RESEARCH ARTICLE

Male bumblebees perform learning flights on leaving a flower but not when leaving their nest

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ABSTRACT

Female bees and wasps demonstrate, through their performance of elaborate learning flights, when and where they memorise features of a significant site. An important feature of these flights is that the insects look back to fixate the site that they are leaving. Females, which forage for nectar and pollen and return with it to the nest, execute learning flights on their initial departure from both their nest and newly discovered flowers. To our knowledge, these flights have so far only been studied in females. Here, we describe and analyse putative learning flights observed in male bumblebees *Bombus terrestris* L. Once male bumblebees are mature, they leave their nest for good and fend for themselves. We show that, unlike female foragers, males always fly directly away from their nest, without looking back, in keeping with their indifference to their natal nest. In contrast, after males have drunk from artificial flowers, their flights on first leaving the flowers resemble the learning flights of females, particularly in their fixation of the flowers. These differences in the occurrence of female and male learning flights seem to match the diverse needs of the two sexes to learn about disparate, ecologically relevant places in their surroundings.

KEY WORDS: Eusocial insect, Bee, Spatial learning, Sex-specific behaviour, Navigation, Foraging

INTRODUCTION

In many animal species, the two sexes, to some degree, know and learn about different things. In eusocial insects, like bees, the roles of females and males are quite distinct. In the bumblebee *Bombus terrestris* L., the species with which we are concerned here, a single female queen lays fertilised eggs. The other females are workers that perform one of several tasks for the benefit of the colony. They may, for instance, tend larvae, guard the colony, explore for nest or food sites, or forage for nectar and pollen, which they bring back to the nest. The workers forage individually and learn the locations of both their nest and good foraging sites. Male *B. terrestris*, in contrast, are not concerned about the state of the colony. They leave their nest to find potential mates and do not return (Goulson, 2010; Paxton, 2005). Indeed, possibly as part of a strategy to avoid inbreeding (Baer, 2003; Gerloff and Schmid-Hempel, 2005; Whitehorn et al., 2009), they may travel as far as 10 km from the colony, where they live as solitary foragers and patrol the terrain for queens (Coppée et al., 2011; Kraus et al., 2009; Paxton, 2005). Whereas males may

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well learn the location of foraging sites near to their patrolling area, they have no reason to learn to return to their nest. Are these differences in life style – in which females forage for the community and males forage only for themselves – reflected in the occurrence of learning flights in the two sexes?

Female wasps and bees on first leaving their nest or a flower perform elaborate flights (Brünnert et al., 1994; Collett, 1995; Collett et al., 2013; Collett and Lehrer, 1993; Hempel de Ibarra et al., 2009; Lehrer, 1993; Opfinger, 1931; Philippides et al., 2013; Stürzl et al., 2016; Tinbergen, 1932; Vollbehr, 1975; Zeil, 1993a,b) lasting sometimes tens of seconds during which they learn the location of that site. These learning flights consist of stereotyped manoeuvres (Collett et al., 2013; Philippides et al., 2013; Stürzl et al., 2016), which seem to be designed to pick up visual information that can guide their return to the site. The duration of flights when leaving a flower is probably related to the reward that the flower gives (Wei et al., 2002; Wei and Dyer, 2009). But flights from the nest seem to be triggered by some appreciation of the nest's significance combined with the insect's lack of knowledge of the nest's location. So far, learning flights have not been studied in male insects. Some observations suggest that honeybee drones initially tend to perform short flights at the hive prior to mating flights, which could well be learning flights (Howell and Usinger, 1933; Witherell, 1971). Here, we first confirm earlier observations (Hempel de Ibarra et al., 2009), that male bumblebees depart directly from the nest without looking back, even though they have fed there. We then investigate whether the flights of males leaving flowers resemble those of female workers.

MATERIALS AND METHODS
Experimental procedures
Experiments were conducted from June 2015 to March 2016 in a greenhouse (8×12 m floor area) at the Streatham campus of the University of Exeter. Male and female worker bumblebees, *Bombus terrestris audax*, from commercially reared colonies (Koppert UK), were marked individually with coloured number tags. *Bombus terrestris* is a ground-nesting species that leaves its nest through a hole in the ground. To mimic this situation, we placed each experimental colony under a table and recorded the flights of naive, male and worker bees when they left their nest through a hole in the centre of the table. We also recorded the bees' departures after they had fed from a flat artificial flower on top of another table (see below; Fig. 1).

The tables (1.5×1.8 m) were covered with white gravel that was frequently raked. Three black cylinders (17×5 cm) were placed around the nest entrance at a distance of 24.5 cm (centre of the landmark). The nest entrance was surrounded by a purple plastic ring (5 cm outer diameter), which was frequently cleaned. A second identically arranged table with a sucrose dispenser (50% w/w) in the centre of another purple ring was placed 5 m away; we refer to the sucrose dispenser surrounded by the purple ring as an artificial flower.

Fig. 1. Experimental set up in a greenhouse: nest and flower tables. The nest table is in the foreground with the nest fixed under the table and its exit through a hole near the array of three cylinders. The flower table is in the background with the artificial flower in the same position relative to the cylinders as the nest hole.

The behaviour of bees leaving the nest and the flower was recorded at 50 frames s^{-1} with video cameras (Panasonic HC-V720, HD 1080p) that were hung 1.35 m above each table. An area of approximately 70×90 cm was captured in an image of 1920×1080 pixels.

Male bumblebees (identified by the presence of claspers) typically emerge as adults once the colony is mature and after some days leave the nest. When a male bumblebee flew out of the nest, we let it fly around the greenhouse before catching it in a butterfly net. Because males were not motivated to feed for many hours after leaving the nest, they were kept overnight in a box and then placed individually on the flower the next day. We videoed males while they were on the flower and their subsequent departure from it. The data for workers came from a separate experiment. Worker bees were initially accustomed to artificial flowers by placing them individually on a similar flower on a third, training table. On their second flight from the nest, the training table was hidden and workers found the experimental flower on the second table by themselves.

Bees and colonies

We analysed data from 30 males from six colonies. After leaving the hive, the males were kept overnight in cages indoors and flew normally on the next day when leaving the flower or returning to it. The flights of 14 female foragers were recorded on their flights to and from the nest and flower. We analysed a bee's first departure from the nest and from the flower. Sometimes, departures from the flower were slightly aberrant, with the bee landing during these flights (*n*=5 workers, *n*=5 males); in such cases, we analysed the second departure instead of the first.

Data analysis

The positions and body orientations of the bees (Fig. 2) were extracted from the video-recordings using custom-written codes in Matlab (Philippides et al., 2013). We define the duration of flights from the nest or the flower as the time it took the bees to cross a 30 cm radius circle centred on the nest entrance or the flower. Similarly, we define cumulative distance as the distance a bee travelled before it crossed a circle of a given radius for the first time.

Both workers and males on their departure from the flower turned back to face and fixate the flower (Lehrer, 1993). Such fixations are

typical of learning flights and we compared the fixations of the two sexes. To extract fixations relative to the flower, we first computed for every frame of each flight the angle between the bee's line of sight to the flower and its longitudinal body axis (ϕ; counterclockwise angles are positive; see Fig. 3B). We then scanned successive frames of each flight, noting the modular angular difference ($\Delta\phi$) between adjacent frames, *n* and *n*+1. If $\Delta\phi$ was >3 deg, we repeated this calculation on the next pair of frames, i.e. frames *n*+1 and *n*+2, continuing the process until $\Delta\phi$ was ≤3 deg. Such a small rotational difference indicated the potential start of what we accept as a fixation. To test whether this was the case, we added the next frame to the two-frame sample. If the modular difference between the minimum and maximum values of the sample of three frames ($\Delta\phi_{min.max}$) was ≤3 deg, we added the next frame to the sample and again tested whether $\Delta\phi_{min.max}$ of the four-frame sample was ≤3 deg. This loop was repeated, sequentially adding frames until $\Delta\phi_{min.max}$ of the whole sample was >3 deg. Provided that the sample size of successive frames with $\Delta\phi_{min.max}$≤3 deg was ≥4 frames, the sample was included as a fixation and we recorded its duration and the median value of ϕ. We then continued to scan neighbouring frames until we encountered the start of another potential fixation ($\Delta\phi$≤3 deg), when once more we tested whether these and subsequent frames met our criteria for a fixation. If they did not, the scanning of neighbouring frames was resumed from the second frame after the potential start. This process continued until the end of the flight and was applied to all male and worker learning flights on departure from the flower.

To test whether the selected fixations were more precisely oriented towards the flower than would be expected from the overall distribution of ϕ across learning flights, we carried out two randomisation tests on male flights that were computed in R (version 3.2.0). In the first test, we combined all the frames of the measured fixation intervals into one sample. For each frame of this sample, we took the absolute value of the difference between ϕ and ϕ=0 deg and averaged these values. This total ('mean absolute difference'; see Fig. 3) was then compared with the mean absolute difference of samples of the same number of frames, which were selected randomly from all the flights. We generated 100,000 random samples and found that none of the values for mean absolute difference of these 100,000 samples were smaller than the mean absolute difference of the real fixation sample (Fig. 3). We therefore rejected the hypothesis that the flower-facing fixations can be obtained by randomly selecting frames from all the flights.

In the second test, we took each fixation separately and calculated the absolute value of the difference between the median ϕ of the fixation and ϕ=0 deg. These absolute values were averaged across all the fixations ('mean of the median absolute difference') and compared with that of random selections of consecutive frames. To do so, we randomly selected groups of consecutive frames from different flights to match the number of fixations and their durations (Fig. 3) and calculated the mean of the median absolute difference of this random sample of groups. As in the first test, we repeated the randomisation procedure 100,000 times. Again, none of the values for the mean of the median absolute difference of these 100,000 samples were smaller than the mean of the median absolute difference of the real fixation sample (Fig. 3).

RESULTS
Departures from the nest and flower

On their departure from the nest, males accelerated directly away without turning back to face the nest (Fig. 2A). Their flights when
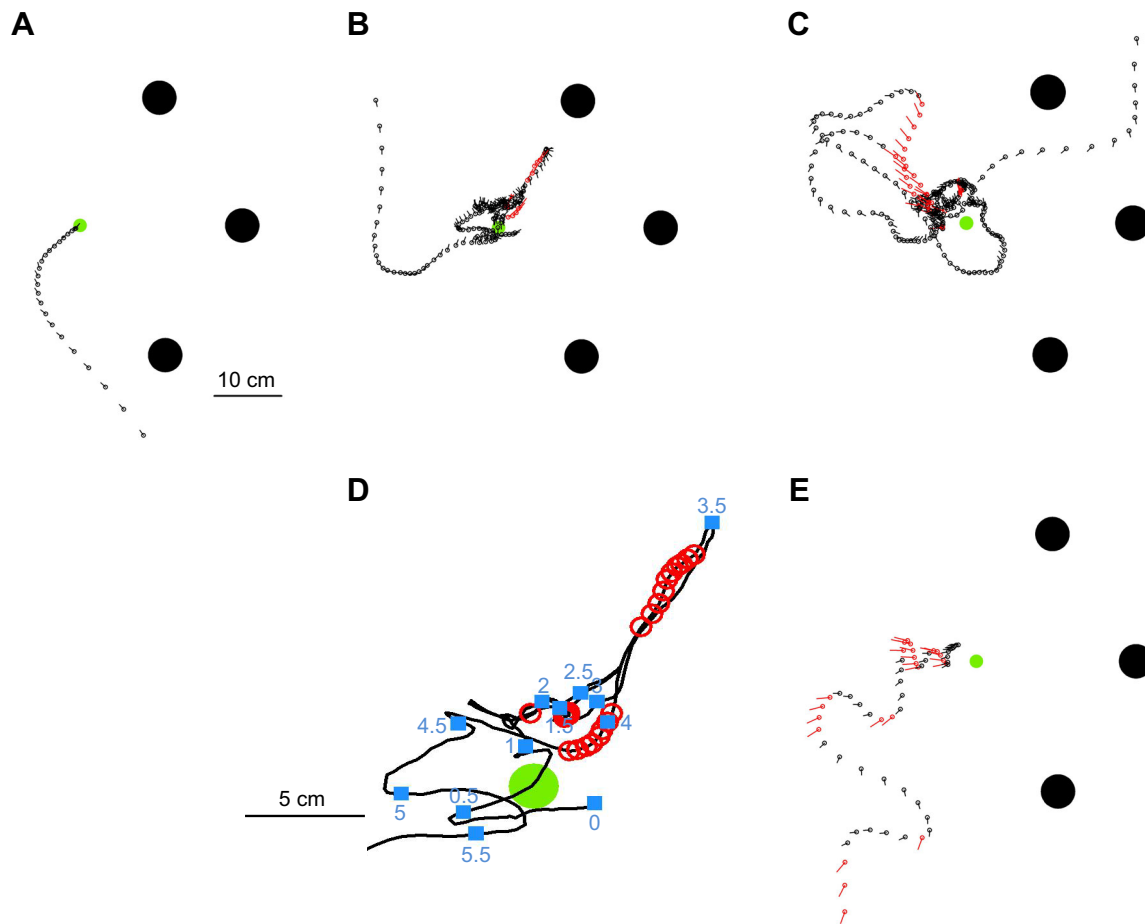
Fig. 2. Example trajectories of male bumblebees. (A) Departure from the nest. (B) Departure from the flower. Flights in A and B are by the same male. (C) Departure from the flower by another bee after its spontaneous return to the flower. (D) Enlarged view of the initial segment of the flight in B. Red circles indicate fixations of the flower (see Materials and methods). Blue squares mark every 0.5 s from the start of the flight. (E) Return to the flower. In all panels except D, each dot shows the position of the bee every 0.04 s and each line shows the orientation of the bee's body. Red circles and lines indicate instances in which the bee faced the flower. Positions of the nest and flower are shown by a green circle. Black circles represent the array of three cylinders. See also Figs S1 and S2.

leaving the flower were significantly longer (Fig. 2B,D). The first departures from the flower were recorded when males were placed on the flower, rather than when they found it by themselves. To check whether this procedure might have disturbed the bees' flights on their departure, we tested workers with the same procedure. The workers' learning flights were of similar duration (see Materials and methods, 'Data analysis') whether they were placed on the flower (N=14, mean±s.e.m. 4.83±1.25 s) or flew there by themselves (N=14, 5.33±1.02 s, Mann–Whitney U-test, U=78.5, Z=−0.90, P=0.37). This similarity suggests that the departure flights of males are also unlikely to be influenced by the way in which a bee reaches the flower. Learning flights after a male's return to the flower support this suggestion (Fig. 2C).

Although males were deprived of food for about a day before being placed on the flower, the time that they spent on the flower was variable. Sometimes males flew away very soon and sometimes they stayed there for 2–3 min (Fig. 4A). We had no direct measurement of when a bee started to drink and the time that it drank when on the flower, but it is reasonable to suppose that drinking time is correlated with time spent on the flower. As males forage for themselves and not for the colony, their motivational state may well be more variable than that of workers. The time that males spent on the flower was correlated with the duration of their flight on departure (Spearman rank, ρ=0.51, P=0.0042; Fig. 4A), suggesting

that a short time spent on the flower, allowing little or no time to drink, is insufficient to trigger learning. For this reason, we excluded males that were in the bottom quartile of time spent on the flower (from 1.8 to 14.4 s) from further analysis.

In several respects, the flights of males leaving flowers resembled those of females. The durations of the flights did not differ significantly (Fig. 4B,C) in contrast to the very short flight durations of males leaving the nest and the very long flights of female workers when they left the nest. The similarities between the durations of male and female flights leaving the flower are mirrored in the cumulative distance plots (Fig. 4D) in which both sexes took a longer, more circuitous route when leaving the feeder (Fig. 2; Figs S1 and S2), than did males leaving the nest.

Flower fixations

A hallmark of learning flights is that bees or wasps look back towards the nest or flower (Collett and Lehrer, 1993; Hempel de Ibarra et al., 2009; Lehrer, 1993; Riabinina et al., 2014; Stürzl et al., 2016), presumably recording views that can guide their return. Whereas bumblebee males almost never faced the nest on leaving it, they, like workers, always looked back when they left the flower. The flight excerpt in Fig. 2D includes three instances (marked in red) of a male facing the flower on departure. The first is a very brief period of hovering at 1.7 s. The second and third are longer, starting
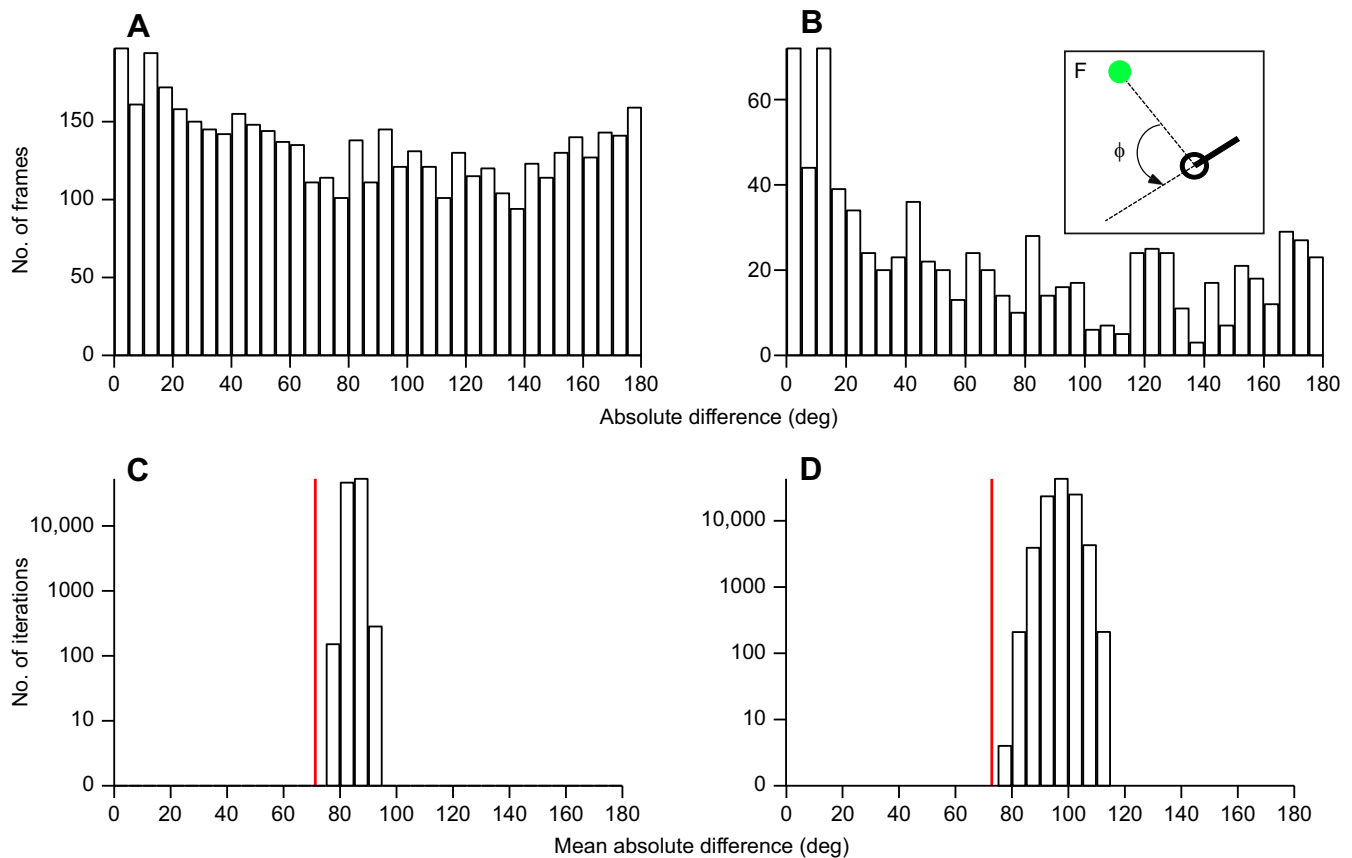
Fig. 3. Analysis of flower fixations in male learning flights. (A,B) Distribution of the absolute values of angles between the male's body orientation and the line from bee to flower (|φ|) for every frame in every flight (4872 frames, *N*=24 males, *n*=24 flights; A) and for every frame in every fixation (821 frames; B). (C,D) Distribution of the mean |φ| of each randomly picked sample of individual frames (C) and groups of frames (D). In both cases, 100,000 samples were randomly selected. The red lines show the measured means of body angle orientation during fixations. Their position outside the distributions of the means of the randomly selected frames and groups of frames demonstrates that the measured distribution of body orientations in fixations is not a random selection from the overall distribution of body orientations during learning flights of male bumblebees. Inset in B shows the angle φ between the flower (F, green circle) and the bee's longitudinal body axis.

at 3.5 s and at 4 s. During the third, the male flies back towards the flower (see Figs S1 and S2 for further examples).

This divergence in facing the flower but not the nest can be seen in plots of the body orientation of males relative to the nest and flower (φ) that include all the frames of all the recorded flights (Fig. 5A). On flights from the flower, the broad peak of the distribution of facing directions relative to the flower (φ) is towards the flower (Fig. 5A, circular mean: 44.02 deg, ρ=0.092, Rayleigh *Z*-test, *Z*=41.93, *P*<0.0001), but on leaving the nest, the peak of the distribution of facing directions is in the direction of departure (circular mean: 177.36 deg, ρ=0.726, Rayleigh *Z*-test, *Z*=615.38, *P*<0.0001): the bee faced the nest for only 0.35% of frames (Fig. 5A).

To what extent are frames in which bees look at the flower grouped together so that the bees fixate the flower for consecutive frames? To examine flower fixations, we extracted periods when the direction in which the bees looked relative to the flower (φ) remained relatively constant (see Materials and methods, 'Data analysis'). Partitioning all the frames of male departures from the flower into those that do and do not fall within these extracted fixations shows a strong peak towards the flower in the distribution of frames within the fixations (Fig. 5B). No such peak is seen for the distribution of frames outside fixations. In addition, a resampling analysis (Good, 2006) shows that the distribution of frames in the fixations has a significantly greater peak in the direction of the

flower than would be expected from the overall distribution of frames from all flights (Fig. 5A, see Fig. 3 for details). It thus seems that bees tend to look at the flower during brief periods of fixation (Fig. 5C).

The modal duration of these fixations was 80 ms in males and females, both when the bees fixated the flower within ±20 deg and when they looked elsewhere (Fig. 6). In both sexes, the distribution of fixations peaked when bees faced the flower (Fig. 5C), but workers spent slightly more of the flight facing the flower than did males. Thus, males faced the flower in 11.03±1.74% (mean±s.e.m.) of all frames and females in 14.42±2.42% of all frames (Mann–Whitney *U*-test, *U*=125.5, *Z*=1.29, *P*=0.20). In both males and females, fixations of the flower occurred most often when bees were close to the flower, within 5–10 cm of its centre (Fig. 5D). The flights of males and females leaving the flower are thus quite comparable.

Returns to flowers

On several occasions, males were recorded when they flew back to revisit the flower (*N*=8, Fig. 2E). These returns resembled those of workers. Like workers returning to the nest (Philippides et al., 2013), the male in Fig. 2E faced the flower at the turning points of its zigzag approach. The flight speeds of males and workers dropped at about the same rate during the bee's approach to the flower (Fig. 7A). Likewise, the path lengths of the bee's approach to the
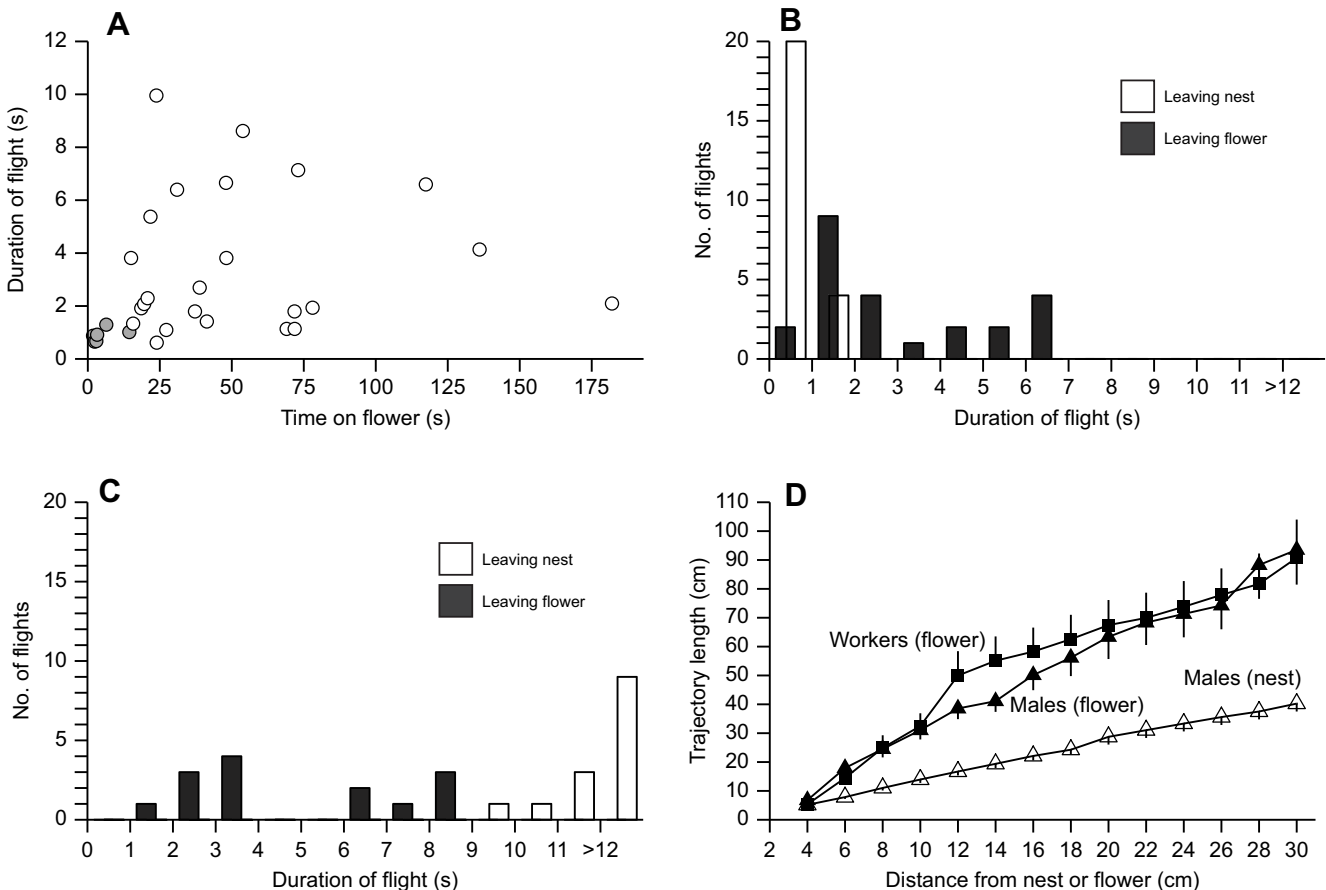
Fig. 4. Some properties of male and female learning flights. (A) Duration of male departure flights from the flower (i.e. time taken to cross a 30 cm radius circle around the flower), plotted against time spent drinking on the flower before departure (N=30 males). Filled circles represent males with a short drinking time (bottom quartile) that were excluded from further analysis (N=6 males). (B) Duration of male departure flights from the nest and flower. (C) Duration of worker departure flights from the nest and flower. The flights of males from the flower were a little shorter (N=24 males, n=24 flights, mean±s.e.m. 3.58±0.54 s) than those of workers (N=14 workers, n=14 flights, 4.94±0.72 s) (Mann–Whitney U-test, U=109, Z=−1.79, P=0.07). Worker flights from the nest lasted longer than the other three categories, i.e. male flights from the nest and flower and worker flights from the flower (14.42±1.20 s). (D) Cumulative trajectory lengths flown by males leaving the nest or flower and by workers leaving the flower. Lengths at different distances from the flower or nest are those measured before the bee first crossed a circle of a given radius to a maximum of 30 cm. The mean±s.e.m. total trajectory length of males leaving the nest was 40.25±2.74 cm and that of males leaving the flower was 98.53±12.05 cm (Wilcoxon, W=21, Z=−3.69, P=0.0002). The mean±s.e.m. trajectory length of workers leaving the flower was 90.75±13.25 cm. It was slightly but not significantly shorter than the trajectories of males leaving the flower (Mann–Whitney U-test, U=159, Z=−0.27, P=0.79). See also Figs S1 and S2.

flower from 30 cm were similar in the two sexes (Fig. 7B). Males faced the flower less often than workers, as seen in a slightly lower peak in the distribution of facing positions (Fig. 7C). Workers faced the flower mostly when they were close to it, but males faced the flower over a broader range of distances (Fig. 7D).

DISCUSSION
Our results show that male and female bumblebees perform flights of a similar structure when leaving flowers, suggesting that males, like workers, perform learning flights when leaving flowers. Although some males, like workers, returned to the flower after their learning flight, we do not know what males have memorised about the flower and its location during the flight. Male bumblebees have recently been found to learn the colours of artificial flowers and approach the rewarded colour while avoiding unrewarded colours (Wolf and Chittka, 2016), but it is unknown whether colour was memorised during a learning flight. The essence of this flight is that it contains periods of directed looking that are presumably coupled to the activation of learning. Thus, the patterns of fixation of a flower by males and females during learning flights (Fig. 5) suggest that both sexes learn something about it – a conclusion that

is reinforced by both males and workers facing the flower during their returns (Fig. 7).

Bumblebee workers forage on a diversity of flowers in different locations, and it may be that learning the colour, shape and odour of a good species is just as or even more important than knowing a flower's exact location within a patch (Heinrich, 1979), though bumblebees can be faithful to the location of a patch, even when the flower species in the patch changes (Ogilvie and Thomson, 2016), indicating some locational learning of flowers. Honeybees can learn the details of a flower's appearance on both arrival and departure (Lehrer, 1993), but they seem to learn location in terms of a flower's proximity to other objects only on departure flights (Lehrer and Collett, 1994). It is unknown whether bumblebees are similar in this respect and whether males differ from females in their learning capacities.

Learning flights can be elicited by several factors such as drinking nectar or leaving a nest. They are also modulated by a variety of factors, like drinking time and sucrose concentration, enclosure in a hive or nest for protracted periods, and difficulty in finding a goal (e.g. Wagner, 1907; Wei et al., 2002; Wei and Dyer, 2009). The duration of a learning flight seems to be correlated with
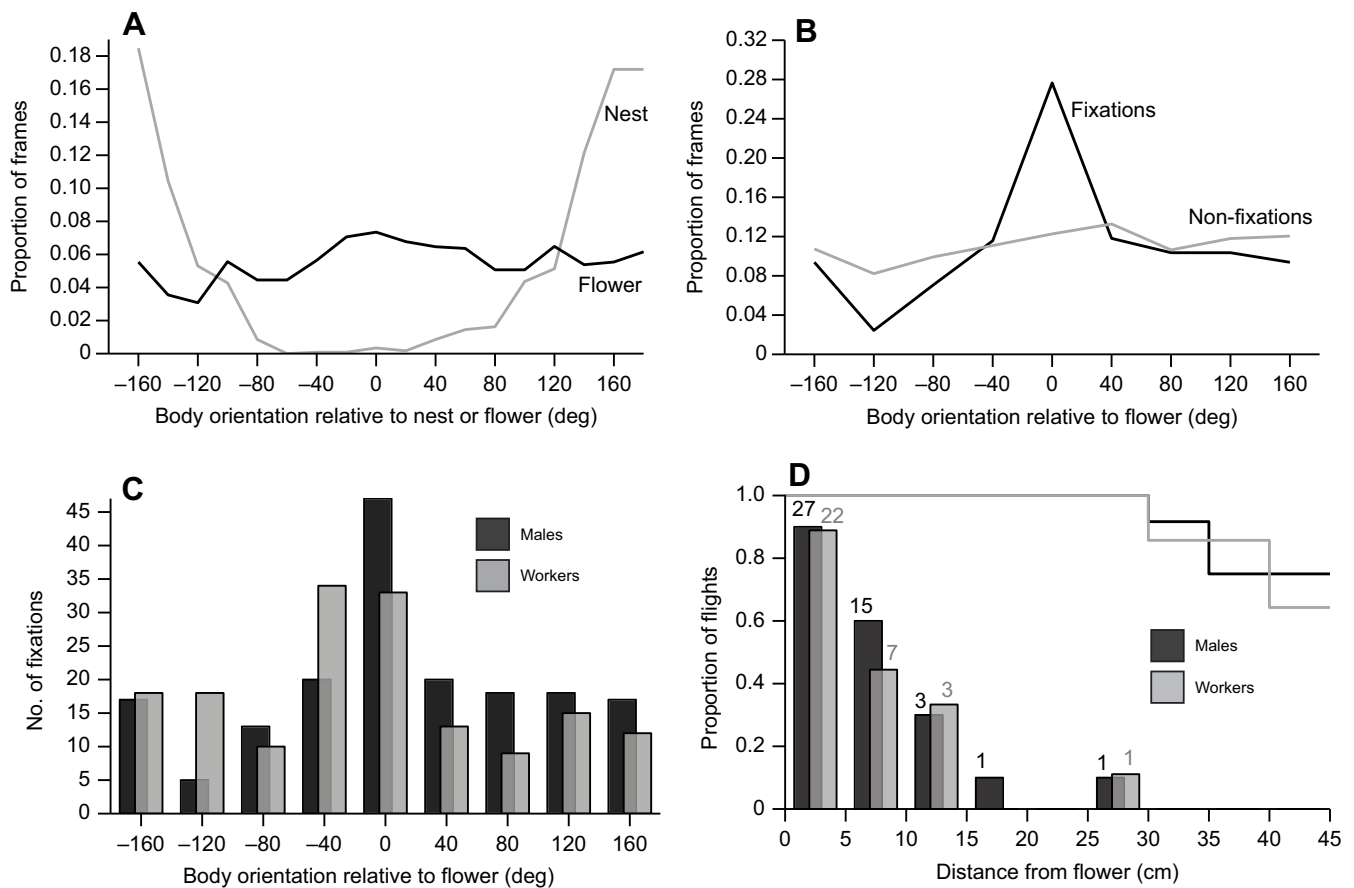
Fig. 5. Fixations of flower and nest during learning flights. (A) Frequency distribution of male body orientation relative to the nest (grey line, 1169 frames, N=24 males) or flower (black line, 4872 frames; N=24 males) on departures from them. Bin width is 20 deg. (B) Distribution of body orientation relative to the flower when all frames of male departure flights are partitioned into those within fixations (821 frames) and those outside fixations (4051 frames). (C) Frequency distribution of male and worker fixations (175 male fixations, 162 worker fixations; N=24 males, N=14 workers) relative to the flower (40 deg bin width). (D) Proportion of flights with at least one flower fixation (ϕ=0±20 deg) within a specified distance from the flower (N=10 males, N=9 workers). The numbers above each 5 cm bin give the total number of fixations falling in that bin. The lines above the histograms show the proportion of flights at each distance that are at least as long as that distance (N=24 males, N=14 workers).

the significance of the place that the bee leaves. Thus, when they leave their nest, workers perform much longer flights than when they leave a flower (Fig. 4). It is still unclear whether bees learn the same things when viewing flowers or the surroundings of the nest entrance.

Males of different bee species have a variety of mating strategies (Goulson, 2010; Paxton, 2005). In bumblebees, the commonest is that of *B. terrestris*, which patrols areas along routes. Other species are territorial and wait, hovering or perched, near a prominent visual object to pounce upon potential passing mates. Might males learn
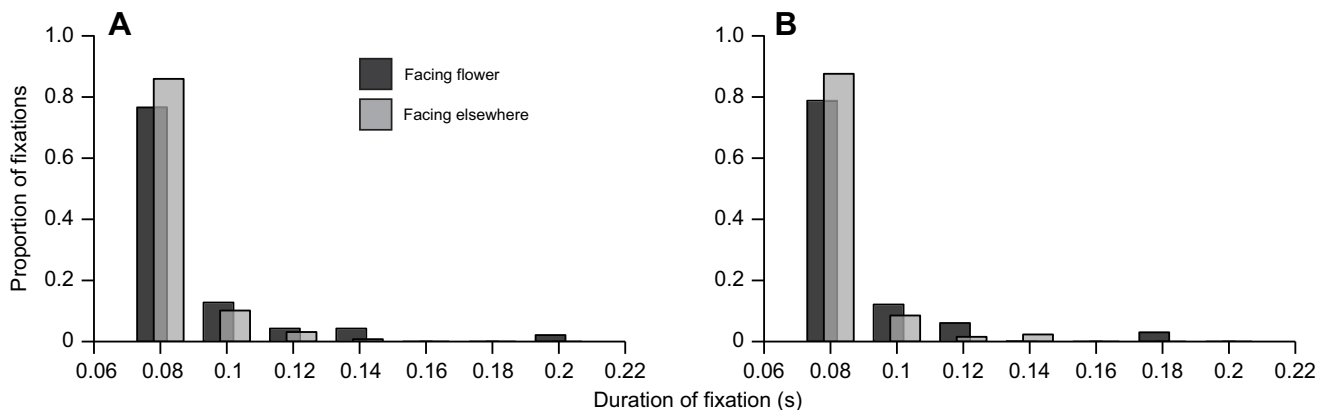

Fig. 6. Duration of fixations in male and female learning flights. Normalised distributions of the duration of all fixations in (A) males (n=175 fixations, N=24 males) and (B) workers (n=162 fixations, N=14 workers). Male and female fixations are partitioned into those in which bees faced the flower (ϕ=0±20 deg; males n=47 fixations, workers n=33 fixations) or did not face the flower (ϕ<−20 deg or ϕ>20 deg).
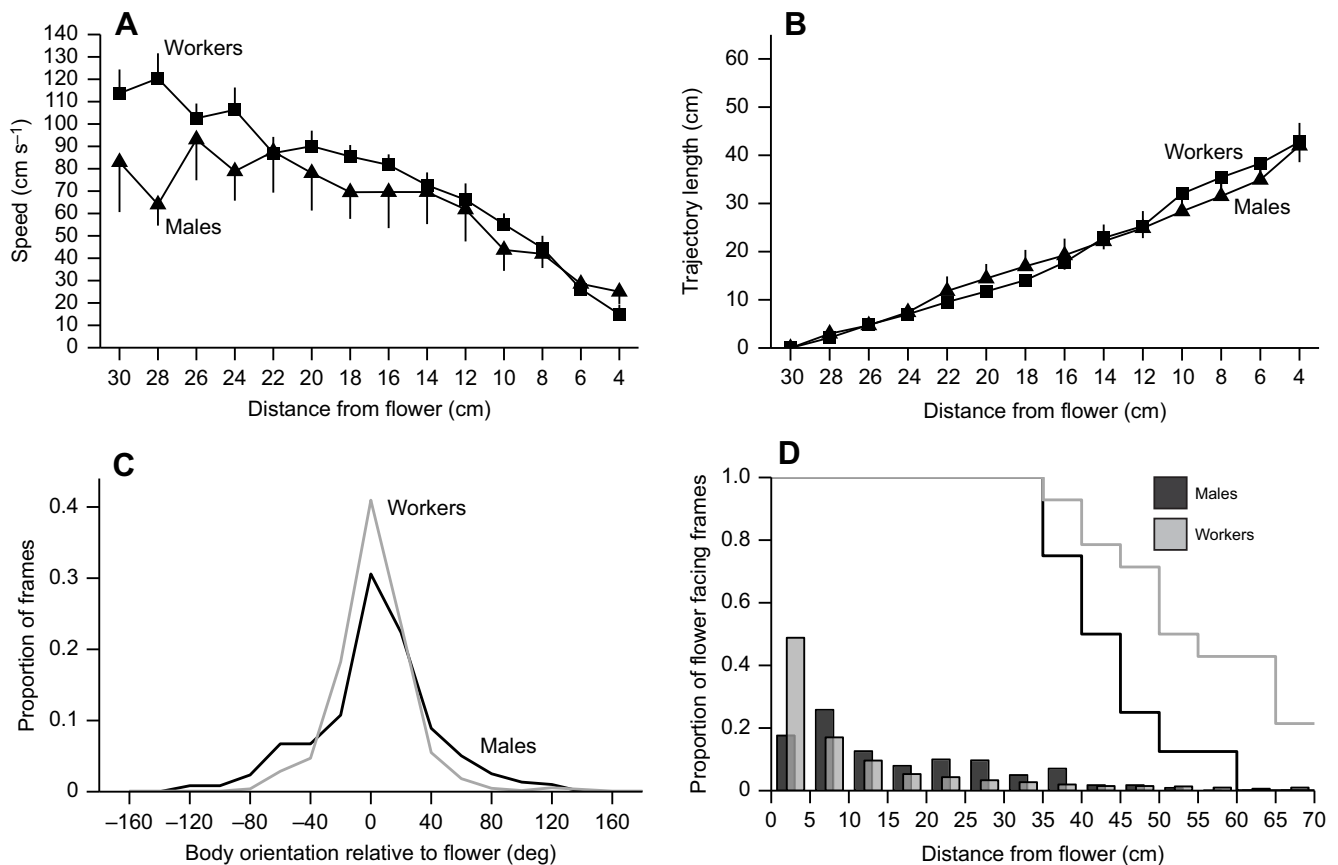
Fig. 7. Comparison of male and worker returns to the flower. (A) Flight speed plotted against distance from the flower (N=8 males, N=14 workers). (B) Cumulative trajectory length as a function of distance from the flower. (C) Frequency distribution of body orientation relative to the flower (males, N=595 frames, workers N=1255). (D) Relative frequency of flower facing (ϕ=0±20 deg) plotted against distance from the flower (males, N=341 frames, workers N=811 frames). The lines above the histograms show the proportion of flights at each distance that are at least as long as that distance (N=8 males, N=14 workers).

their visually specified hovering positions, as do patrolling halictine bees (Barrows, 1976)? Honeybee drones are quite different from bumblebees. They make excursions from their nest to drone aggregation sites to find and mate with queens (Galindo-Cardona et al., 2015; Loper et al., 1992; Witherell, 1971). When unsuccessful, they return to the nest for feeding, as do some male carpenter bees (Leys, 2000; Wittmann and Scholz, 1989). Does the occurrence of learning flights of honeybee and carpenter bee males also fit with their life style: learning flights when leaving the hive (to which they return for sustenance), instead of at flowers (which they do not visit)?

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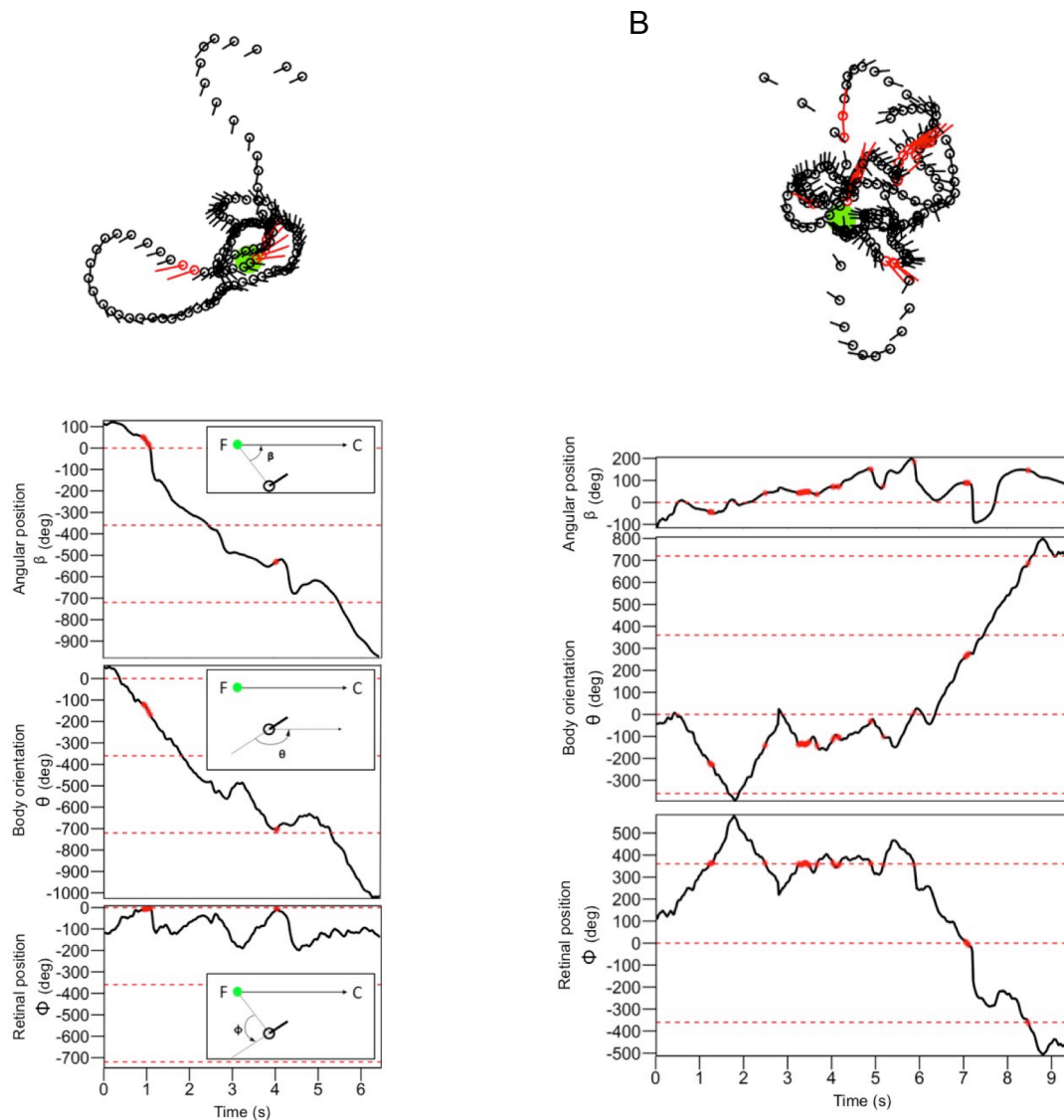
Figure S1. Further example trajectories of a bumblebee male (A) and worker (B) leaving the flower.

In some learning flights bees turn for long periods in the same direction, rotating clock- or counter-clockwise through several complete revolutions. In other flights bees alternate their direction of rotation. Each dot depicts the position of the bee every 40 ms. The line shows the bee's body orientation. Red circles and lines indicate when the bee faces the flower. Green circle shows the position of the flower. Time plots show the bee's cumulative angular position (β) (Zeil, 1993a), its body orientation (θ) relative to the line between the flower and central landmark (F-C), and the position of the flower relative to the bee's longitudinal axis (ϕ, 'Retinal' position for short). Arrows (inset) point in a positive direction. Moments in which the bee faced the flower ($\pm10°$) are shown in red.
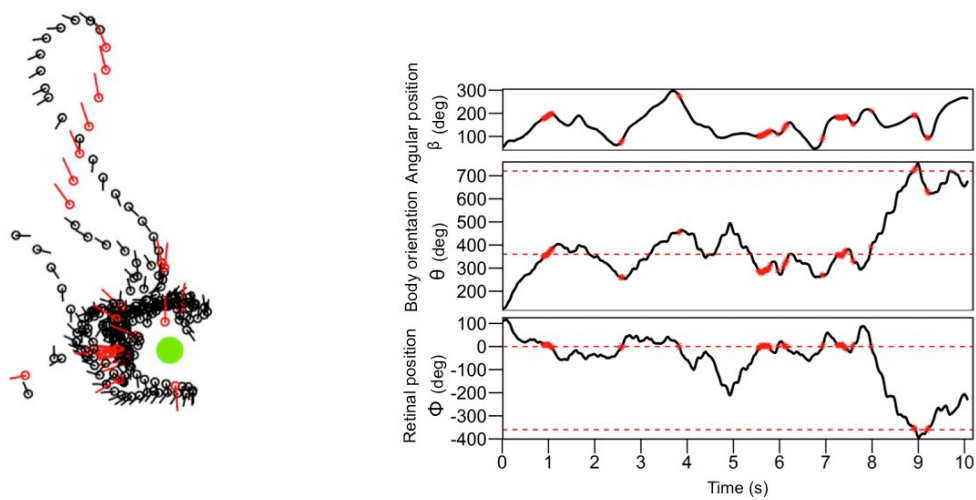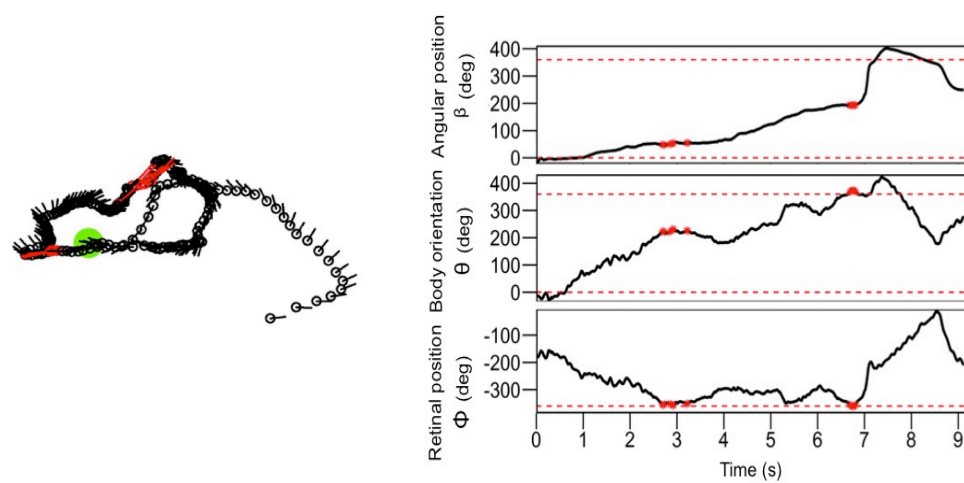
Figure S2. Further similarities in the learning flights of a bumblebee male (A) and worker (B) leaving the flower. For details see Figure S1.