Harmonic radar tracking reveals that honeybee drones navigate between multiple aerial leks

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Male honeybees (drones) are thought to congregate in large numbers in particular “drone congregation areas” to mate. We used harmonic radar to record the flight paths of individual drones and found that drones favoured certain locations within the landscape which were stable over two years. Surprisingly, drones often visit multiple potential lekking sites within a single flight and take shared flight paths between them. Flights between such sites are relatively straight and begin as early as the drone’s second flight, indicating familiarity with the sites acquired during initial learning flights. Arriving at congregation areas, drones display convoluted, looping flight patterns. We found a correlation between a drone’s distance from the centre of each area and its acceleration toward the centre, a signature of collective behaviour leading to congregation in these areas. Our study reveals the behaviour of individual drones as they navigate between and within multiple aerial leks.

Keywords: *Apis mellifera*, drone, drone congregation area, harmonic radar, honeybee, insect mating systems, insect navigation, lek, orientation flight, queen flight

Highlights:

- Flight paths of individual honeybee drones were tracked using harmonic radar
- Convoluted flights were concentrated in four drone congregation areas
- Drones commonly move between lek-like congregation areas during a single flight
- Acceleration patterns suggest a mechanism to maintain congregation area cohesion

Introduction

A major mystery regarding honeybee (*Apis mellifera*) mating behaviour, regards where mating takes place and how drones (males) and queens find one another. Drones (males) attempt to mate with virgin queens in flight and typically undertake 1-6 flights per day (Witherell, 1971; Reyes *et al.*, 2019), over an average of 7 non-consecutive days (Reyes *et al.*, 2019), until they mate successfully or die of predation or old age (mean age at death: 21 days, (Witherell, 1971; Reyes *et al.*, 2019)). A long-standing hypothesis suggests that drones gather in large numbers, up to many thousands at a time (Koeniger *et al.*, 2005), in locations that are not only stable from day to day, but reappear in the same places year after year (Ruttner and Ruttner, 1966; Strang, 1970; Loper, Wolf and Taylor, 1992). Support for this drone congregation area hypothesis comes from studies using tethered queens or pheromone lures to sample drone abundance (Zmarlicki and Morse, 1963; Ruttner and Ruttner, 1972; Taylor, 1984; Galindo-Cardona *et al.*, 2012), but there is limited evidence that such gatherings occur in the absence of the methods used to detect them (Loper, Wolf and Taylor, 1987, 1992) and other lure studies have yielded contradictory evidence (Butler and Fairey, 1964; Currie, 1987).

Nearly all investigations of drone congregations have relied on pheromone lures or tethered queens, leading to concerns that apparent congregation areas may have been created by the lures themselves. Apparent congregations can be created by releasing large amounts of pheromone (Butler, 1967; 1970; Tribe, 1982), and drones return frequently to locations at which they have encountered queen pheromone (Butler and Fairey, 1964), so such artificial congregations may be long-lasting. Several authors report that drones were rapidly attracted to pheromone lures in almost any location (Butler and Fairey, 1964; Tribe, 1982), including 800m out to sea (Butler and Fairey, 1964), leading Butler and Fairey to conclude that drones must be dispersed widely and evenly throughout the landscape (Butler and Fairey, 1964). While lure-sampling studies in hilly regions have reported patterns of attraction to lures suggestive of distinct drone congregations (Ruttner, 1966; Ruttner and Ruttner, 1966), this has been hard to replicate in flatter areas (Ruttner, 1966; Currie, 1987). To demonstrate the existence of drone congregation areas with certainty, it is necessary to show that drones congregate in these areas without the presence of such bait.

Two previous studies have used radar technology to attempt to characterize the movements of drones. Loper et al. (1987), used an X-band (9.4Ghz) marine radar to confirm that drones, were present at purported drone congregation areas even in the absence of queens. However, since caged queens had been used to identify these locations to begin with, it was impossible to rule out the possibility that the congregations had become established as a result of the lures. In a more ambitious study, Loper and others used radar to survey the numbers of drones observed in different locations around a large apiary and built up a picture of drone movements, in the aggregate, although they could not identify or track the flight paths of individual drones (Loper, Wolf and Taylor, 1992). They described a network of 18km of shared flyways in which thousands of drones followed very similar routes throughout the landscape. These flyways were 50-100m wide and often ran parallel (but no closer than 60m) to treelines and roadways. They identified 26 different locations they believed to be drone congregation areas (Loper, Wolf and Taylor, 1992). Congregation areas had diameters around 100m and tended to be higher than flyways (around 30m) but were described as an ‘inverted cone’ in which fewer drones were found at higher altitudes (Loper, Wolf and Taylor, 1992). In a sub-experiment, Loper et al. (1992) monitored two of these purported congregation areas throughout the course of one afternoon to observe how the number of drones varied with time of day. They reported a maximum of 68 drones at a congregation at any one time, which is very low compared to the numbers found by other studies (Koeniger *et al.*, 2005).

Almost nothing is yet known of the flight dynamics of individual drones, how they explore the landscape, how their behaviour changes at congregation areas, or whether they are faithful to a single congregation area. Among vertebrates with lek mating systems – characterized by spatial clusters of large numbers of males, who are there solely to attempt to mate and do not provide any direct benefits to females, such as food or territory (Bradbury, 1977; Alcock, 1987) – males show high levels of fidelity to a single lek (Apollonio, Festa-Bianchet and Mari, 1989; Figenschou, Folstad and Liljedal, 2004; Gibson *et al.*, 2014; Fremgen *et al.*, 2017); it is not known whether lekking insects are similarly faithful to a single site, although there is some evidence that at least one species of wasp may be (Nielsen and Nielsen, 1953). Additionally, a body of literature on the placement and composition of congregations rests on the central assumption that the use of pheromone- or queen-lures does not alter drone behaviour. The only support for this comes from a single radar study (Loper, Wolf and Taylor, 1992), which contradicts most other literature in suggesting that congregations are smaller, more numerous and closer together than previously thought, and which thus requires further investigation.

Results

Use of the landscape by drones

We tracked the flights of honeybee drones (*Apis mellifera*) from three hives in a hay meadow set within an agricultural landscape at Rothamsted Research, Hertfordshire, UK, over two years, from June-September 2016 and from May-July 2017. Drones were allowed to leave and enter the hives at will. They were tracked by harmonic radar when they chose to fly. We recorded 648 *substantial flight segments* – defined as a series of positional fixes from the radar which could be unambiguously identified as being made by a single drone, lasting at least 30s, in which the bee moved at least 15m from its starting position – from at least 78 individual drones.

Drones were detected across the entire trackable area of the site, with high traffic corridors extending Southeast and terminating in hotspots in the same locations (Figure 1). We found drone activity was very similar in both years (Figure 1C, E). Drones from different hives converged on similar routes (Figures 2, S1, S2) suggesting the use of common heuristic movement rules (see Supplemental information).

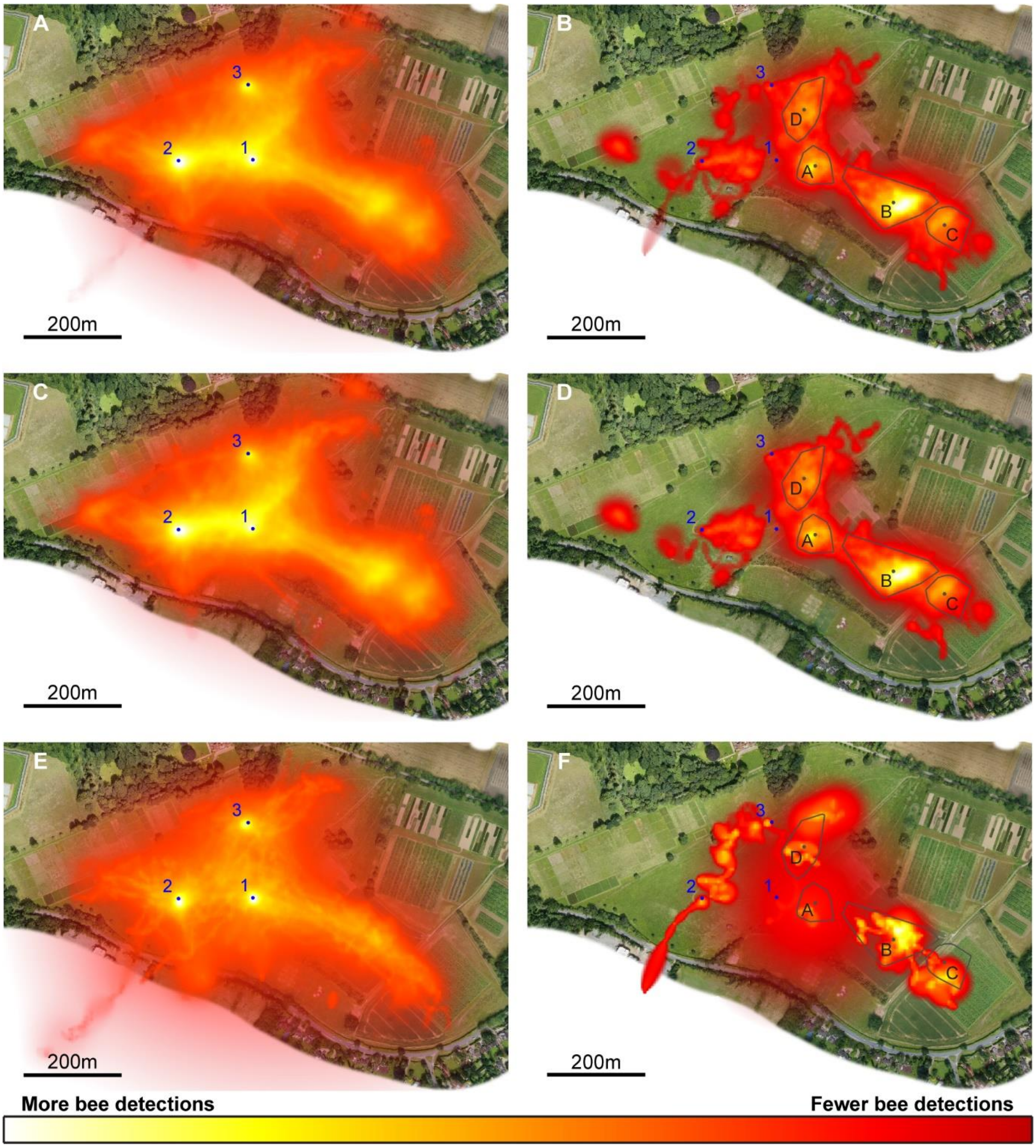

Figure 1. Landscape use by drones

A) Heat map showing all drone flight activity recorded in 2016-2017 superimposed on an aerial orthomosaic image of the field site. Hive locations are marked by blue circles and numbered. Areas with brighter, yellower colouration were more visited by drones. N = 1174 tracks. **B)** Heat map showing all convoluted sections of flight recorded in 2016-2017, whose centre of mass was greater than 50m from all active hives. The centre of mass of each cluster of data points that we identified as a probable drone congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. This is a rough estimate of the boundary of each congregation area, for illustrative purposes only. N = 111 tracks. **C)** Heat map showing all drone activity recorded in 2016. N = 835 tracks. **D)** Heat map showing convoluted sections of flight recorded in 2016, whose centre of mass was greater than 50m from all active hives. N = 94 tracks **E)** Heat map showing all drone activity recorded in 2017. N = 339 tracks **F)** Heat map showing convoluted sections of flight recorded in 2017, whose centre of mass was greater than 50m from all active hives. N = 17 tracks.

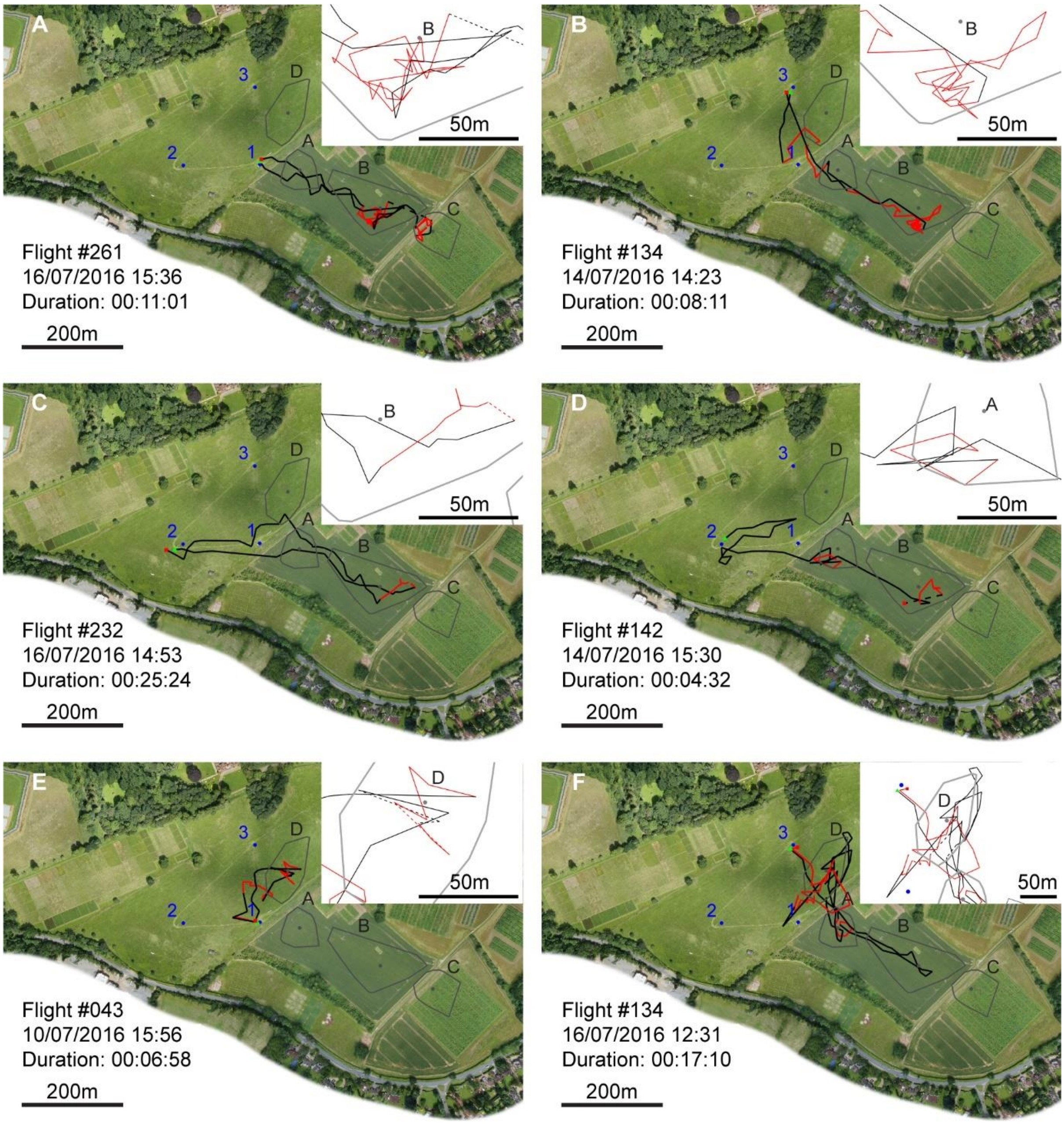

Figure 2. Example flight paths showing convergence on similar routes

A) Flight path of a drone from hive 1 passing through congregation areas A, B and C, and showing evidence of convoluted flight at locations B and C. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable drone congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. Insets for each panel: zoomed view showing details of convoluted flight at congregation areas. **B)** Example flight from hive 3 showing convergence in both the route taken and the destination with the flight in A). **C-D)** Example flights from hive 2 visiting congregation areas A and B and showing convergence in route and destination with the flights shown in other panels. Note that only the outbound portion of the flight in D) is shown; either this drone did not return to the hive or the return flight was not detected. **E)** Example flight from hive 1 showing a visit to congregation area D. **F)** Example flight from hive 3 showing visits to congregation areas D, A and B, with convoluted flight at D and A.

Identifying potential drone congregation areas

Previous studies either sampled drones at discrete locations or used radar to monitor drone flight in the aggregate, but could not identify or track the flight paths of individual drones (Loper, Wolf and Taylor, 1987, 1992). Consequently, little is yet known about the flight paths taken by individual drones. Our data show that drone flights typically consisted of periods of straight, direct flight, interspersed with periods of convoluted, looping flight (Figure 2). We developed a simple algorithm to classify flight into straight and convoluted sections (Figure 2; see Transparent methods, Supplemental information). We identified 425 sections of convoluted flight in 329 flights (51% of all substantial flight segments). Multiple convoluted sections occurred in 67 flights (20.3% of all flights containing convoluted sections). The mean duration of convoluted sections of flight was 134.0s ± 17.3 (means ± standard error, throughout). Among flights that contained convoluted sections, convoluted flight accounted for 56.3% ± 2.0 of the total flight duration.

We used a clustering algorithm to reveal geographically clustered activity in convoluted flights. We identified four clusters of drone positions with data points contributed by at least 10 different tracks (Figure 1B; Table S1). Examination of individual drone tracks confirms the importance of these probable drone congregation areas, with numerous flights approaching these areas along relatively direct flight paths and abruptly changing to convoluted flight (Figure 2).

Orientation flight and route development

We recorded 19 complete first flights of drones, comparable to orientation flights in workers (Capaldi *et al.*, 2000). First flights remained within around 100m of the hive, and frequently consisted of multiple loops in different directions from the hive (Figure 3). In this aspect, they more closely resemble the initial flights of bumblebee (*Bombus terrestris*) workers (Osborne *et al.*, 2013; Woodgate *et al.*, 2016), than honeybee workers, which typically perform a single loop per flight (Capaldi *et al.*, 2000). Notably, drones performing orientation flights never undertook convoluted flight at congregation areas.

Figure 3. Orientation flights

A) Example flight path of the first flight (orientation flight) ever undertaken by a drone from hive 1. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. Insets for each panel: zoomed view showing details of flight path. **B)** Orientation flight of a drone from hive 3. **C-D)** Orientation flights of two drones from hive 2, showing the typical range of distances reached from the hive.

For four drones, we recorded 6-8 consecutive flights, beginning with their first ever orientation flight (Figures 4, S3). Typically, one or two localised orientation flights were followed by an abrupt switch to flights travelling much further from the hive, passing through one or more congregation areas. Drones may thus need fewer orientation flights than typically undertaken by workers (mean 5.6 ± 2.9, (Capaldi *et al.*, 2000)). We attempted to track the flight of virgin queens for comparison, but with little success (see Figure S4, Supplemental information).

Figure 4. Example flight paths showing consecutive flights of drone #48

The first six flights ever undertaken by drone #48. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. **A)** The drone's first ever flight was very brief, less than two minutes with convoluted flight directly in front of the hive entrance and a brief loop toward the Northwest. **B)** The second flight was much more extensive with loops passing through congregation areas D and A, followed by a longer flight through area C and appearing to continue even further, disappearing over a road that forms the Southeastern border of our field site. The portions of flight we were able to detect were fairly straight, going directly to the congregation areas and showing no evidence of systematic search. **C-F)** Subsequent flights by the same drone were even more direct, passing through congregation areas A, B and C, occasionally making convoluted flight at these locations, and apparently continuing across the road on two more occasions (E, F).

Dynamics of flight at hives and congregation areas

Drones from all hives visited all four congregation areas in both years (Table S1; Supplemental information), although area A was less commonly visited in 2017, while it is possible that the centre of area C shifted Southwards (Figure 1D, F). Among vertebrates with lek mating systems, males show high levels of fidelity to a single lek (Apollonio, Festa-Bianchet and Mari, 1989; Figenschou, Folstad and Liljedal, 2004; Gibson *et al.*, 2014; Fremgen *et al.*, 2017). We found that it was common for drones to visit and perform convoluted flight at more than one congregation area during the same flight, connected by periods of much straighter flight (Figure 2A, D, F). We identified tracks in which either the bee performed a section of convoluted flight whose center of mass (mean coordinates of every data point) was within 50m of a cluster centre, or in which the bee stayed within 50m of a cluster centre for at least 21s (seven revolutions of the radar). This included periods in which the signal was lost, provided the positional fixes either side of the missing period were within 50m of a cluster centre: this can occur if the bee flies too high for the radar to detect. There were 154 such flights which visited at least one congregation area (representing 23.7% of all flights recorded), 37 (24.0%) of which visited more than one congregation.

We found a linear relationship between a drone's position relative to the congregation area or hive and its acceleration conditioned on its position, in both East-West and North-South directions of travel (all $P < 0.005$; Figures 5, S5; Table S2). The x-intercepts (the location at which the acceleration is zero) were very close to the cluster centre in all cases (mean ± S.E.: x-direction = -2.17m ± 2.30; y-direction = 0.15m ± 2.13; Table S2; Figure S5). In other words, the further drones moved from the centre of a congregation area or hive during convoluted flight, the more strongly they accelerated back toward the centre. Such patterns of acceleration function as an effective force – with individuals behaving as though they are trapped in an elastic potential well (Katz *et al.*, 2011; Kelley and Ouellette, 2013) – and promote swarm cohesion (Kelley and Ouellette, 2013). Other characteristic properties of swarms, notably including midge mating swarms (Kelley and Ouellette, 2013), are that their distributions of velocity and position have Gaussian cores. This was true of our convoluted flight data at congregation areas (Figures S6, S7). Taken together, these statistical properties of drone's convoluted flight suggest that this flight resembles swarming. Our data on flight dynamics suggest that congregation areas have roughly symmetrical cores of 30-50m diameter (see Supplemental information).

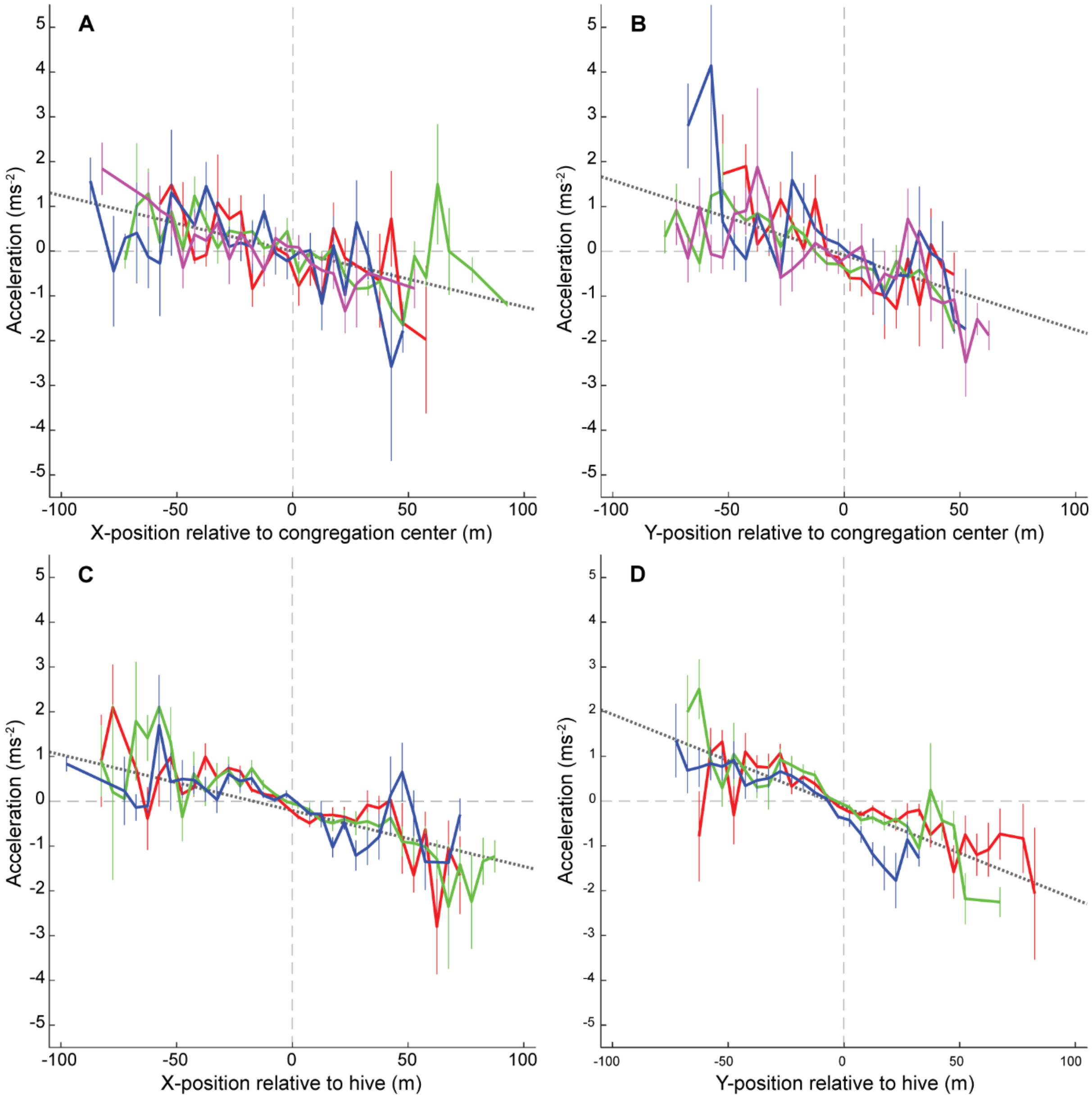

Figure 5. Mean acceleration as a function of position relative to the centre of congregation areas or hives

A) Mean x-component of acceleration calculated over bins of 5m in the x-direction (East-West) from the centre of each congregation area. Red line: area A; green line: area B; blue line: area C; magenta line: area D. Narrow vertical bars show SE for each bin. Vertical dashed reference line indicates centre of congregation area or hive. Horizontal dashed reference line indicates mean acceleration equal to zero. Grey dotted line shows regression line through all binned data. **B)** Mean y-component of acceleration (North-South) for the same locations. **C)** Mean x-component of acceleration calculated over bins of 5m in the x-direction from each hive location. Red line: hive 1; blue line: hive 2; green line: hive 3. **D)** Mean y-component of acceleration for the same locations. Scatterplots showing the full distributions at each location are shown in Figure S5.

The dynamics of flight at congregation areas differed from those at hives: the distributions of position and velocity, which at congregations resembled those of midge mating swarms, have much smaller cores in the case of flight at hives (Figures S8, S9). We tested for a difference in kurtosis, a measure of how 'heavy-tailed' each distribution is. The kurtosis of the hive-flight position distributions was significantly greater than that for congregation areas ($F_{1,6}$ = 34.97, P = 0.002; Figure S10A), while the velocity distributions showed a similar, but non-significant, trend ($F_{1,6}$ = 5.46, P = 0.067, Figure S10B). There was no effect of direction (x- or y-) on the kurtosis values (position: $F_{1,6}$ = 0.15, P = 0.714, Figure S10A; velocity: $F_{1,6}$ = 0.32, P = 0.594; Figure S10B). Flight at swarms was significantly faster than at hives (swarms, 5.05ms^{-1} ± 0.14; hives, 3.03ms^{-1} ± 0.10; $F_{1,300}$ = 16.02, P = 0.007; c.f. mean speed of straight flight sections, 4.77ms^{-1} ± 0.07, Figure S10C), but there was no difference in the duration of convoluted flight sections (swarms, 111.4s ± 25.2; hives, 141.6s ± 23.3; $F_{1,303}$ = 0.45, P = 0.515; Figure S10D). These results demonstrate that the convoluted flights recorded at congregation areas differ their flight dynamics from those around hives, likely reflecting different functions, with hive-flight probably not a form of swarming.

There were no significant differences between the four congregation areas in the duration of convoluted flight sections ($F_{3,80}$ = 0.67, P = 0.574; Figure S10E; Table 1), but the mean speed of convoluted flight sections at congregation area A was greater than at areas B or C ($F_{3,80}$ = 4.63, P = 0.005; pairwise comparisons using Tukey's method: A vs B, P = 0.016; A vs C, P = 0.035; all other pairwise comparisons, P > 0.05; Figure S10F; Table 1).

Discussion

Using harmonic radar tracking, we have recorded the behaviour of individual honeybee drones as they explore the landscape and search for mates, revealing a characteristic switch between relatively straight periods of flight to a tightly looping pattern, often multiple times in the same flight. These individual tracks show the signature of collective behaviour: convoluted flights were clustered in four areas of our experimental site, and the flight dynamics of drones suggest the mechanism by which group cohesion is maintained, demonstrating that these areas are swarms (Kelley and Ouellette, 2013). These results reveal the internal structure of drone congregation areas (Taylor, 1984; Koeniger *et al.*, 2005; Koeniger, Koeniger and Pechhacker, 2005; Galindo-Cardona *et al.*, 2012).

It was common in our study for drones to visit more than congregation area within a single flight, with around a quarter of flights that featured convoluted flight at a congregation area, or lingered in the area too long to be merely passing through, going on to do the same at other congregations. Travel between neighbouring areas was particularly common, perhaps facilitated by their locations on shared flyways (Loper, Wolf and Taylor, 1992). Bouts of convoluted flight in our dataset were relatively short, with a mean duration of little over two minutes, perhaps suggesting that drones routinely patrol between swarm locations, lingering only briefly in each to search for the presence of a queen.

The dominant hypothesis for the purpose of congregation areas is that they function akin to leks (Zmarlicki and Morse, 1963; Baudry *et al.*, 1998; Koeniger *et al.*, 2005) and facilitate mating (see Supplemental information). Among lekking species of birds, mammals and fish, individual males show a high degree of fidelity to a particular lek site (Apollonio, Festa-Bianchet and Mari, 1989; Figenschou, Folstad and Liljedal, 2004; Gibson *et al.*, 2014; Fremgen *et al.*, 2017). Switching between leks is rare (Fremgen *et al.*, 2017) and regular movement between leks within a day, or even a breeding season, is unknown. Males of many insect species form dense, lek-like aerial swarms, above visual cues known as swarm markers, near treetops or at hilltops (Sullivan, 1981; Alcock, 1987; Shelly and Whittier, 1997; Van Veen, Sommeijer and Meeuwsen, 1997). These often maintain a relatively stable size and shape even as individuals leave and others arrive, leading Sullivan (1981) to hypothesise that individual males move between adjacent swarms. There is no previous experimental support for this hypothesis, however, and one study suggested male mosquitos were faithful to a particular swarm over a period of several days (Nielsen and Nielsen, 1953). Our radar tracks provide the best evidence for a mating strategy in which individuals travel between multiple aerial leks whose locations are fixed. Tracking or capture-mark-recapture studies of other swarming insects may reveal similar movements between swarms.

We identified four apparent congregation areas, each of which was visited by drones from all three hives and across both year of tracking. Nonetheless, there were some differences between them: areas B and C were frequently visited in both years but area A was much less visited in 2017 than in 2016 and flight speeds during convoluted flight at area A were higher than at B or C. Although area D was visited as often as area C, a high proportion of visitors came from hive 3, and passed through en route to areas B and C. It is possible that while some congregation areas remain stable from year to year and are defined by the features of the landscape, others may be less permanent and influenced by the positions of colonies or other factors. Loper et al. (1992) reported occasional transient “bubbles” of drone activity within flyways, but areas A and D in our study appear to be more stable than that, with activity recorded in both areas over two years. Further work may reveal whether the term drone congregation area presently confuses multiple discrete phenomena.

Our results on flight dynamics explain how congregations can remain stable, even though individual drones do not remain there for prolonged periods: the relationship observed between acceleration and distance from the centre will tend to function to draw individuals back in toward the centre creating an emergent potential well that keeps drones bound to the congregation (Okubo, 1986; Kelley and Ouellette, 2013). The congregation thus takes on physical properties, emerging from the collective behaviour of the individuals within it. Drones thus use the same mechanisms for swarm cohesion as midges or mosquitos but on a far larger spatial scale (our congregations had a radius of approximately 50m, c.f. approximately 10cm for swarms of *Chironomus riparius* midges (Kelley and Ouellette, 2013)). Individual drones tended to perform convoluted flight for 2-3 minutes at a time but if drones leaving the congregation are replaced by newly arriving ones, the congregation itself can remain stable for far longer periods (Sullivan, 1981).

The congregation areas and flyways we have identified were frequented by drones across two years, demonstrating, in concert with the results of Loper et al. (1992), that swarms in relatively restricted volumes can remain stable over multiple years. This adds perspective to previous reports that the broad areas of drone activity revealed by lure-sampling studies persist over long periods (Strang, 1970; Ruttner and Ruttner, 1972). No individual drones could possibly visit a drone congregation area in multiple years, since they do not survive over winter. The locations of drone congregations, therefore, must be discoverable by individual drones rather than being learned from others. Our data show that orientation flights of drones typically do not take them far enough from their hive to discover congregations, and that drones switch from orientation to making direct flights to congregation areas within one or two flights, without obvious signs of systematic searching. Cues to congregation area locations must be perceivable from relatively close to the hive and, since drones from all hive locations visited the same congregations, must be perceivable from many locations. Previous authors have suggested several landscape properties that might determine where drone congregations form: low parts of the skyline (Ruttner and Ruttner, 1966, 1972), distance from tree cover (Zmarlicki and Morse, 1963; Ruttner and Ruttner, 1966; Galindo-Cardona *et al.*, 2012), and South facing aspect (Galindo-Cardona *et al.*, 2012). None of these, however, are sufficient to predict exactly where swarms will form. Our flight tracks demonstrate that drones share routes through the landscape, as well as destinations. These flyways (Loper, Wolf and Taylor, 1992) might play a role in helping drones locate congregations, potentially explaining why it has proved so difficult to find any combination of cues that defines individual congregation areas. Reconstruction, from radar track data, of the views experienced by drones as they navigate to and from drone congregation areas promises to reveal the cues they use.

It has been long hypothesised that drones gather in large numbers at drone congregation areas (Taylor, 1984; Koeniger *et al.*, 2005; Koeniger, Koeniger and Pechhacker, 2005; Galindo-Cardona *et al.*, 2012), but this has been challenged (Butler and Fairey, 1964; Currie, 1987), because almost all evidence for these congregations comes from studies using either caged queens or pheromone lures to attract drones. Such studies cannot with certainty refute the alternative hypothesis that these sampling methods, themselves, cause the congregations. This debate was partially resolved when Loper et al. (1992) used radar tracking to demonstrate that drones congregated in repeatable locations in the absence of lures. However, their observations departed from the consensus emerging from lure-sampling studies in several ways: the clusters of activity that Loper et al. identified as drone congregation areas were much smaller than previously assumed (100m diameter, with a peak of 68 drones observed at any one time (Loper, Wolf and Taylor, 1992); c.f. 220m x 260m during the South African winter, enlarging to 500m x 1000m in summer (Tribe, 1982); a mean of 11,750 drones estimated at a single congregation using lure-sampling (Koeniger *et al.*, 2005)), and were found much closer together. Loper et al. (1992) also suggested that shared flyways around the landscape might be more important than the congregations themselves. They were unable to track individuals, but our work now corroborates most of their unusual findings: using different methodology we also estimated our congregations to be approximately 100m across and identified shared flyways between them. We found four such locations at close proximity. The placement of congregations B and C, either side of a roadway, appears to agree with the suggestion that congregations form where terrain features are interrupted (Loper, Wolf and Taylor, 1992).

Why do radar studies of drone activity depart from the observations of lure sampling studies? The most likely explanation is that the superior spatial and temporal resolution of radar monitoring has revealed the internal structure present in drone congregation areas. We suggest that the locations described as drone congregation areas by previous authors (Zmarlicki and Morse, 1963; Taylor, 1984; Koeniger *et al.*, 2005; Koeniger, Koeniger and Pechhacker, 2005; Galindo-Cardona *et al.*, 2012) are likely to actually comprise several distinct swarms and their associated flyways. Our data demonstrate that these substructures, and not just the broad region favoured by drones, are themselves stable over a timescale of years. If, as our data suggest, individual drones move between congregation areas, remaining for only short periods at each, the congregations may never have more than a small number of drones present at once. Aerial traps, though, will not only catch drones present when the lure is raised, but all those that subsequently arrive (while few are able to leave), gradually depleting the population of an entire network of congregations and flyways. This may also partly explain why the supposedly enormous aggregations of drones have proven difficult to locate when much smaller swarms of midges, mosquitos or wasps are readily discovered (Sullivan, 1981; Shelly and Whittier, 1997). Another explanation for the discrepancies between radar and lure-sampling studies could be that the presence of queens or pheromone-lures alters drone behaviour sufficiently to interrupt the normal structure of congregation areas, causing them to expand or perhaps inducing several, ordinarily distinct congregations to merge (Ni and Ouellette, 2016). Careful experiments using radar to monitor drone activity in the presence of lures could resolve the question of whether congregations are smaller in the absence of lures or whether drone congregation areas have an internal structure which radar tracking is only now starting to reveal.

Limitations of the study

Due to the logistical problems involved in moving the harmonic radar, we monitored the movements of drones in just one location. We partially mitigated this issue by tracking bees from three different hives, demonstrating that the behaviours we uncovered are not completely idiosyncratic to a single spatial location, but the three hives were close enough that bees from each encountered a substantially similar landscape. Repetition of this work in other locations will establish how the networks of flyways and stable congregation areas identified in our work and by Loper et al. (1992) are influenced by landscape structure. Loper er al. (1992) found that flight at congregation areas was higher than in flyways, although drones were rarer and rarer as elevation increased. We angled the harmonic radar to maximise our ability to track bees across the entire network of flyways and congregations, so it is likely that further flight activity took place at congregation areas too high for us to detect. Current harmonic radar technology doesn’t allow us to identify individual bees when several transponders are used. Solving this problem would open up the potential to investigate interactions between drones, and between drones and queens.

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Author contributions

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Declaration of interests

The authors declare no competing interests.

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Figure legends

Figure 1. Landscape use by drones

A) Heat map showing all drone flight activity recorded in 2016-2017 superimposed on an aerial orthomosaic image of the field site. Hive locations are marked by blue circles and numbered. Areas with brighter, yellower colouration were more visited by drones. N = 1174 tracks. **B)** Heat map showing all convoluted sections of flight recorded in 2016-2017, whose centre of mass was greater than 50m from all active hives. The centre of mass of each cluster of data points that we identified as a probable drone congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. This is a rough estimate of the boundary of each congregation area, for illustrative purposes only. N = 111 tracks. **C)** Heat map showing all drone activity recorded in 2016. N = 835 tracks. **D)** Heat map showing convoluted sections of flight recorded in 2016, whose centre of mass was greater than 50m from all active hives. N = 94 tracks **E)** Heat map showing all drone activity recorded in 2017. N = 339 tracks **F)** Heat map showing convoluted sections of flight recorded in 2017, whose centre of mass was greater than 50m from all active hives. N = 17 tracks.

Figure 2. Example flight paths showing convergence on similar routes

A) Flight path of a drone from hive 1 passing through congregation areas A, B and C, and showing evidence of convoluted flight at locations B and C. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable drone congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. Insets for each panel: zoomed view showing details of convoluted flight at congregation areas. **B)** Example flight from hive 3 showing convergence in both the route taken and the destination with the flight in A). **C-D)** Example flights from hive 2 visiting congregation areas A and B and showing convergence in route and destination with the flights shown in other panels. Note that only the outbound portion of the flight in D) is shown; either this drone did not return to the hive or the return flight was not detected. **E)** Example flight from hive 1 showing a visit to congregation area D. **F)** Example flight from hive 3 showing visits to congregation areas D, A and B, with convoluted flight at D and A.

Figure 3. Orientation flights

A) Example flight path of the first flight (orientation flight) ever undertaken by a drone from hive 1. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. Insets for each panel: zoomed view showing details of flight path. **B)** Orientation flight of a drone from hive 3. **C-D)** Orientation flights of two drones from hive 2, showing the typical range of distances reached from the hive.

Figure 4. Example flight paths showing consecutive flights of drone #48

The first six flights ever undertaken by drone #48. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. **A)** The drone's first ever flight was very brief, less than two minutes with convoluted flight directly in front of the hive entrance and a brief loop toward the Northwest. **B)** The second flight was much more extensive with loops passing through congregation areas D and A, followed by a longer flight through area C and appearing to continue even further, disappearing over a road that forms the Southeastern border of our field site. The portions of flight we were able to detect were fairly straight, going directly to the congregation areas and showing no evidence of systematic search. **C-F)** Subsequent flights by the same drone were even more direct, passing through congregation areas A, B and C, occasionally making convoluted flight at these locations, and apparently continuing across the road on two more occasions (E, F).

Figure 5. Mean acceleration as a function of position relative to the centre of congregation areas or hives

A) Mean x-component of acceleration calculated over bins of 5m in the x-direction (East-West) from the centre of each congregation area. Red line: area A; green line: area B; blue line: area C; magenta line: area D. Narrow vertical bars show SE for each bin. Vertical dashed reference line indicates centre of congregation area or hive. Horizontal dashed reference line indicates mean acceleration equal to zero. Grey dotted line shows regression line through all binned data. **B)** Mean y-component of acceleration (North-South) for the same locations. **C)** Mean x-component of acceleration calculated over bins of 5m in the x-direction from each hive location. Red line: hive 1; blue line: hive 2; green line: hive 3. **D)** Mean y-component of acceleration for the same locations. Scatterplots showing the full distributions at each location are shown in Figure S5.

Supplemental figure legends

Figure S1. Heat maps showing drone activity broken down by hive of origin, related to Figure 1

A) Heat map showing all drone flights from hive 1, recorded over both years 2016-2017, superimposed on an aerial orthomosaic image of the field site. Hive locations are marked by blue circles and numbered. Areas with brighter, yellower colouration were more visited by drones. N = 256 tracks. **B)** Heat map showing all drone flights from hive 2. N = 375 tracks. **C)** Heat map showing all drone flights from hive 3. N = 131 tracks.

Figure S2. Example flight paths showing probable shared flyway, related to Figures 1, 2

A) Flight path of a drone from hive 1 returning from an unknown location to the Northeast of the trackable area of the site. The outbound portion of this flight was not detected by the radar. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. **B)** Outbound flight path of a drone from hive 1, showing convoluted flight at congregation area D and leaving the trackable area to the Northeast. Curved flight path shows convergence with track shown in A and is likely to be the same drone. **C)** Inbound flight to hive 2 to destination to the Northeast showing convergence in route and destination with flights from other hives in other panels. **D)** Complete flight from hive 3 to destination to the Northeast showing convergence in route and destination with flights from other hives shown in other panels.

Figure S3. Example flight paths showing consecutive flights of drone #39, related to Figures 3, 4

The first eight flights ever undertaken by drone #39. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. **A)** The drone's first flight was typical of orientation flights, remaining close to the hive with convoluted flight centred on the hive location and no evidence of exploratory flight further afield. **B)** The second flight was very similar in structure. **C)** The third flight, taking place approximately 15 minutes after the drone had returned from its second flight, showed an abrupt change in structure. The track is missing some data, suggesting the drone flew too high or low for the radar to detect, but the data we do have show that the drone went much further from the hive, passing through congregation areas A and B. The portions of flight we recorded were fast and direct, with no evidence of orientation-flight-like convolution or of systematic search. **D-H)** The remaining flights by this drone were very similar: direct flights passing through congregation areas A and B. **H)** The drone did not return from its eighth flight; it is unknown whether it mated successfully or died.

Figure S4. Example flight paths showing first and subsequent flights of virgin queens, related to Figures 3, 4

A) First flight ever undertaken by queen #02. Sections of flight classified as straight are depicted in black; sections of flight classified as convoluted are shown by red lines. Gaps of greater than 30s between consecutive data points are indicated by dashed lines. The start of the track is marked by a green triangle and the end by a red rectangle. Hives are marked by blue circles and numbered. The centre of mass of each cluster of data points that we identified as a probable drone congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. It was common for first flights to remain within 10m of the hive entrance. **B)** Second flight undertaken by the same queen, #02, during the same day as her first flight. The bee largely made loops in a very restricted area near the hive entrance, with occasional larger loops, centred on the hive. **C)** First flight of queen #77. Queens were kept in mating nuclei at the location marked with a blue circle and labelled 'Q'. **D)** Third flight of queen #09, showing longer range looping flight. **E)** Second flight of queen #21, showing flight to the North, during which the queen appears to have mated. **F)** First flight of queen #75. The bee lost her transponder and the flight is incomplete, but it returned having mated.

Figure S5. Mean acceleration as a function of position relative to the centres of congregation areas or hives, related to Figure 5

A-D) Distance from the centre of each congregation area in the x-direction (East-West) plotted against the x-component of acceleration in the x-direction. Grey dotted lines in each panel show the regression lines for each distribution. **E-H)** Distance from the centre of each congregation area in the y-direction (North-South) plotted against the y-component of acceleration in the y-direction. **I-K)** Distance from each hive location vs the x-component of acceleration. **L-N)** Distance from each hive location vs the y-component of acceleration. There is a statistically significant negative slope to all distributions indicating that the further drones travel from the centre of the congregation or hive, the more strongly they accelerate back toward the centre. **O)** Positions of convoluted sections of flight. The centre of mass of each cluster of data points that we identified as a probable congregation area is marked by a grey circle and labelled A-D. Convex hull polygons containing all data points assigned to each cluster are outlined in grey. The centre of mass of each convoluted section of flight classified as taking place at congregation area A is represented by a red circle; those at area B by green circles; those of area C by blue circles; and those at area D by magenta circles.

Figure S6. Histograms and normal probability plots showing the distributions of bee position during sections of convoluted flight at four congregation areas, related to Figure 5

A-D) Histograms of the x-position (East-West, relative to cluster centre) of every data point in any convoluted section whose centre of mass was within 50m of each congregation area centre. **E-H)** Normal probability plots for the distributions shown in A-D. **I-L)** Histograms of the y-position (North-South, relative to cluster centre) of every data point in any convoluted section whose centre of mass was within 50m of each congregation area centre. **M-P)** Normal probability plots for the distributions shown in I-L. Distributions are approximately Gaussian at their centres, deviating only toward the edges.

Figure S7. Histograms and normal probability plots showing the distributions of bee velocity during sections of convoluted flight at four congregation areas, related to Figure 5

A-D) Histograms of the x-component of velocity (East-West) of every data point in any convoluted section whose centre of mass was within 50m of each congregation area centre. **E-H)** Normal probability plots for the distributions shown in A-D. **I-L)** Histograms of the y-component of velocity (North-South) of every data point in any convoluted section whose centre of mass was within 50m of each congregation area centre. **M-P)** Normal probability plots for the distributions shown in I-L. Distributions are approximately Gaussian at their centres, deviating only toward the edges.

Figure S8. Histograms and normal probability plots showing the distributions of bee position during sections of convoluted flight around three hives, related to Figure 5

A-C) Histograms of the x-position (East-West, relative to hive position) of every data point in any convoluted section whose centre of mass was within 50m of each hive. **D-F)** Normal probability plots for the distributions shown in A-C. **G-I)** Histograms of the y-position (North-South, relative to hive position) of every data point in any convoluted section whose centre of mass was within 50m of each hive. **J-L)** Normal probability plots for the distributions shown in G-I. Distributions are narrower than those at swarm locations and fit a Gaussian distribution less well, showing a higher degree of kurtosis.

Figure S9. Histograms and normal probability plots showing the distributions of bee velocity during sections of convoluted flight around three hives, related to Figure 5

A-C) Histograms of the x-component of velocity (East-West) of every data point in any convoluted section whose centre of mass was within 50m of each hive. **D-F)** Normal probability plots for the distributions shown in A-C. **G-I)** Histograms of the y-component of velocity (North-South) of every data point in any convoluted section whose centre of mass was within 50m of each hive. **J-L)** Normal probability plots for the distributions shown in G-I. Distributions are narrower than those swarm locations and may fit a Gaussian distribution less well.

Figure S10. Differences in flight dynamics between convoluted flight sections occurring at congregation areas and those near hives, related to Figure 5

A) Boxplots showing the kurtosis of distributions of drone positions in the x-direction (East-West), or y-direction (North-South) relative to the centre of each congregation area or hive; flights at hives show significantly heavier-tailed distributions than those at congregations. Asterisks denote results of statistical analysis: ns: non-significant; *: P<0.05; **: P<0.01; ***: P<0.001 **B)** Boxplots showing kurtosis of distributions of drone velocity in the x- and y-directions. **C)** Boxplots showing the duration of convoluted sections of flight whose centre of mass lies within 50m of the centre of a congregation area or of a hive. Only hive sites that were populated at the time the convoluted section occurred are included. **D)** Boxplots showing mean speed of flight during convoluted sections of flight at congregation areas or hives; flight in the congregations was significantly faster than that at hives. **E)** Boxplots showing duration of convoluted flight at each congregation area. **F)** Boxplots showing mean speed of sections of convoluted flight at each congregation area; bees flew faster at area A than at areas B or C.

Figure S11. Heat maps demonstrating that detection of convoluted flight is robust to variation in the parameters used, related to Figures 1, S1, Transparent methods

A-I) Heat maps showing all convoluted sections of flight recorded in 2016-2017, whose centre of mass was greater than 50m from all active hives. Hive locations are marked by blue circles and numbered. Areas with brighter, yellower colouration were more visited by drones. Each panel shows the sections of convoluted flight detected by our algorithm when a different combination of two parameters was used (the duration of the moving window over which straightness of the track was calculated, and the threshold minimum vector length used to differentiate straight from convoluted flight). In general, shorter windows or resultant vector lengths result in fewer data points being classified as belonging to convoluted flight, while longer windows or vector lengths result in more data points being classified as convoluted flight. In practice, the same sections of flight are typically identified, with data points added to or removed from the start and end of these periods of convoluted flight as the parameters change. In the aggregate, while the boundaries of the regions visited by convoluted flight are changeable, depending on the exact combinations of parameters used, they expand and contract around four constant hotspots, corresponding to the four congregation areas identified in the main text. N = panel A, 57 tracks; B, 79 tracks; C, 113 tracks; D, 79 tracks; E, 111 tracks; F, 146 tracks; G, 92 tracks; H, 135 tracks; I, 165 tracks.