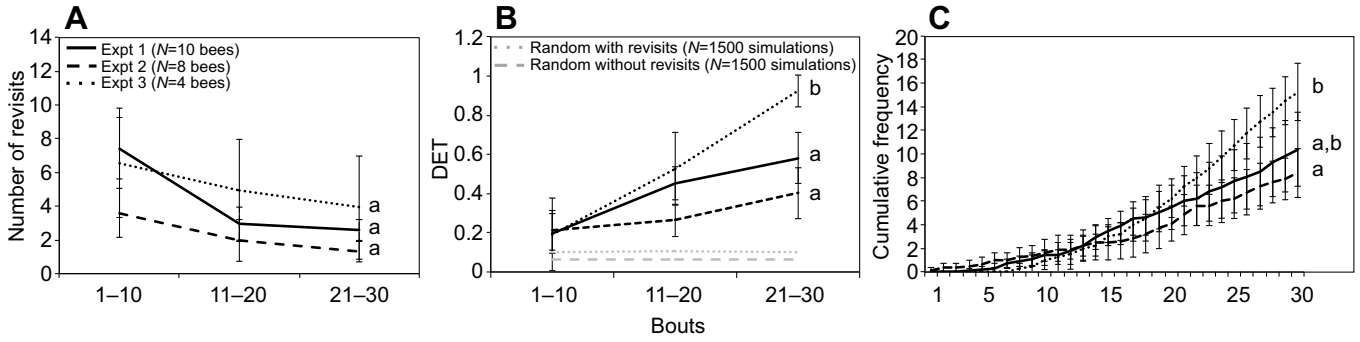

Fig. 2. Foraging performance. (A) Mean frequency of immediate revisits to flowers, (B) mean determinism (DET) value (sequence repeatability) and (C) mean cumulative frequency of favourite sequence (the most common four-flower visitation sequence, excluding revisits, used by each bee). Means are given with 95% CI. *N* is the number of replicates. Different lowercase letters next to curves indicate significant pairwise differences between experiments (two-tailed pairwise Wilcoxon tests with Bonferroni correction, $P<0.017$) for the last bin of 10 bouts (A,B) or the last bout (C).

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without the necessity of learning metric relationships between all main locations (Lihoreau et al., 2012; Reynolds et al., 2013). Learning of route segments and gradual rearrangement of their utilisation order allows for a dynamic optimisation of flight paths and finding of novel solutions in responses to environmental perturbations, such as the addition or removal of resources (Lihoreau et al., 2010).

Growing evidence shows that honeybees flexibly use private and social information in a context-dependent manner when foraging (Grüter and Leadbeater, 2014). Our study indicates that private information is sufficient to support complex spatial strategies in these insects. Trapline foraging may efficiently complement cooperative foraging to exploit resources in the vicinity of the hive (where dance recruitment does not occur) or in environments in which resources are less clumped or not large enough to sustain multiple foragers at once (early or late in the season). In contrast to dance communication (Dornhaus and Chittka, 1999), the ability to rely on individual memory to search and exploit foods is observed in a large diversity of bee species (Janzen, 1971; Lihoreau et al., 2010, 2012; Ohashi et al., 2007), including the most socially advanced, suggesting that trapline foraging is ancestrally shared in this insect group.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
M.L. designed the experiments. A.B. collected the data. A.B. and M.L. analysed the data. A.B. and M.L. wrote the manuscript.

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Supplementary information
Supplementary information available online at
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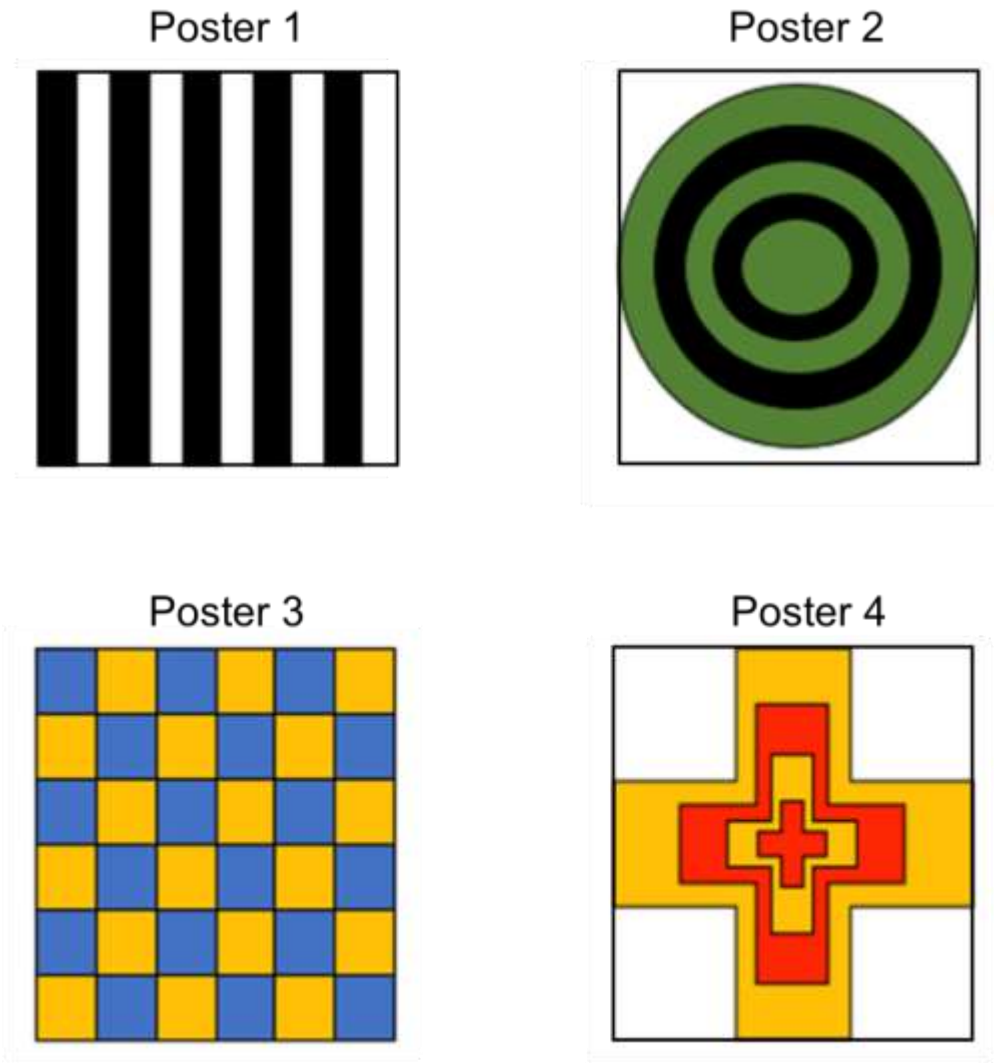

Fig S1: Appearance of the geometric-patterned posters used in the lab (experiment 1). Each poster (dimension A0) was positioned on a different wall of the flight room, providing 2D visual landmarks to bees (see precise locations in Fig. 1A).

(A) Schematic view of the experimental field

(B) Panoramic photo of the field

Fig S2: Experimental field. Observations were conducted on a flat ploughed land at the INRA Domaine Langlade (France, 43°30'10.5"N 1°32'20.1"E). (A). The 300 x 150 m experimental field (delimited in red) was surrounded by bushes, treelines, paths and roads, creating a visual panorama that could be used by bees for navigation. The location of the hive is indicated by the white square. The pre-training flower (F0) and the experimental flowers (F1-F4) are showed for the large array of flower (experiment 3). The black arrow indicates north. (B) Panoramic view of the experimental field (photograph by AB).

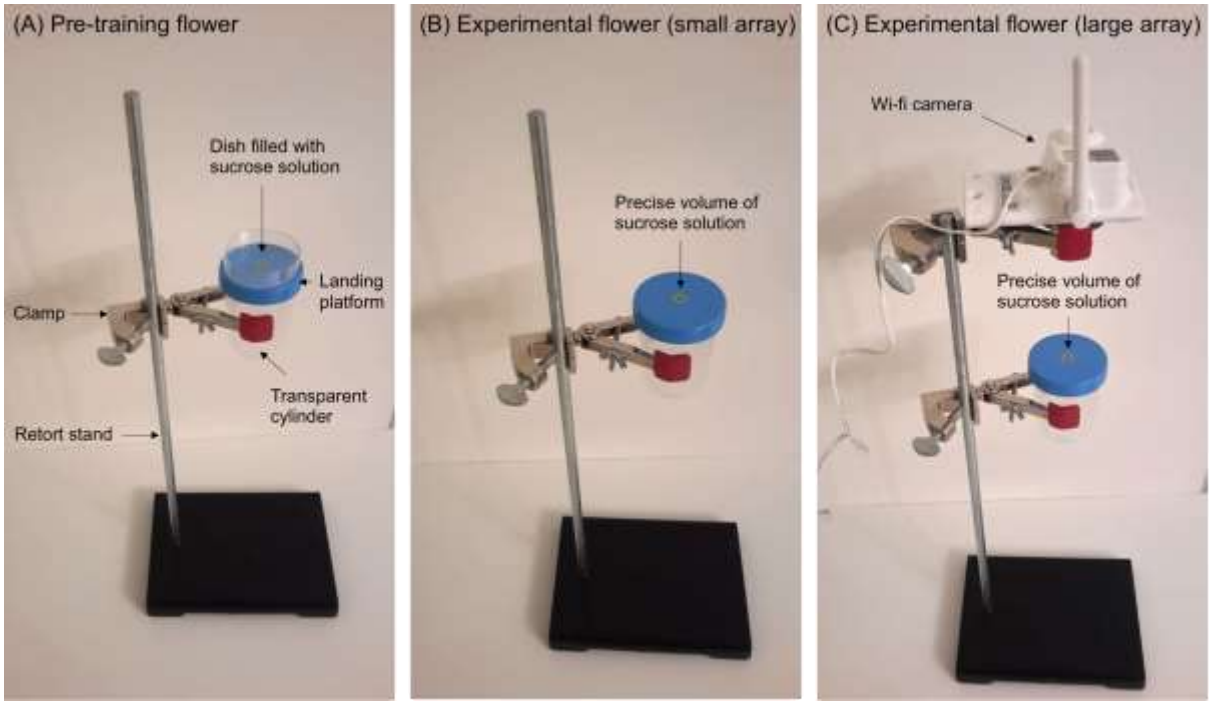

Fig S3: Design of the artificial flowers. Flowers consisted of a blue plastic landing platform (diameter = 6cm) sitting on a transparent plastic cylinder (diameter min = 5.5 cm). Each flower was hold 30 cm above ground by a clamp attached to a 50 cm retort stand. A yellow mark in the middle of the landing platform indicated the location of the sucrose reward. (A) For pre-training, a small petri dish (diameter = 6 cm, volume = 110 ml) filled with sucrose solution was placed on the landing platform to provide bees with *ad libitum* reward. (B) For testing bees in the small spatial scale array of flowers (experiments 1 and 2), a precise volume of sucrose reward (min = 5 µL, max= 15 µl) was added by the experimenter using an electronic dispenser (HandyStep electronic). (C) For testing bees in the larger spatial array, a wi-fi camera (D-Link DCS-2330L) was placed 20 cm above each flower (50 cm above ground) to visualise the landing platform on a computer screen. The cameras and the computer were powered with a portable generator (Mechafer).

(A) Experiment 1: small array in the lab

	Bee 1	Bee 2	Bee 3	Bee 4	Bee 5	Bee 6	Bee 7	Bee 8	Bee 9	Bee 10
Bout1	41	14	341	41	4312	14	41	143	41	41
Bout2	41	14	41	41	4123	14	41	14	41	4
Bout3	4132	4123	14	4123	4132	143	41	143	41	14
Bout4	143	1234	143	143	1432	123	41	434	41	4132
Bout5	123	1432	4321	432	4321	3214	41	23	1423	3214
Bout6	1432	1234	1432	1	1324	321	413	134	1	4321
Bout7	412	123	4321	4321	1234	1234	4132	413	1423	4321
Bout8	1234	12	4123	3214	3421	321	4132	1234	1432	4321
Bout9	1234	12	4321	4321	1423	1234	1243	1324	4123	4321
Bout10	4123	123	4132	342	3421	123	4321	1432	1234	4321
Bout11	123	234	4132	324	3421	3124	1432	1432	1324	4321
Bout12	123	231	3142	4321	1234	123	4321	1234	123	2134
Bout13	1234	2341	4132	321	4231	1234	4321	1234	1	3214
Bout14	4123	123	1432	2314	1234	1234	4321	1234	1234	3214
Bout15	4123	2314	1234	3214	1432	3214	4321	1234	1234	3214
Bout16	4123	231	4123	4321	3124	231	4321	1234	231	2314
Bout17	2314	23	4123	4321	1234	123	4321	1234	1234	3214
Bout18	123	1423	2314	3124	3214	231	1234	1234	2341	2143
Bout19	1234	2314	2314	431	1234	1234	4321	1234	1234	3241
Bout20	4123	432	4132	3124	4321	123	4321	1234	2341	3214
Bout21	4123	123	4123	312	3241	1234	4321	1234	4123	3214
Bout22	1234	4123	3214	3142	23	1234	4321	1324	132	2314
Bout23	4123	1423	2314	3124	1234	1234	4321	1234	2341	3214
Bout24	2314	123	1234	3124	23	1234	4321	1234	23	3241
Bout25	4123	1234	4123	4321	1324	1234	4321	1342	2341	4321
Bout26	4123	4132	4123	3142	1342	1234	3214	1234	1234	4321
Bout27	14	2314	1234	2134	1342	123	4321	1234	1234	2314
Bout28	4123	1234	1234	4321	231	1234	4321	1234	1234	2314
Bout29	1234	1234	1234	2143	2	123	4321	1234	1342	3214
Bout30	1234	1234	1234	3421	3421	1234	4321	1234	23	3214

(B) Experiment 2: small array in the field

	Bee 11	Bee 12	Bee 13	Bee 14	Bee 15	Bee 16	Bee 17	Bee 18
Bout1	131	1324	4132	134	4132	3241	1	1432
Bout2	1324	3214	2314	134	1324	23	4321	412
Bout3	413	432	4132	132	1432	324	1432	3214
Bout4	1324	1342	132	142	1324	321	2143	1423
Bout5	123	1324	4132	12	1342	231	1234	4213
Bout6	321	3241	4123	241	4321	2314	4321	2314
Bout7	123	4132	1234	123	3214	3124	4312	4132
Bout8	132	4123	132	4	1324	2314	4321	123
Bout9	321	1324	1234	13	1423	3421	4123	1423
Bout10	132	41	1432	4	1324	2314	4321	1423
Bout11	1234	4321	4123	4132	1234	234	4321	1423
Bout12	132	132	4231	132	4321	4312	1324	1324
Bout13	3214	4132	132	4	4123	3124	4321	1234
Bout14	321	321	4123	1234	4132	2341	4321	1324
Bout15	234	3241	1234	341	1324	3142	1234	4123
Bout16	314	4132	4321	124	1324	2314	123	412
Bout17	134	1324	413	1324	4132	2314	1234	1324
Bout18	324	1324	4123	324	4321	3412	1234	1234
Bout19	1324	324	4123	341	1234	1432	4321	1234
Bout20	3214	234	4321	1342	4123	3142	1324	1234
Bout21	1234	1324	4123	1324	4123	2314	4321	1234
Bout22	1324	1324	4123	1342	4123	1342	4321	241
Bout23	3241	321	4132	34	4132	4321	3	1324
Bout24	1234	4123	4321	134	4123	2341	4321	1234
Bout25	1324	3214	132	134	4123	143	1243	3214
Bout26	1324	14	4123	1324	1342	134	4321	1234
Bout27	1324	1324	4321	1342	1234	4132	4321	1324
Bout28	1234	324	1234	1342	4123	4321	32	1234
Bout29	1432	1342	1234	1234	4123	1432	4132	1234
Bout30	1234	1324	4123	4123	4132	3412	4321	1234

(C) Experiment 3: large array in the field

	Bee 19	Bee 20	Bee 21	Bee 22
Bout1	123	324	12	1
Bout2	143	321	124	1
Bout3	123	234	1423	12
Bout4	21	34	134	21
Bout5	132	314	142	123
Bout6	123	413	321	123
Bout7	132	13	123	1323
Bout8	123	34	1234	12
Bout9	123	1243	1234	123
Bout10	1234	4321	1324	13
Bout11	132	234	1234	134
Bout12	124	4321	132	123
Bout13	13	4321	123	1234
Bout14	1234	321	12	13
Bout15	1234	2134	1234	1234
Bout16	1234	3214	123	123
Bout17	1234	4321	1234	132
Bout18	1234	1432	1234	1324
Bout19	1234	4321	1234	1234
Bout20	1234	4321	123	1234
Bout21	1234	4321	1234	1234
Bout22	1234	432	1234	1234
Bout23	1234	4321	1234	123
Bout24	1234	4321	1234	1234
Bout25	1234	4321	1234	1234
Bout26	1234	4321	1234	1234
Bout27	1234	4321	1234	1234
Bout28	1234	4321	2134	1234
Bout29	1234	4321	1234	1234
Bout30	1234	4321	1234	1432

Fig. S4: Four-flower visitation sequences (excluding revisits) for each bee in experiments 1-3. Numbers (1-4) in tables refer to unique flowers (see details in Fig. 1), and colour codes refer to a unique flower sequence. Incomplete sequences (not included in the analyses of sequence repeatability) are in white. Sequences in columns are sorted in chronological order (from foraging bout 1 to foraging bout 30).