

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

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10

11 **Keywords**

12 Insect, bee, learning, flight, navigation, flower

13

14 **Summary statement (max 30 words)**

15 Bumblebee males leave their nest directly, but they perform learning flights when they leave
16 artificial flowers, during which they turn back and fixate the flowers.

17

18 **Abstract**

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

33

34 **Introduction**

35 In many animal species the two sexes, to some degree, know and learn about different things.
36 In eusocial insects, like bees, the roles of females and males are quite distinct. In the
37 bumblebee, *Bombus terrestris* L., the species with which we are concerned here, a single
38 female queen lays fertilised eggs. Other females are workers that perform one of several tasks
39 for the benefit of the colony. They may, for instance, tend larvae, guard the colony, explore
40 for nest or food sites, forage for nectar and pollen which they bring back to the nest. The
41 workers forage individually and must learn the locations of both their nest and of good
42 foraging sites. Male *Bombus terrestris*, in contrast, are not concerned about the state of the
43 colony. They leave their nest to find potential mates and do not return (Goulson, 2010;
44 Paxton, 2005). Indeed, possibly as part of a strategy to avoid inbreeding (Baer, 2003; Gerloff
45 and Schmid-Hempel, 2005; Whitehorn et al., 2009), they may travel as far as 10 km where
46 they live as solitary foragers and patrol the terrain for queens (Coppée et al., 2011; Kraus et
47 al., 2009; Paxton, 2005). Whereas males may well learn the location of foraging sites near to
48 their patrolling area, they have no reason to learn to return to their nest. Are these differences
49 in life style - foraging for the community by females and foraging for themselves by males -
50 reflected in the occurrence of learning flights in the two sexes?

51

52 Female wasps and bees on first leaving their nest or a flower perform elaborate flights
53 (Brünnert et al., 1994; Collett, 1995; Collett et al., 2013; Collett and Lehrer, 1993; Hempel de
54 Ibarra et al., 2009; Lehrer, 1993; Opfinger, 1931; Philippides et al., 2013; Stürzl et al., 2016;
55 Tinbergen, 1932; Vollbehre, 1975; Zeil, 1993a; Zeil, 1993b) lasting sometimes tens of seconds
56 during which they learn the location of that site. These learning flights consist of stereotyped
57 manoeuvres (Collett et al., 2013; Philippides et al., 2013; Stürzl et al., 2016), which seemed
58 to be designed to pick up visual information that can guide their return to the site. The
59 durations of flights when leaving a flower are probably related to the reward that the flower
60 gives (Wei et al., 2002; Wei and Dyer, 2009). But flights from the nest seem to be triggered
61 by some appreciation of the nest's significance combined with the insect's lack of knowledge
62 of the nest's location. So far, learning flights have not been studied in male insects. Some
63 observations suggest that honeybee drones initially tend to perform short flights at the hive
64 prior to mating flights which could well be learning flights (Howell and Usinger, 1933;
65 Witherell, 1971). We find here, confirming earlier observations (Hempel de Ibarra et al.,
66 2009), that male bumblebees with no attachment to their natal nest, even though they have
67 fed there, depart directly from the nest without looking back. We now investigate whether the
68 flights of males leaving flowers resemble those of female workers.

69

70 **Materials and Methods**

71

72 *Experimental procedures*

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

81

82 The tables (1.5x1.8m) were covered with white gravel that was frequently raked. Three black
83 cylinders (17x5cm) were placed around the nest entrance at a distance of 24.5 cm (centre of
84 the landmark). The nest entrance was surrounded by a purple plastic ring (5 cm outer
85 diameter), which was frequently cleaned. A second identically arranged table with a sucrose
86 dispenser (50% w/w) in the centre of another purple ring, was placed 5m away. We refer to
87 the sucrose dispenser and purple ring as an artificial flower. The behaviour of bees leaving
88 the nest and the flower was recorded at 50 frames per second with video cameras (Panasonic
89 HC-V720, HD 1080p) that were hung 1.35m above each table. An area of appx. 70x90cm
90 was captured in an image of 1920x1080 pixels.

91

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

102

103 *Bees and colonies*

104 We analysed data from 30 males from 6 colonies. The males after leaving the hive were kept
105 overnight in cages indoors and flew normally when leaving the flower or returning to it. The
106 flights of 14 female foragers were recorded on their flights to and from the nest and flower.
107 We analysed a bee's first departure from the nest and flower, respectively. Sometimes,
108 departures from the flower were slightly aberrant with the bee landing during these
109 flights (n=5 workers, n=5 males). We then analysed the second departure instead of the first.

110

111 *Data analysis*

112 The positions and body orientations of the bees (Fig. 2) were extracted from the video-
113 recordings using custom-written codes in Matlab (Philippides et al., 2013). Angles are
114 measured with counter-clockwise direction positive and clockwise negative. We measure the
115 duration of flights from the nest or the flower as the time it took the bees to cross a 30cm
116 radius circle centred on the nest entrance or the flower. Similarly, we measure cumulative
117 distance as the distance a bee travels before it crosses for the first time a circle of a given
118 radius.

119

120 Both workers and males on their departure from the flower can be seen to look back and face
121 it. We adopted the following procedure in order to analyse these flower fixations. We first
122 extracted all fixations relative to the flower. To do so, we took the angular position of the
123 bee's longitudinal axis relative to the flower (φ) (Fig. 3) and scanned successive frames of
124 each flight, noting the modular angular difference (diff φ) between adjacent frames, n and
125 n+1. If diff φ was $>3^\circ$, we repeated this calculation on the next pair of frames i.e. frames n+1
126 and n+2, continuing the process until diff φ was $\leq 3^\circ$. Such a small rotational difference
127 indicated the potential start of what we accept as a fixation. To test whether it was indeed a
128 start, we added the next frame to the two-frame sample. If the modular difference between
129 the minimum and maximum values of the sample of three frames (φ [diff.min.max]) was $\leq 3^\circ$,
130 we added the next frame to the sample and again tested whether φ [diff.min.max] of the four-
131 frame sample was $\leq 3^\circ$. This loop was repeated, sequentially adding frames until φ
132 [diff.min.max] of the whole sample was $>3^\circ$. Provided that the sample size of successive
133 frames with φ [diff.min.max] $\leq 3^\circ$ was ≥ 4 frames, the sample was included as a fixation and
134 we recorded its duration and the median value of φ . We then continued to scan neighbouring
135 frames until we encountered the start of another potential fixation (φ [diff]) $\leq 3^\circ$, when once

136 more we tested whether these and subsequent frames met our criteria of a fixation. If they did
137 not, the scanning of neighbouring frames was resumed from the 2nd frame after the potential
138 start. This process continued until the end of the flight and was applied to all male and worker
139 learning flights at the flower.

140

141 To test whether the selected fixations were more precisely oriented towards the flower than
142 would be expected from the overall distribution of φ across learning flights, we carried out
143 two randomisation tests that were computed in R (version 3.2.0). In the first test, we
144 combined all the frames of the measured fixation intervals into one sample. For each frame of
145 this sample we took the absolute value of the difference between φ and $\varphi=0^\circ$ and averaged
146 these values. This total (Mean[abs.diff]) (see Fig. 3) was then compared with the
147 Mean[abs.diff]s of samples of the same number of frames which were selected randomly
148 from all the flights. We generated 100,000 random samples and found that none of the
149 Mean[abs.diff]s of the 100,000 were smaller than the Mean[abs.diff] of the real fixation
150 sample (Fig. 3). We therefore rejected the hypothesis that the flower-facing fixations can be
151 obtained by randomly selecting frames from all the flights.

152 In the second test, we took each fixation separately and calculated the absolute value of the
153 difference between the median φ of the fixation and $\varphi=0^\circ$. These absolute values were
154 averaged across all the fixations (Mean[median.abs.diff]) and compared with that of random
155 selections of consecutive frames. Thus, we randomly selected groups of consecutive frames
156 from different flights to match the number of fixations and their durations (Fig. 3) and
157 calculated the Mean[median.abs.diff] of this random sample of groups. As in the first test, we
158 repeated the randomisation procedure 100,000 times. Again, none of the
159 Mean[median.abs.diff]s of the 100,000 were smaller than the Mean[median.abs.diff] of the
160 real fixation sample (Fig. 3).

161 **Results**

162

163 *Departures from nest and flower*

164 Males on their departure from the nest accelerated directly away without turning back to face
165 the nest (Fig. 2A). The males' flights when leaving the flower were significantly longer and
166 more complex (Fig. 2B, D). The first departures from the flower were recorded when males
167 were placed on the flower, rather than when they found it by themselves. To check whether
168 this procedure might have disturbed the bees' flights on their departure, we tested workers

169 with the same procedure. The workers' learning flights were of similar duration (see *Data*
170 *analysis*) whether they were placed on the flower (N=14, Mean=4.83s±1.25) or flew there by
171 themselves (N=14, Mean=5.33±1.02, Mann-Whitney-U test, U=78.5, Z=-0.90, p=0.37). This
172 similarity suggests that the departure flights of males are also unlikely to be influenced by the
173 way in which a bee reaches the flower. Learning flights after a male's return to the flower
174 support this suggestion (Fig. 2C).

175

176 Although males were deprived of food for about a day before being placed on the flower, the
177 time that they spent on the flower was variable. Sometimes males flew away very soon and
178 sometimes they stayed there for 2-3 minutes (Fig. 4A). We had no direct measurement of
179 when a bee started to drink and how long it drank when on the flower, but it is reasonable to
180 suppose that drinking time is correlated with time spent on the flower. Since males forage for
181 themselves and not for the colony, their motivational state may well be more variable than
182 that of workers. The time that males spent on the flower is correlated with the duration of
183 their flight on departure (Spearman Rank, rho=0.51, p=0.0042, Fig. 4A), suggesting that a
184 short time spent on the flower, allowing little or no time to drink, is insufficient to trigger
185 learning. For this reason, we have excluded males that were in the bottom quartile of time
186 spent on the flower (from 1.8 to 14.4s) from further analysis.

187

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

194

195 *Flower fixations*

196 A hallmark of learning flights is that bees or wasps look back towards the nest or flower
197 (Collett and Lehrer, 1993; Hempel de Ibarra et al., 2009; Lehrer, 1993; Riabinina et al., 2014;
198 Stürzl et al., 2016), presumably recording views that can guide their return. Whereas
199 bumblebee males almost never faced the nest on leaving it, they, like workers, always did
200 when they left the flower. The flight excerpt in Figure 2D includes three instances (marked in
201 red) of a male facing the flower on departure. The first is a very brief period of hovering at

202 1.7s. The second and third are longer, starting at 3.5s and at 4s. During the third, the male
203 flies back towards the flower (see Fig. S1 and S2 for further examples).

204

205 This difference between facing flowers but not the nest can be seen in plots of the body
206 orientation of males relative to the nest and flower (φ) that includes all the frames of all the
207 recorded flights (Fig. 5A). On flights from the flower, the broad peak of the distribution of
208 facing directions relative to the flower (φ) is in its direction (Fig. 5A, circular mean: 44.02° , r
209 $=0.092$, Rayleigh Z test, $Z=41.93$, $P<0.0001$), but on leaving the nest, the peak of the
210 distribution of facing directions is in the direction of departure (circular mean: 177.36° , r
211 $=0.726$, Rayleigh Z test, $Z=615.38$, $P<0.0001$): the bee faced the nest on only 0.35% of
212 frames (Fig. 5A).

213

214 To what extent are frames in which bees look at the flower grouped together so that the bees
215 fixate the flower for consecutive frames? To examine flower fixations, we extracted periods
216 in which the bees' looking directions relative to the flower (φ) remained relatively constant
217 (see *Data analysis*). A partition of all the frames of male departures from the flower into
218 those that do and do not fall within these extracted fixations shows a strong peak towards the
219 flower in the distribution of frames within the fixations (Fig. 5B). No such peak is seen for
220 the distribution of frames outside fixations. In addition, a resampling analysis (Good, 2006)
221 shows that the distribution of frames in the fixations is significantly more peaked in the
222 direction of the flower than would be expected from the overall distribution of frames from
223 all flights (Fig. 5A, see Fig. 3 for details). It thus seems that bees tend to look at the flower
224 during brief periods of fixation (Fig. 5C).

225

226 The modal duration of these fixations was 80ms in males and in females, both when the bees
227 fixated the flower within $\pm 20^\circ$ and when they looked elsewhere (Fig. 6). While in both sexes
228 the distribution of fixations peaked when bees faced the flower (Fig. 5C), workers spent very
229 slightly more of the flight facing the flower than did males. Thus, males faced the flower in
230 $11.03\% \pm 1.74\text{SE}$ of all frames and females in $14.42\% \pm 2.42\text{SE}$ of all frames (Mann-Whitney-
231 U, $U=125.5$, $Z=1.29$, $p=0.20$). In both males and females fixations of the flower occurred
232 most often when bees were close to the flower, within 5-10cm of its centre (Fig. 5D). The
233 flights of males and females leaving the flower are thus quite comparable.

234

235 *Returns to flowers*

236 On several occasions males were recorded when they flew back to revisit the flower (N=8,
237 Fig. 2E). These returns resembled those of workers. Like workers returning to the nest
238 (Philippides et al., 2013), the male in Fig. 2E faced the flower at the turning points of its
239 zigzag approach. The flight speeds of males and workers dropped at about the same rate
240 during the bees' approaches to the flower (Fig. 7A). Likewise, the path lengths of the bees'
241 approach to the flower from 30cm were similar in both sexes (Fig. 7B). Males faced the
242 flower less often than workers, as seen in a slightly lower peak in the distribution of facing
243 positions (Fig. 7C). Workers faced the flower mostly when they were close to it, but males
244 faced the flower over a broader range of distances (Fig. 7D).

245

246 **Discussion**

247 Our results show that male and female bumblebees perform flights when leaving flowers that
248 have a similar structure in the two sexes suggesting that males, like workers, perform learning
249 flights when leaving flowers. Although some males, like workers, returned to the flower after
250 their learning flight, we do not know what males have memorised about the flower and its
251 location during the flight. Male bumblebees have recently been found to learn the colours of
252 artificial flowers and approach the rewarded colour while avoiding unrewarded colours (Wolf
253 and Chittka, 2016), but it is unknown whether colour was memorised during a learning flight.
254 The essence of this flight is that it contains periods of directed looking that are presumably
255 coupled to the activation of learning. Thus, the males' and females' patterns of fixation of a
256 flower during learning flights (Fig. 5) suggest that both sexes learn something about it; a
257 conclusion that is reinforced by both males and workers facing the flower during their returns
258 (Fig. 7).

259

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

269

270 Learning flights can be elicited by several factors such as drinking nectar or leaving a nest.
271 They are also modulated by a variety of factors, like drinking time and sucrose concentration,
272 enclosure in a hive or nest for protracted periods, and difficulty in finding a goal (e.g.
273 Wagner, 1907; Wei et al., 2002; Wei and Dyer, 2009). The duration of a learning flight seems
274 to be correlated with the significance of the place that the bee leaves. Thus, workers leaving
275 their nest perform much longer flights than when they leave a flower (Fig. 4). It is still
276 unclear whether bees learn the same things when viewing flowers or the surroundings of the
277 nest entrance.

278

279 Males of different bee species have a variety of mating strategies (Goulson, 2010; Paxton,
280 2005). In bumblebees the commonest is that of *B. terrestris* which patrols areas along routes.
281 Other species are territorial and wait, hovering or perched, near a prominent visual object to
282 pounce upon potential passing mates. Might males learn their visually specified hovering
283 positions, as do patrolling halictine bees (Barrows, 1976)? Honeybee drones are quite
284 different from bumblebees. They make excursions from their nest to drone aggregation sites
285 to find and mate with queens (Galindo-Cardona et al., 2015; Loper et al., 1992; Witherell,
286 1971). When unsuccessful they return to the nest for feeding, as also do some male carpenter
287 bees (Leys, 2000; Wittmann and Scholz, 1989). Does the occurrence of learning flights of
288 honeybee and carpenter bee males also fit with their life style: learning flights when leaving
289 the hive (to which they return for sustenance), instead of at flowers (which they don't visit)?

290

291 **Acknowledgments**

292

293 We thank Andrew Philippides for providing Matlab scripts, Ka Yee Chow for help with
294 experiments and Matthew Collett for discussion.

295

296 **Competing interests**

297 No competing interests declared

298

299 **Author contributions**

300 T. R. initially observed male flights from a flower. All authors contributed to the design of
301 the research; T.R. and E. F. collected data; T. R. analyzed the data; T.R., T.S.C. and N.H.
302 designed the analysis and wrote the paper, with inputs from E.F.

303

304 **Funding**

305 Financial support came from the Leverhulme Trust (RPG-2012-677).

306

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1 **Figure 1. Experimental set up in greenhouse: nest and flower tables**

2 The nest table is in the foreground with the nest fixed under the table and its exit through a
3 hole near the array of three cylinders. The flower table is in the background with the artificial
4 flower in the same position relative to the cylinders as is the nest hole.

5

6 **Figure 2. Example trajectories of male bumblebees**

7 (A) Departure from nest. (B) Departure from flower. Flights in A and B are by the same
8 male. (C) Departure from a flower by another bee after its spontaneous return to the flower.
9 (D) Enlarged view of the initial segment of the flight in panel B. Red circles indicate
10 fixations of the flower (see text). Blue squares mark the time from the start every 0.5s. (E)
11 Return to flower. In all panels except D, each dot shows the position of the bee every 0.04s
12 and each line the orientation of the bee's body. Red circles and lines indicate instances in
13 which the bee faces the flower. Positions of nest and flower are shown by a green circle. See
14 also Figures S1 and S2.

15

16 **Fig. 3 Analysis of flower fixations in male learning flights**

17 (A,B) Distributions of the absolute values of angles between the males' body orientation and
18 the line from bee to flower ($|\varphi|$) for every frame in every flight (4872 frames, N=24 males,
19 n=24 flights; A) and for every frame in every fixation (821 frames; B). (C,D) Distributions of
20 the mean $|\varphi|$ of each randomly picked sample of individual frames in C and groups of frames
21 in D. In both cases, 100,000 random samples were randomly selected. The red lines show the
22 measured means of body angle orientation. Their position outside the means of the randomly
23 selected frames and group of frames demonstrate that the measured distribution of body
24 orientations in fixations is not a random selection from the overall distribution of body
25 orientations during learning flights of male bumblebees. Inset shows the angle ' φ ' between the
26 flower and the bee's longitudinal body axis.

27

28 **Figure 4. Some properties of male and female learning flights**

29 (A) Duration of male departure flights from the flower (i.e. time taken to cross a 30 cm radius
30 circle around the flower) is plotted against time spent drinking on the flower before departure

31 (N=30 males). Filled circles depict males with short drinking time (bottom quartile) that were
32 excluded from further analysis (N=6 males). (B) Durations of male departure flights from
33 nest and flower. (C) Durations of worker departure flights from nest and flower. The flights
34 of males from the flower were a little shorter (N=24 males, n=24 flights,
35 Mean=3.58s±0.54SE) than those of workers (N=14 workers, n=14 flights,
36 Mean=4.94s±0.72SE) (Mann-Whitney-U, U=109, Z=-1.79, p=0.07). Worker flights from the
37 nest lasted longer than the other three categories (Mean=14.42s±1.20SE). (D) Cumulative
38 trajectory lengths flown by males leaving the nest or flower and by workers leaving the
39 flower. Lengths at different distances from the flower or nest are those measured before the
40 bee first crosses a circle of a given radius to a maximum of 30 cm. The mean total trajectory
41 length of males leaving the nest was 40.25cm±2.74SE) and of males leaving the flower was
42 98.53cm (±12.05SE; Wilcoxon, W=21, Z=-3.69, p= 0.0002). The mean trajectory length of
43 workers leaving the flower was 90.75 cm (±13.25SE). It was slightly but not significantly
44 shorter than the trajectories of males leaving the flower (Mann-Whitney-U, U=159, Z=-0.27,
45 p=0.79). See also Figures S1 and S2.

46

47 **Figure 5. Fixations of flower and nest during learning flights**

48 (A) Frequency distributions of males' body orientation relative to the goal when leaving nest
49 (black line, 1169 frames) or flower (grey line, 4872 frames; N=24 males). Bin width is 20°.
50 (B) Distributions of body orientation relative to flower when all frames of male departure
51 flights are partitioned into frames within fixations (821 frames) and frames outside fixations
52 (4051 frames). (C) Frequency distributions of male and worker fixations (175 male, 162
53 worker fixations; N=24 males, N=14 workers) relative to the flower (40° bin width). (D)
54 Proportion of flights which have at least one flower fixation ($\phi = 0^\circ \pm 20^\circ$) within a specified
55 distance from the flower (N=10 males, N=9 workers). The numbers above each 5cm bin give
56 the total number of fixations falling in that bin. The lines above the histograms show the
57 proportion of flights at each distance that are at least as long as that distance (N=24 males,
58 N=14 workers).

59

60 **Figure 6. Durations of the fixations in male and female learning flights**

61 Normalised distributions of the duration of all fixations in (A) males (n=175 fixations; N=24
62 males) and (B) workers (n=162 fixations; N=14 workers). Male and female fixations are

63 partitioned into those in which bees faced ($\varphi=0^\circ\pm 20^\circ$), males ($n_f=47$ fixations), workers
64 ($n_f=33$ fixations); or did not face the flower ($\varphi<-20^\circ$ or $\varphi>20^\circ$).

65

66 **Figure 7. Comparisons of male and worker returns to flower**

67 (A) Flight speed plotted against distance from flower (N=8 males, N=14 workers). (B)

68 Cumulative trajectory length as a function of distance from flower. (C) Frequency

69 distributions of body orientation relative to flower (males N=595 frames, workers N=1255).

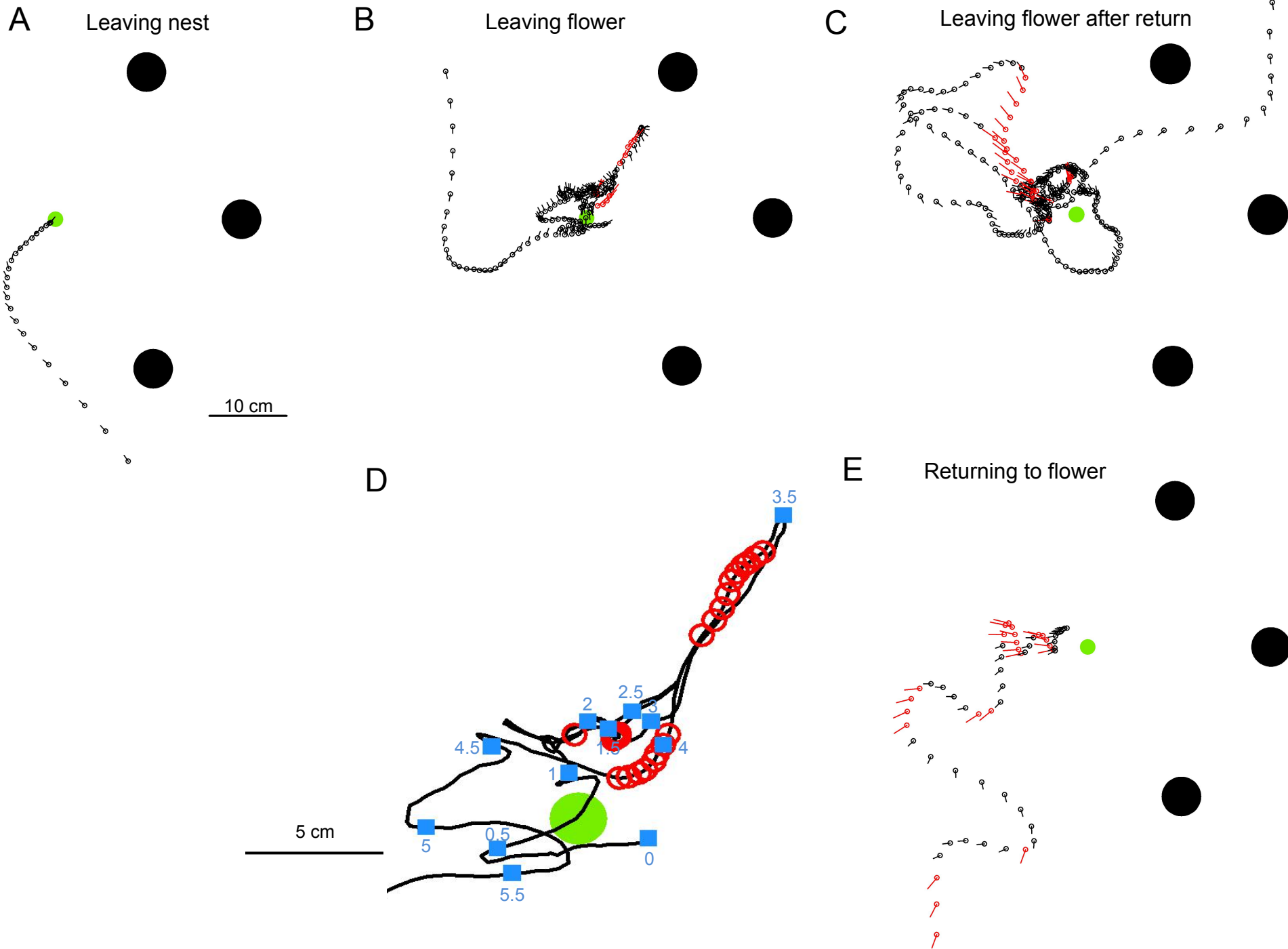
70 (D) Relative frequency of flower facing ($\varphi = 0^\circ\pm 20^\circ$) plotted against distance from flower

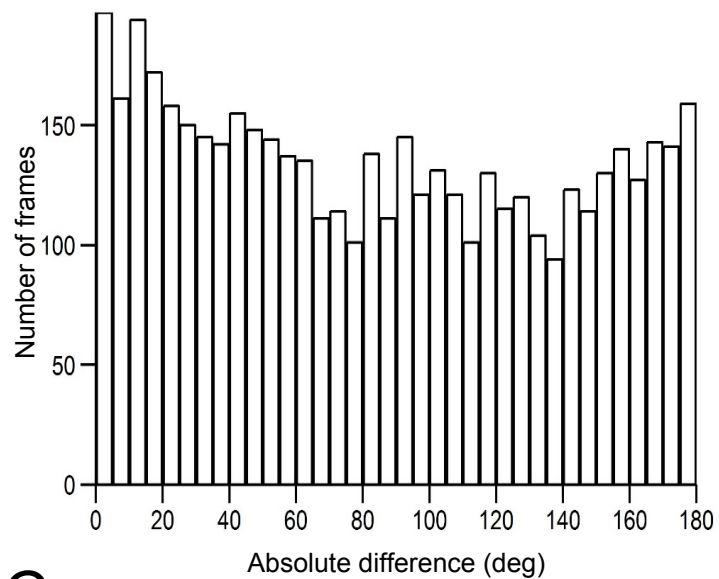
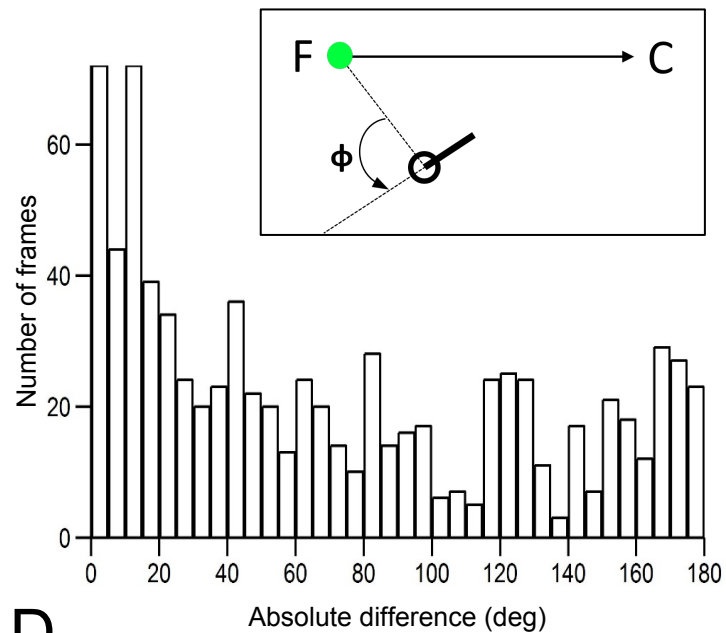
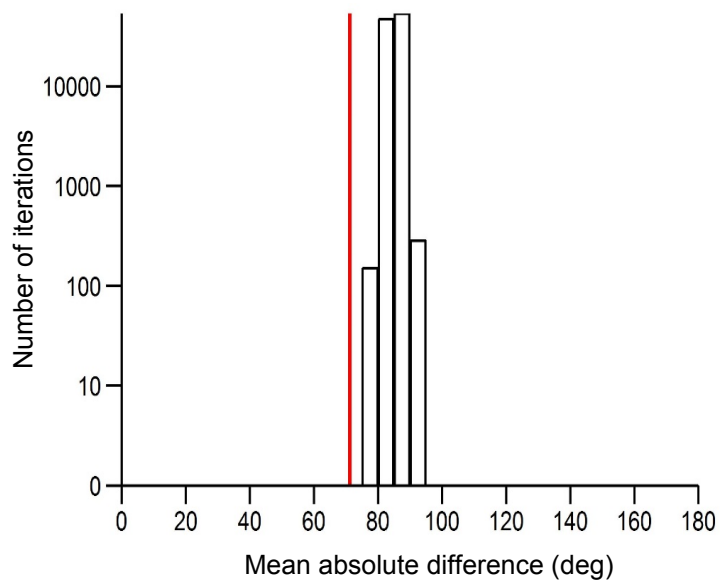
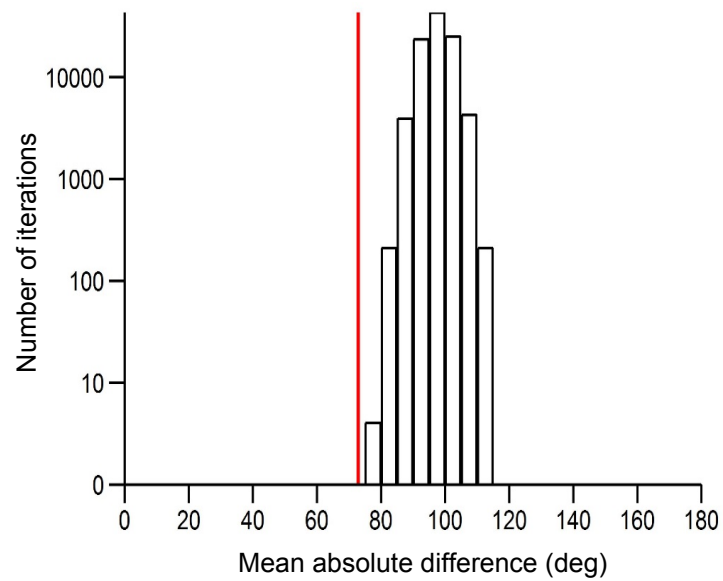
71 (males, N= 341 frames, workers N=811 frames). The lines above the histograms show the

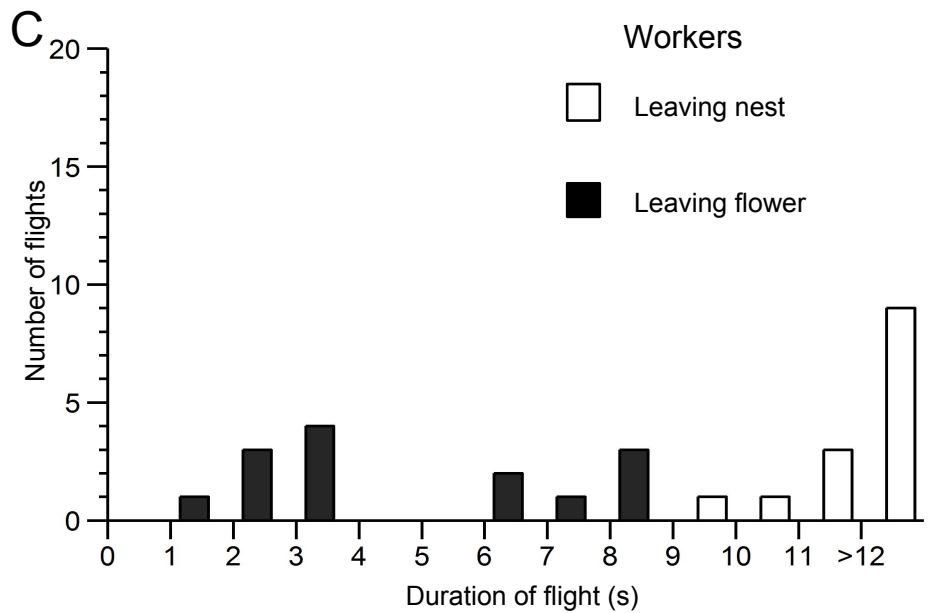
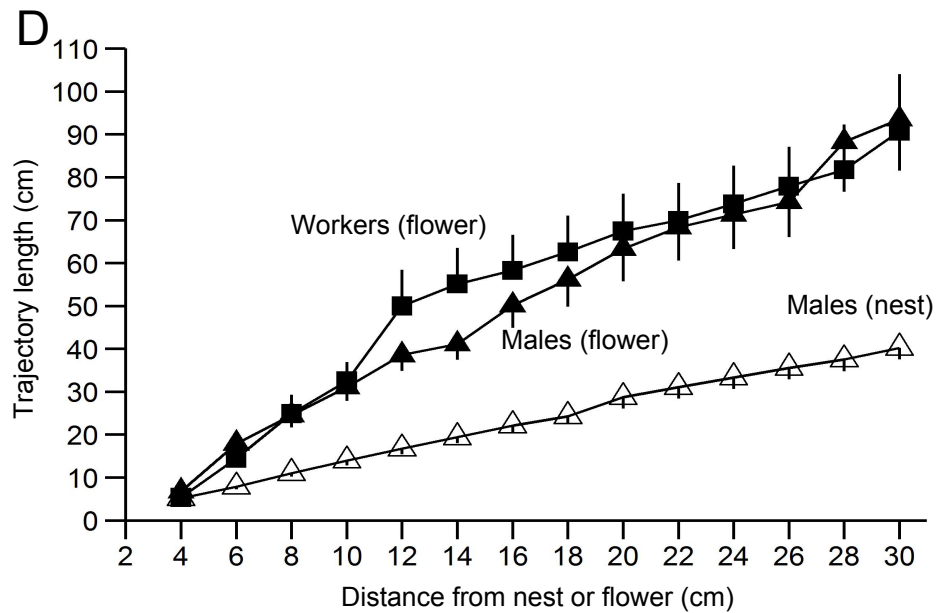
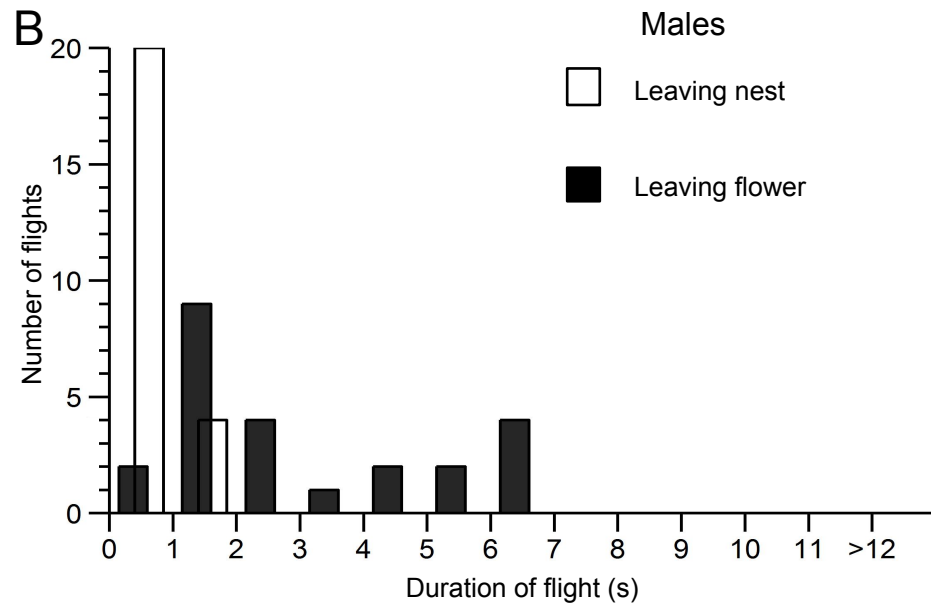
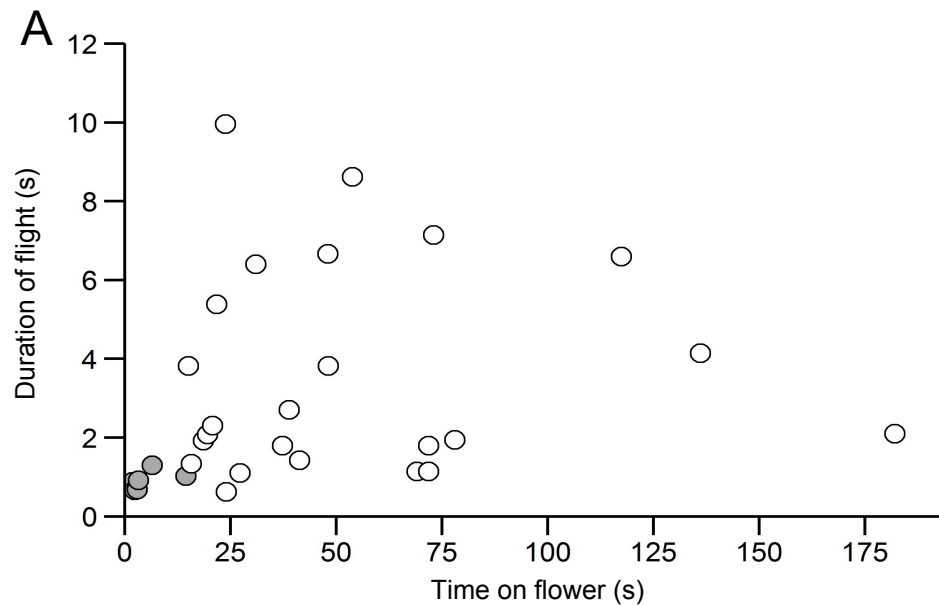
72 proportion of flights at each distance that are as least as long as that distance (N=8 males,

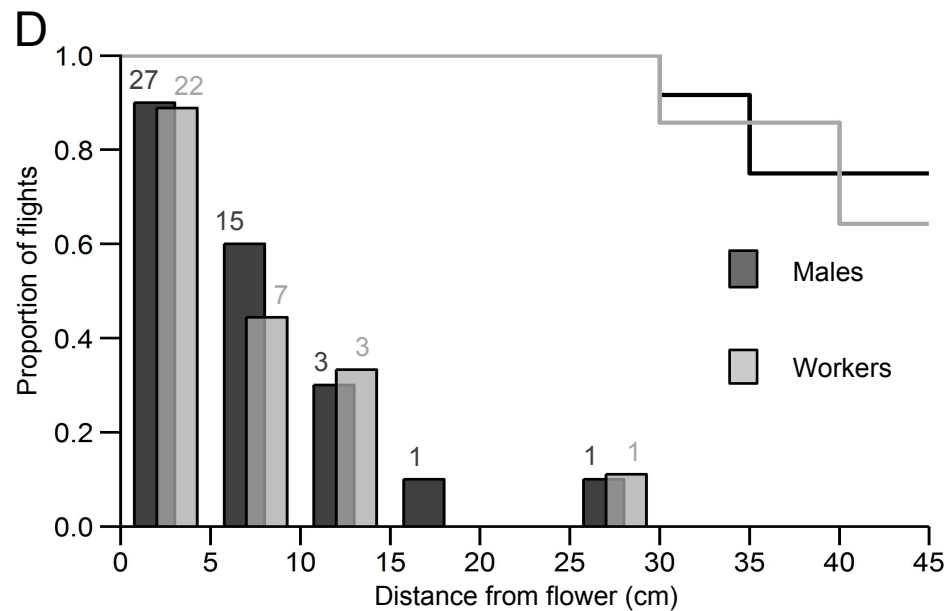
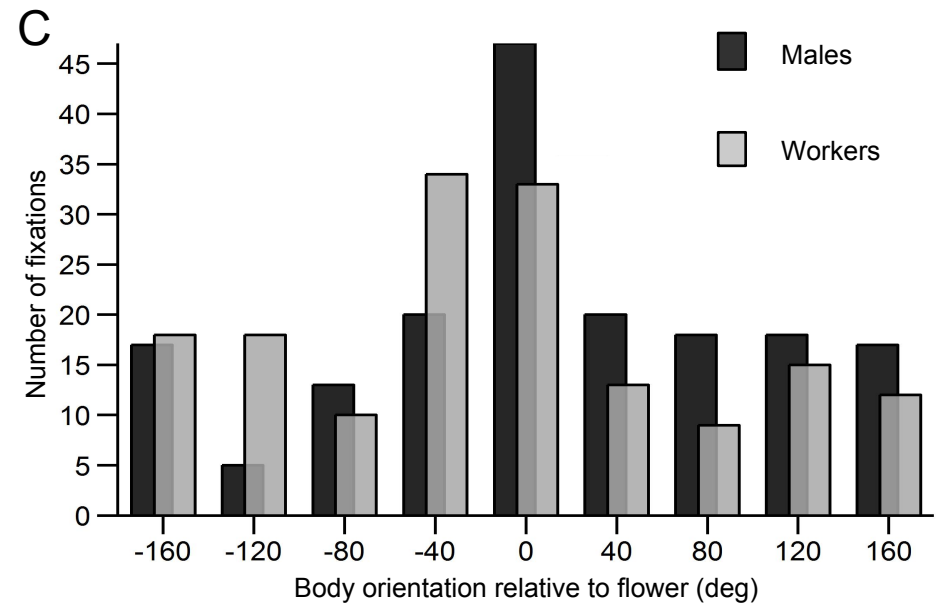
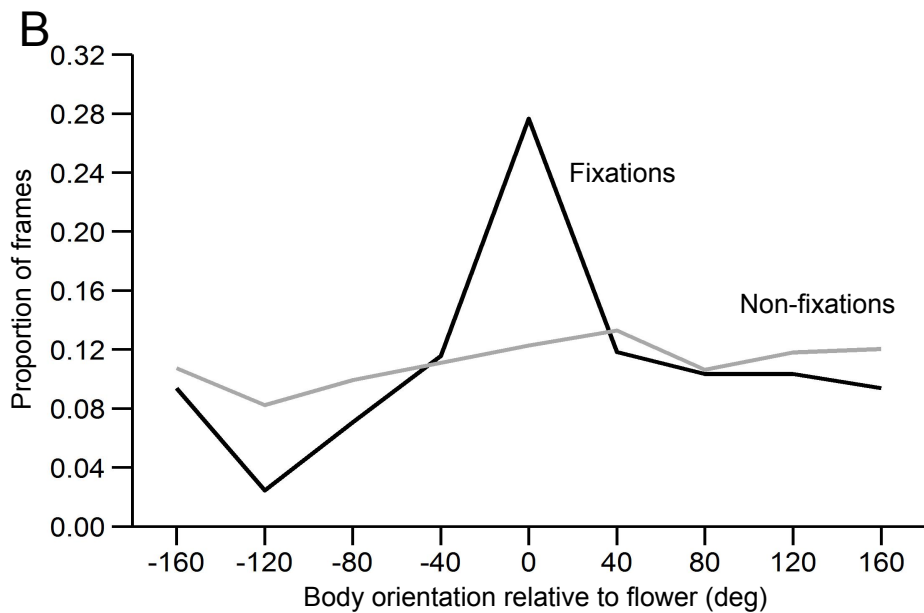
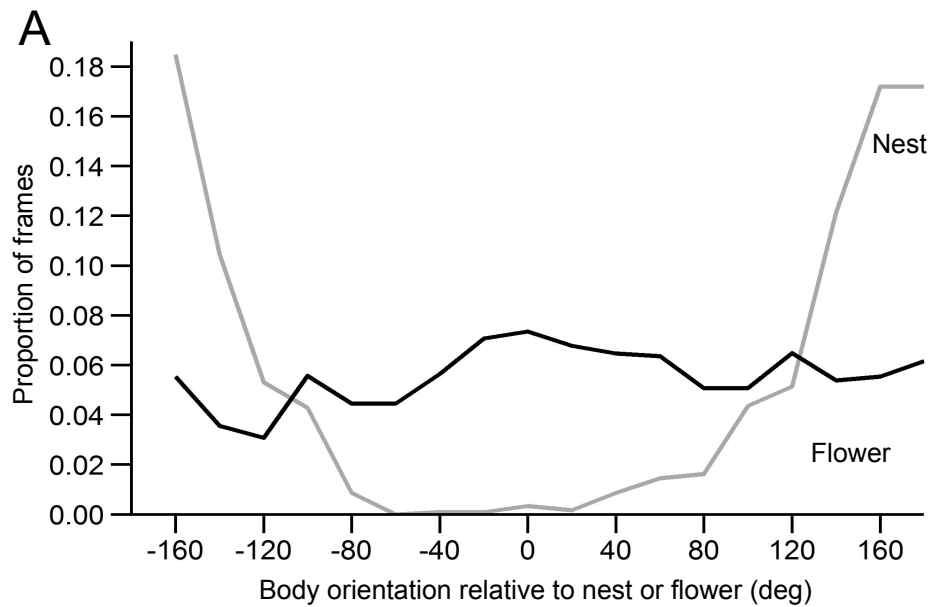
73 N=14 workers).

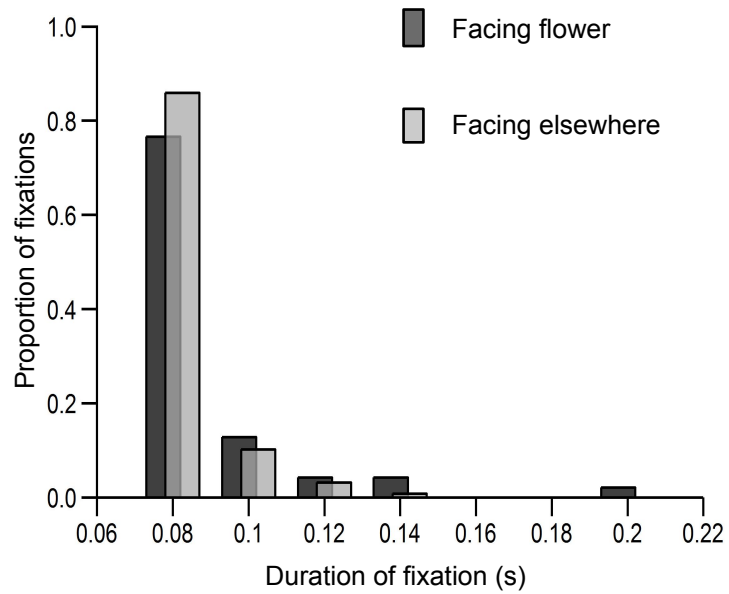




A**B****C****D**





A**B**