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How does an informed minority of scouts guide a honeybee swarm as it flies to its new home?

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When a honeybee swarm lifts off to fly to a new nest site, only the scouts know in what direction the swarm must fly, and they constitute only about 5% of the bees in a swarm. Nevertheless, a swarm will fly quickly and directly to its destination. How does the small minority of informed scouts indicate the swarm's flight direction to the large majority of uninformed bees? Two hypotheses have been suggested. The first proposes that the flying scouts streak through the swarm cloud in the direction of the goal, thereby indicating the travel direction visually (vision hypothesis). The second proposes that flying scouts release pheromones from their Nasanov glands at the front of the cloud of flying bees, thereby indicating the travel direction chemically (olfaction hypothesis). We tested both hypotheses by studying the flights of normal swarms and comparing them to the flights of swarms composed of bees whose Nasanov glands were sealed shut. Our results support the vision hypothesis and contradict the olfaction hypothesis. We identified fast-flying bees ('streakers') in swarms, as predicted by the vision hypothesis, but we found no effect of sealing the Nasanov glands of swarming bees. Sealed-bee swarms were perfectly capable of flying directly to a new nest site.

In many animal species, individuals move about in groups as they perform seasonal migrations, travel to food sources and return to safe havens (Boinski & Garber 2000; Krause & Ruxton 2002). An intriguing question about such group movements is how they are oriented. In some species, all individuals in a group share a genetically determined propensity to travel in a certain direction (Berthold & Querner 1981; Berthold et al. 1992), or all are involved in choosing a particular travel direction (Neill 1979; Grünbaum 1998). In other species, relatively few of the individuals within a group have pertinent information about the group's travel destination, usually because of differences between individuals in age or experience, and these informed individuals guide those that are not informed. For example, a few informed individuals within a fish school can determine the foraging movements of the group and can steer a group towards a target (Reebs 2000; Swaney et al. 2001). In this study, we investigated a striking form of group movement that relies on guidance by a small subset of informed individuals: the flight of a honeybee swarm.

A swarm of honeybees consists of one queen and several thousand workers. Swarms are generally produced in the spring, when large colonies divide themselves for reproduction. In this process of colony fissioning, the mother queen and approximately half the worker bees leave the parental nest to establish a new colony, while a daughter queen and the balance of the workers stay behind to perpetuate the old colony (reviewed in Winston 1987). The swarm bees leave en masse, forming a cloud of bees just outside the parental nest, but within about 20 min they coalesce into a football-sized cluster at an interim site, usually a nearby tree branch. From here they choose a nest site.

Several hundred scout bees fly from the swarm cluster to search out tree cavities and other potential dwelling places. The dozen or so scouts that find suitable cavities report their locations by means of waggle dances performed on the surface of the bivouacked swarm, and other scouts decode the dances, visit the sites themselves, and may dance in turn. There ensues a process of 'friendly

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competition' among the scouts affiliated with the different sites, at the end of which one site comes to dominate in visits and dancing (Lindauer 1955; Seeley & Visscher 2004). Once this agreement is reached, the swarm takes flight again and moves to the chosen site, often several kilometres away (Seeley & Morse 1977; Villa 2004).

An intriguing feature of the flight of a honeybee swarm is that only about 5% of a swarm's members have visited the new nest site before swarm liftoff (Seeley et al. 1979). Furthermore, the other 95% of the swarm's members have remained quiescent throughout the decision-making process, that is, they have not paid attention to the dances indicating the location of their future home. Therefore, most of the bees in an airborne swarm do not know in what direction they must fly until the scouts give them this information. How do the scouts do so? Two mechanisms of swarm guidance have been proposed. Lindauer (1955) observed in airborne swarms that some bees fly through the swarm cloud at high speed and in the correct travel direction, seemingly 'pointing' the direction to the new nest site. Lindauer suggested that these fast-flying bees (which we call 'streakers') are scouts that have visited the chosen nest site, and that their behaviour guides the other, uninformed, bees towards their new home. We refer to Lindauer's hypothesis as the vision hypothesis. An alternative to the vision hypothesis is the olfaction hypothesis of Avitabile et al. (1975), who proposed that the scouts provide guidance by releasing assembly pheromone from their Nasanov glands (a gland between the last two tergites of the bee's abdomen) on one side of the swarm cloud, thereby creating an odour gradient that can guide the other bees in the swarm.

So far, neither the vision hypothesis nor the olfaction hypothesis has been tested empirically, although other investigators have confirmed Lindauer's report that there are streakers in flying swarms (Seeley et al. 1979; Dyer 2000). The vision hypothesis has been tested theoretically in a modelling study in which a small proportion of the bees in a simulated swarm repeatedly fly through the centre of the swarm in the direction of the nest site (Janson et al. 2005). The simulated swarms behave much like real swarms, which indicates that streakers are, in principle, able to guide swarms. This modelling study shows, however, only that the vision hypothesis is a possible mechanism of swarm guidance; it does not prove that it is the actual mechanism.

We tested both the vision and olfaction hypotheses of swarm guidance using real honeybee swarms. We studied the flights of both normal honeybee swarms and swarms in which each bee's Nasanov gland was sealed shut.

METHODS

Study Sites

Our main study site was the Liddell Field Station of Cornell University at Ithaca, New York, U.S.A. We set up swarms, one at a time, on the edge of a large, unmowed field (330 × 800 m) bounded by woods. Near the centre of this field stands a large white ash tree, *Fraxinus americana*, on which we mounted, 4 m off the ground, a small, unoccupied hive (a six-frame nucleus box). This bait hive provided the swarms with an attractive nest site in a controlled location. To enhance the hive's attractiveness to the bees, we put inside it a frame of old, empty comb and a pheromone lure containing an artificial blend of the main compounds in the secretion of the Nasanov gland of worker bees (Brushy Mountain Bee Farm, Moravian Falls, North Carolina, U.S.A.). On the eastern edge of the field, 270 m from the tree-mounted hive, we set up our swarms. Each swarm was placed on a swarm mount (Weidenmüller & Seeley 1999), positioned in the centre of a 20 × 20-m mowed area. Within this mowed area, we erected 36 1.3-m stakes, 4 m apart, to create a grid for measuring the length and width of each swarm cloud immediately after liftoff. We also erected a 6-m pole, with 1-m markings, to measure the heights of the top and bottom of each swarm cloud. We mowed several paths between the swarm mount and bait hive so that we could easily follow our swarms once they were in flight. Every 30 m along the path that ran directly from the mount to the hive, we erected a distance marker consisting of a 2-m stake topped with a bright flag.

We used a second study site to record the flight of one swarm over a greater distance than was possible at our main study site. This second site, 7 km from the main one, was a much larger (1200 × 2000 m) field that was completely mowed. We established one swarm in the middle of this field using the same mount as for our main study site. We also placed two bait hives in trees on the edge of the field, as described above, but the swarm flew instead to a hollow tree more than 3 km outside the field.

Swarm Preparation

All our swarms were artificial swarms prepared from colonies headed by 'New World Carniolan' queens (mainly *Apis mellifera carnica*) purchased from Strachan Apiaries, Yuba City, California, U.S.A. We worked with swarms of two sizes: large ones (ca. 11 500 bees) for making general observations on swarms in flight, and small ones (ca. 4000 bees) for the experimental test of the olfaction hypothesis. The size of the large swarms corresponds to the median size of natural swarms, and the size of the small swarms is within the size range of natural swarms (Fell et al. 1977).

We prepared each large swarm by removing the queen from an established colony in a normal hive, caging her in a small queen cage (3.2 × 10 × 1.6 cm), suspending the queen cage in a larger 'package' cage (15 × 25 × 25 cm) of wood with wire screen sides, and then shaking 1.5 kg of the colony's worker bees (ca. 11 500 bees) into the cage using a large funnel. The worker bees quickly clustered around their caged queen. We kept the caged bees indoors at room temperature and fed them a granulated sucrose:water solution (1:1 by volume) ad libitum until the bees started to produce wax scales 3–4 days later. We then placed the swarm on the swarm mount; we opened the swarm cage, fastened the caged queen to the mount, and shook the worker bees on to the base of the mount.

The workers then clustered around their caged queen, and some of them, the nest site scouts, flew off to search for possible nesting cavities.

The small swarms were prepared differently from the large swarms, with each bee receiving either a paint seal over the Nasanov gland (treatment swarms) or a paint dot on the thorax (control swarms). For each swarm, we first collected batches of worker bees in wire cages (10 × 10 × 25 cm) using the large funnel, putting about 1000 bees in each cage. We then shook bees from these cages into plastic zip-lock freezer bags (ca. 40 bees in each bag). We placed 10–20 bee-filled bags into a refrigerator (4 °C) until the bees were motionless. We then emptied one bag at a time, spreading the chilled bees in a single layer on a container of reusable ice ('blue ice') to keep them immobile. To prepare a swarm of bees with sealed Nasanov glands, we applied a thick layer of paint (Testors Gloss Enamel, The Testor Corporation, Rockford, U.S.A.) over the entire dorsal surface of the distal end of each bee's abdomen. To prepare a control swarm of unsealed bees, we applied paint to each bee's thorax instead of her abdomen. Each batch of painted bees was then transferred from the blue ice to a paper towel, to help the bees to warm up and the paint to dry. When the bees began to crawl about, we checked their paint marks before placing them in a 'package' cage, as above, that contained their queen, confined in a queen cage. The bees eventually recovered fully from being chilled and clustered around the queen. A sugar solution feeder provided the caged bees with food. Once we had prepared all 4000 bees in a swarm, we treated the swarm as described above for the large swarms (i.e. we fed them with sugar solution until wax scales were produced, then released them on the swarm mount). We prepared three treatment (sealed-bee) swarms and three control (unsealed-bee) swarms. When placing the treatment swarms on the swarm mount, we assisted the bees in clustering around their queen by tying an artificial Nasanov lure to the stand until the bees had formed a cluster.

Flight Data Recording: Large Swarms

We studied the flights of five large swarms. Three made 270-m flights to our bait hive and two made considerably longer flights to hollow trees. The three swarms that made relatively short flights flew along a route known in advance (straight from swarm mount to bait hive), which enabled us to record their flights with precision. We encouraged these three swarms to fly to our hive in the field, rather than to some tree in the forest, by steadily monitoring the waggle dances performed on each swarm and removing any dancers that advertised sites other than our hive. We did not censor the dances in the other two swarms which flew to hollow trees. One of the two long-flight swarms was observed at the primary study site and the other was observed at the secondary study site. We hoped that by letting these two swarms make long flights, they would show us the maximum flight speed of a swarm.

Four large swarms lifted off at the primary study site. In each case, the cloud of flying bees remained essentially stationary for about a minute after all the bees had taken flight, and during this time we estimated the dimensions of each airborne swarm. To do so, we counted the number of metres in the 20 × 20-m grid over which the swarm extended when viewed from the side (i.e. looking along a line perpendicular to the flight direction) and when viewed from the back (i.e. looking along the line of flight). We also recorded the heights of the top and the bottom of each swarm with the aid of the metre marks on the 6-m pole. We recorded observations with continuously running tape recorders that we started when each swarm began to take-off.

We measured flight speed for each swarm in one of two ways depending on whether the swarm made a short-distance flight to our hive or a long-distance flight to a tree. For each of the three swarms that flew to our bait hive, and hence along a route with flagged stakes at 30-m intervals, we recorded when the centre of the swarm passed over each stake. For each of the two swarms that flew to a far-off tree, we ran beneath the swarm and planted a flagged stake every 30 s for as long as we could stay with the swarm. We later retraced the flight paths of the two swarms and measured the distances between the stakes.

For the three swarms that flew to the hive, we also recorded the time that each swarm needed to enter the hive ('entry time'). We measured this as the interval between when the front of a swarm reached the hive and when the air became quiet again. A swarm produces a loud buzzing sound while the bees are flying about outside their new home, but this drops off as the bees land at its entrance and move inside.

Flight Data Recording: Small Swarms

All but one of the six small swarms that were used to test the olfaction hypothesis performed a 270-m flight from swarm mount to bait hive. The one (control) swarm that did not fly to the bait hive also flew towards the bait hive, but continued flying past it a few hundred metres to take up residence in a hollow tree in the woods. For these swarms, as for the large swarms, we baited the hive with a pheromone lure to make our hive attractive to the bees. Using the small swarms to test the olfaction hypothesis required that we eliminate the artificial pheromone from the hive before each swarm flew to it. We did this at least 30 min before each swarm took flight, by replacing the bait hive that contained a swarm lure with one that had never contained a swarm lure. The scout bees showed no signs of being disturbed by this swapping of hives. In one case (treatment swarm 3) the artificial pheromone lure was removed from the nestbox only moments before the swarm moved into the bait hive and this bait hive was not replaced by a clean one, because the events overtook the observer.

For each of the six small swarms (three treatment and three control), we recorded its dimensions when starting flight, speed throughout flight, and entry time at the end of flight (except in the case of the control swarm that flew past the bait hive), using the methods described above for the large swarms. At the end of each swarm's flight, we counted the bees on the front of the bait hive that were standing in the scenting posture: abdomen raised and abdomen tip tilted to expose the Nasanov gland. This behaviour is normally performed to emit Nasanov pheromone, but in the case of our treatment swarms little or no such pheromone was emitted. We made these counts every minute for 10 min (or less when the counts became unreliable because of the large number of bees landing near the hive entrance), starting when the front of a swarm reached the tree with the bait hive. Finally, within an hour of when each treatment (sealed-bee) swarm had moved into the bait hive, we checked the seals of these bees. To do so, we sampled and inspected 250 bees using the following methods: after removing the bait hive's lid to expose the swarm bees, an experimenter randomly plucked one bee at a time from inside the hive, pinched her between thumb and index finger, and observed her as she tried to sting. Each bee curled her abdomen strongly while trying to sting, so it was easy to see whether the paint seal over her Nasanov gland was intact or broken.

Photographic Analysis

To investigate the variation in flight speed and flight direction among the individual bees within a flying swarm, we took photographs of the second large swarm during its flight to the bait hive. Photographs were made with a 35–100-mm zoom lens mounted on a camera body for 35-mm film. We used colour transparency film with a slow film speed (DIN 64) and took the photographs with a moderately long exposure time (1/30 s). The camera was positioned 20 m from the centre of the swarm and the axis of photography was perpendicular to the axis of swarm flight (Fig. 1). The camera was positioned as low as possible (about 1 m off the ground) so that the background for most of the swarm was clear sky. This set-up yielded photographs that captured a 10-m-wide image at the distance of the swarm centre (20 m) and in which individual bees appeared as small, dark streaks on a light background. In each photograph there was a 45-cm size reference, either the swarm mount or a portable marker, positioned near the centre of the swarm. We analysed two of the photographs of large swarm 2: one taken 33 s after the swarm had completed liftoff, and was starting to move away from the mount, and one taken 57 s later (90 s after liftoff), when the swarm was moving steadily (although still slowly) and the centre of its cloud had reached the 30-m mark. Each photograph was analysed by projecting it on to a white surface to create an enlarged (600 × 900 mm) image. We measured the length (mm) and the angle (degrees, relative to horizontal) of each dark streak that was in focus in the enlarged image ($N = 1333$ and 1553 streaks, representing 12 and 13% of the bees in the swarms).

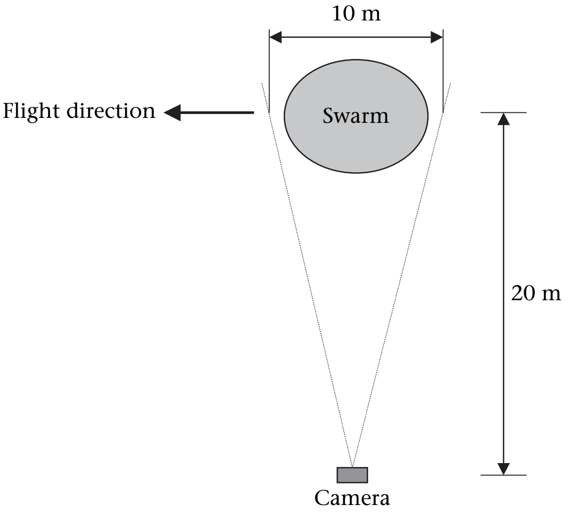

Figure 1. Bird's-eye view of the layout used to photograph flying swarms. The camera (bottom) was 20 m from the swarm (top) and photographs were taken at an angle of 90° relative to the swarm's travel direction. The recorded image was 10 m wide at 20 m, so included most of the swarm.

Because each photograph had a size reference and recorded the bees' movements during a known interval (1/30 s), we were able to calculate for each photograph the conversion factor between streak length and flight speed (for both photographs: 1 mm of streak length = 0.3 m/s of velocity in the plane of the photograph). This conversion factor is accurate only for bees whose distance from the camera matched that of the size reference, i.e. 20 m. Although some bees were closer and some were more distant, those whose distance from the camera was not within 1.5 m of 20 m were not in focus in the photograph and so were not included in this analysis. The maximum errors of our flight speed estimates were, therefore, ±8% of 20 m. Thus, for example, a bee whose streak was 10 mm long in the enlarged photograph was a bee whose flight speed, in the plane of the photograph, was 3 m/s. For the bees in the photograph, we used streak lengths to evaluate the distribution of flight speeds and streak angles to get a distribution of flight angles relative to the horizontal, i.e. the swarm's travel direction. We could not tell the polarity (movement left versus movement right) of each streak, so we assumed that each bee was flying in the general direction of the swarm's movement (i.e. from right to left in the photograph). In principle, the bees' flight angles could range from $-90°$ (streak straight down) through $0°$ (streak horizontal) to $+90°$ (streak straight up), but most of the flight angles were $\pm 45°$. Finally, in analysing the second photograph, which recorded the swarm when it was well under way, we measured streak length and streak angle separately for the upper and lower halves of the photograph. We did so to compare the distributions of flight speed and flight angle between the upper portion of the swarm and the swarm as a whole.

Flight Speed Measurements: Individual Bees

To estimate the maximum flight speed that a worker bee can achieve in straight-line flight, we measured the flight durations of 20 bees as each bee flew to and from sugar water feeders 500, 700 and 900 m along a line extending from their hive. The slope of the regression line that relates flight duration (to or from the feeder) and flight distance indicates the speed of bees in straight-line flight; it is not affected by time spent in circling flight at the end of each trip, as the bee prepares to settle at the hive entrance or bee feeder. To stimulate the bees to fly at top speed, we worked with bees from a hungry colony as they exploited a rich feeder (Seeley 1995). To make the study colony (which inhabited a two-frame observation hive) hungry, we removed its honey stores. To make the feeder highly desirable, we loaded it with a highly concentrated (2.5 M/litre) sucrose solution that the bees could collect ad libitum. Twenty bees from this colony were trained to the feeder and marked with paint for individual identification. Once these 20 bees were marked, all additional bees arriving at the feeder were captured to prevent crowding at the feeder and to prevent the colony's 'nectar' influx from becoming high; under these conditions, foragers remain highly motivated to forage. For each bee, we recorded the time spent making one flight from hive to feeder and one flight from feeder to hive, for each of the three distances between hive and feeder. Flight durations were measured by two observers, one at the hive and one at the feeder. Both were equipped with a stopwatch and a two-way radio. To measure the duration of a bee's outward flight, the observer at the hive started a stopwatch when he saw a marked bee leave the hive, alerted the observer at the feeder to look for the arrival of this bee, and then stopped his stopwatch when the observer reported that the bee of interest had landed at the feeder. To measure the duration of a bee's homeward flight, the roles of the two observers were reversed. The feeder was positioned in three successive locations south of the observation hive, 500, 700 and 900 m. We used the same 20 bees for all feeder locations. Wind speed and direction were recorded at 30-s intervals with an anemometer and wind vane mounted on a 5-m mast at the observation hive.

RESULTS

Flights of Large Swarms

The large swarms, when airborne, formed clouds of flying bees 8–12 m long (horizontal axis in travel direction), 6–8 m wide (horizontal axis perpendicular to travel direction) and 3–4 m high (Table 1). We estimated the volume of each swarm's cloud by multiplying the measurements of length, width and height, and we used this estimate to calculate the density of bees in each swarm's cloud, knowing that each swarm contained approximately 11 500 bees. The range of density estimates was 30–80 bees/m^3 (mean 50 bees/m^3). At this density, adjacent bees are separated, on average, by 27 cm. The three swarms that performed a 270-m flight to the bait hive needed 275–322 s to do so (i.e. time elapsed from when a swarm completed liftoff to when the front of the swarm reached the tree holding the hive). The range of entry times for these three swarms was 10 min 22 s to 24 min.

Table 1. Measurements for three large swarms that flew 270 m to a bait hive and one large swarm that flew more than 1000 m to a hollow tree

	Length (m)	Width (m)	Height (m)	Density (bees/m^3)	Flight time (s)	Entry time (min:s)
Swarm 1	12	8	4	30	297	24:00
Swarm 2	8	6	3	80	322	12:30
Swarm 3	12	8	3	40	275	10:22
Swarm 4	8	8	3	60	ND	ND

Each swarm contained approximately 11 500 bees. The dimensions of each swarm were measured shortly after liftoff. ND = no data.

The pattern of change in speed during the flight was similar for these three swarms (Fig. 2). Each one accelerated steadily for the first 90 m, reached a peak flight speed of 6–7 km/h (1.7–1.9 m/s) after flying 90–120 m, reduced its speed after 210–240 m, moved slowly during the final 30 m, and finally stopped at the tree holding the bait hive.

For the three large swarms that flew only 270 m to the bait hive we suspected that the peak recorded flight speeds of 6–7 km/h (1.7–1.9 m/s) did not represent the maximum speeds that flying swarms can achieve. We therefore allowed two swarms to make long-distance flights to hollow trees. Based on the dances performed by these swarms' scouts shortly before liftoff, we estimated that these two swarms made flights of over 1000 and 4000 m to their new homes. Tall grass and trees limited our ability to keep in contact with these swarms to only 347 and 1323 m, respectively, that is, for only about the first third of each swarm's flight. Nevertheless, for these two swarms we recorded markedly higher maximum flight speeds (9.6 km/h or 2.7 m/s and 11.3 km/h or 3.2 m/s) than for the first three swarms (Fig. 3). The maximum speed of the second swarm remained stable for the last 5 min that we were able to follow the swarm.

Flights of Small Swarms

Both treatment and control swarms, when airborne, formed similar-sized clouds of flying bees (treatment swarms: 8 m long, 8–10 m wide, 2–3 m high; control swarms: 8–10 m long, 6–8 m wide, 3 m high; Table 2). The density estimates were also similar for the two types of swarms (treatment swarms: 17–31 bees/m^3, mean 22 bees/m^3; control swarms: 20–29 bees/m^3, mean 22 bees/m^3). At a density of 22 bees/m^3, adjacent bees are separated, on average, by 36 cm.

Both treatment and control swarms flew quickly and directly to the bait hive (control swarm 1 flew to the bait hive but then continued past it to occupy a hollow tree). The mean ± SD flight time for the three treatment swarms (346.7 ± 27.6 s) was not significantly different from that for the control swarms (267.0 ± 0.0 s; Student's *t* test: $t_3 = 2.183$, $P = 0.12$). The mean entry time for the three treatment swarms (17 min 22 s) was, however, significantly higher than that of the two control swarms for which we had entry time measurements (8 min 53 s; Student's *t* test: $t_3 = 5.612$, $P = 0.01$). The entry time for treatment swarm 3 was much shorter than that of the other two treatment

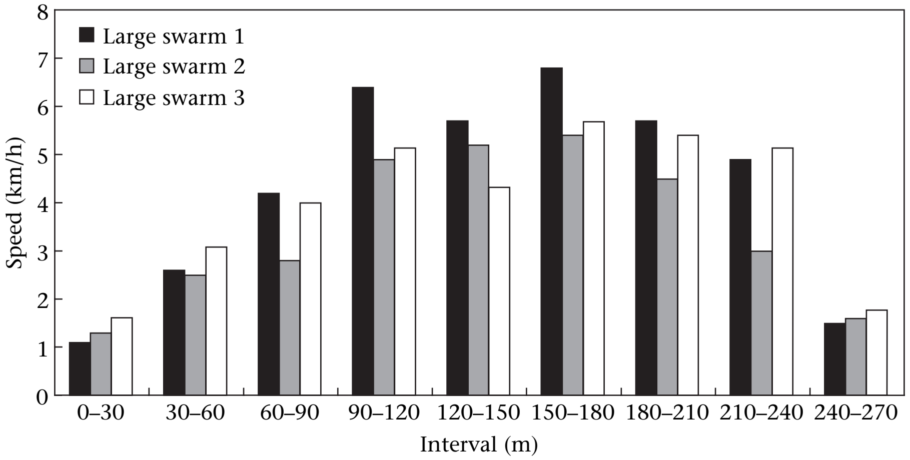

Figure 2. Flight speed patterns of the three large swarms that flew 270 m to a bait hive. We measured each swarm's speed throughout its flight as time elapsed per 30 m of flight.

swarms, probably because in this swarm, but not the other two, we did not replace the bait hive that contained a pheromone lure with an unscented bait hive.

The pattern of change in speed during flight was similar for treatment and control swarms (Fig. 4). As occurred with the large swarms, the small swarms accelerated steadily for the first 90 m, reached peak flight speeds after flying 90–120 m, slowed after flying 210–240 m, moved slowly during the final 30 m, and finally stopped at the tree supporting the bait hive. The only deviation from this pattern came with control swarm 1, which flew past the bait hive and did not slow down when nearing it. The maximum speeds of the treatment swarms (6.8, 3.6 and 6.8 km/h) were similar to those of the control swarms (6.7, 6.4 and 7.2 km/h), with the obvious exception of treatment swarm 2. This swarm flew much more slowly than the other swarms (maximum speed only 3.6 km/h), probably because it flew against a fierce headwind; the other swarms encountered at most a slight breeze.

The counts of bees performing the scenting behaviour (Fig. 5) on the front of the bait hive showed no obvious difference between treatment (Fig. S1 in the Supplementary Material) and control swarms.

Of the 250 bees sampled from each treatment swarm after it had moved into the bait hive only 0.8% (swarms 1 and 2) and 1.6% (swarm 3) of the bees had broken seals.

Flight Patterns of Individuals

While watching the flying swarms, we observed conspicuous differences between individuals in flight speed and pattern. Most bees within a swarm flew slowly and with curved flight paths, but some flew rapidly and linearly in the direction of the swarm's destination. The latter bees (streakers) appeared to be mainly in the upper region of a swarm.

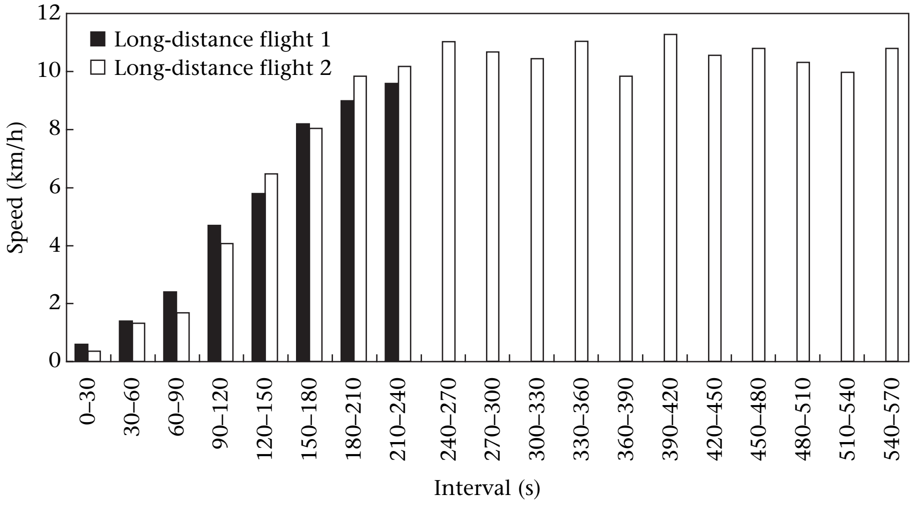

Figure 3. Flight speed patterns of the two large swarms that flew more than 1000 m (swarm 4) and more than 4000 m (swarm 5) to hollow trees. We measured each swarm's speed throughout the first third of its flight (i.e. as long as we could run along with the swarm; 347 m for swarm 1 and 1323 m for swarm 2) from distance covered per 30 s of flight.

Table 2. Measurements for six small swarms that flew 270 m to a bait hive (one continued flying past the hive)

	Length (m)	Width (m)	Height (m)	Density (bees/m^3)	Flight time (s)	Entry time (min:s)
Treatment swarm 1	8	8	2	31	288	21:45
Treatment swarm 2	8	10	3	17	405	19:36
Treatment swarm 3	8	10	3	19	347	10:45
Control swarm 1	8	6	3	28	ND	ND
Control swarm 2	10	8	3	17	267	09:00
Control swarm 3	8	8	3	20	267	08:45

Each swarm contained approximately 4000 bees. Treatment swarms: bees whose Nasanov glands were painted shut; control swarms: bees that received paint but did not have their Nasanov glands painted shut. The dimensions of each swarm were measured shortly after liftoff. ND = no data.

Shortly after liftoff, the streaks representing individual bees in the enlarged (600 × 900 mm) photographic image (Fig. S2a in the Supplementary Material) were nearly all shorter than 10 mm, representing bees whose flight speeds in the plane of the photograph were less than 3 m/s (Fig. 6a). There were a few longer streaks (10–35 mm) representing bees that were flying more rapidly (3–10.5 m/s). When the swarm had increased its speed and had travelled 30 m (Fig. S2b in the Supplementary Material) fewer bees produced extremely short (1–3 mm) streaks, indicating that fewer bees were still moving slowly in the plane of the photograph (Fig. 6b). The streak length distribution for the top portion of the swarm was shifted noticeably to higher values relative to the streak length distribution for the swarm as a whole (Student's t test: $t_{81} = -6.97$, $P < 0.001$; Fig. 6b). This result implies that the bees in the top portion of the swarm were flying either more rapidly or more in alignment with the swarm's travel direction, or both, than were bees in the swarm as a whole.

The distributions of streak angles shortly after liftoff and 57 s later when the swarm was en route, for the whole swarm, were significantly different, with the latter

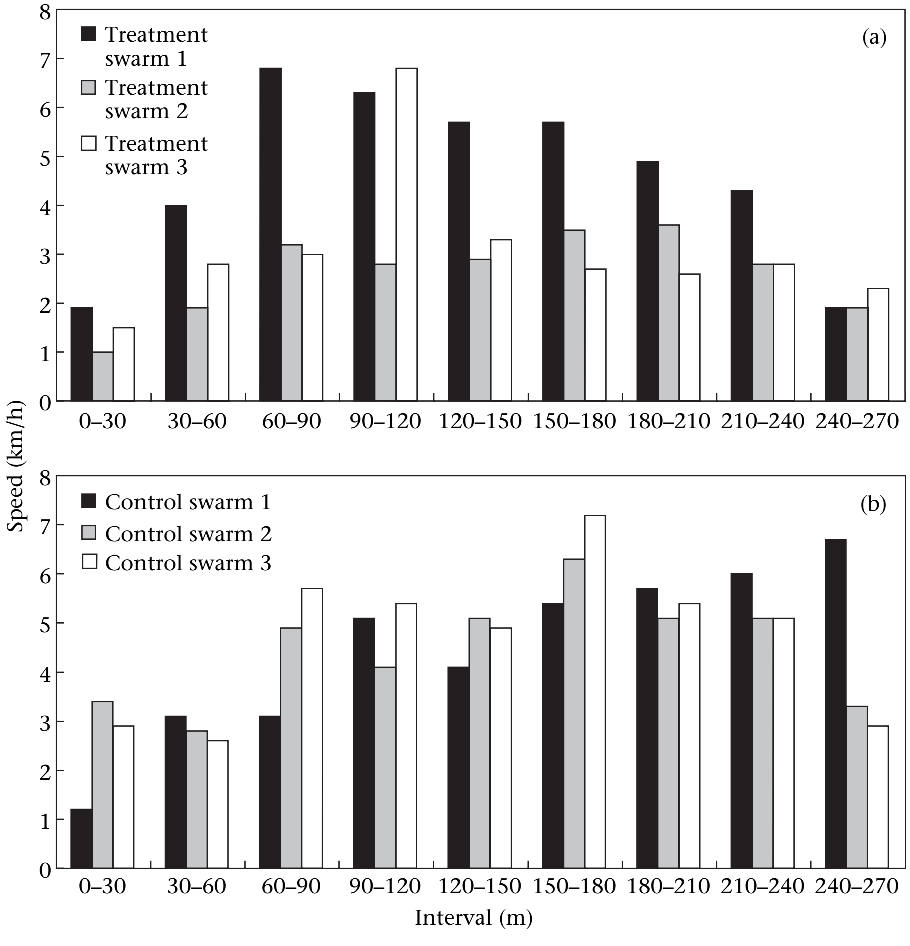

Figure 4. Flight speed patterns of the six small swarms. (a) Three treatment swarms (Nasanov glands sealed) and (b) three control swarms (Nasanov glands not sealed). All flew to the bait hive at 270 m, except control swarm 1, which flew past it en route to a hollow tree. We measured each swarm's speed as time elapsed per 30 m of flight between swarm mount and bait hive.

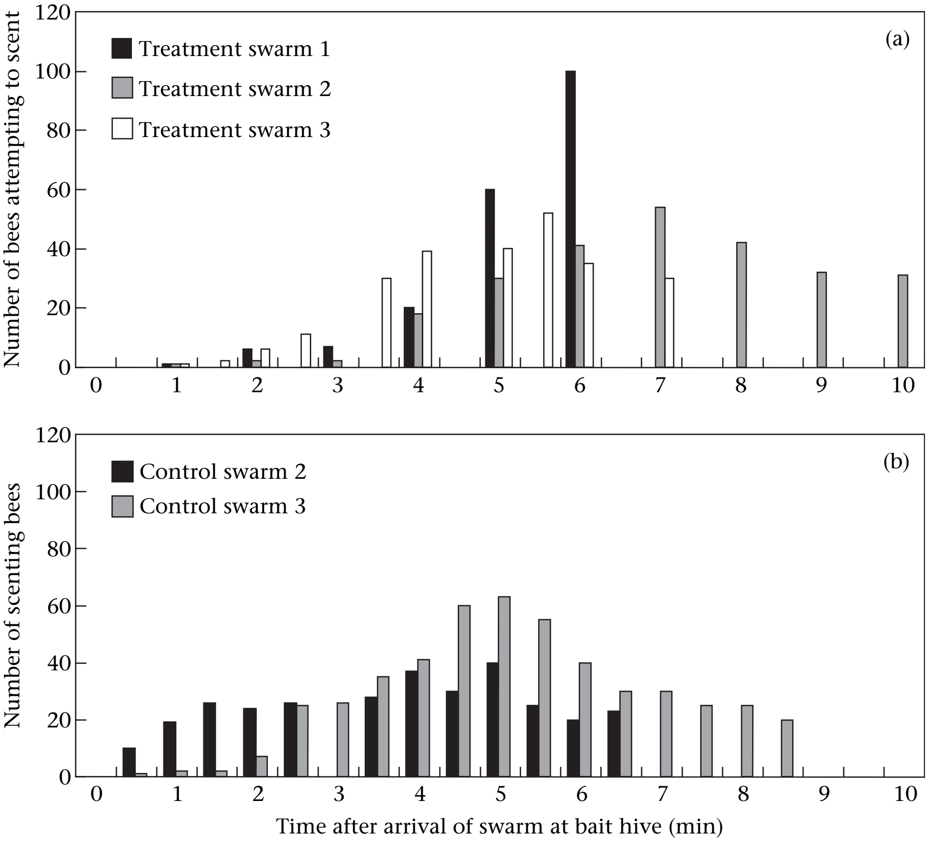

Figure 5. Number of bees trying to secrete Nasanov pheromone ('scenting') for (a) treatment swarms (Nasanov glands sealed) and (b) control swarms (Nasanov glands not sealed) in the first 10 min after the arrival of the swarm at the bait hive. Data for control swarm 1 are missing because this swarm did not move into the bait hive.

distribution clustered more tightly around the travel direction (Watson–Williams test for differences in two distributions, Zar 1996: $F_{1,698} = 4.90$, $P = 0.027$; Fig. 7a). This result implies that as the swarm started its flight, its bees increasingly adopted flight directions that were aligned with the direction of swarm movement. For the distributions of streak angles for bees in the upper and lower halves of the image of the swarm en route we found no difference between the streak angles for bees in the upper and lower halves of the swarm ($F_{1,397} = 2.67$, $P = 0.103$; Fig. 7b). For bees shortly after liftoff, the distributions of streak angles for bees with streak lengths of over 15 mm were more aligned with the swarm's movement than were those of bees with streaks shorter than 15 mm ($F_{1,413} = 4.01$, $P = 0.04$; Fig. 7c). This difference disappeared when we compared the distributions of streak angles between slow and fast bees, when the swarm was en route ($F_{1,503} = 2.81$, $P = 0.09$; Fig. 7d) when all the bees showed relatively high alignment with the swarm's movement direction.

Maximum Speed of Flying Bees

Figure 8 shows the two regression lines relating flight distance and flight time for bees flying either to or from a highly desirable food source. The slope of the line for outward flights, made by essentially empty foragers, is 9.45 m/s and that for homeward flights, made by foragers with loads of sugar solution, is 6.57 m/s. The flight speed measurements were all made on one day, when the average wind speed was just 0.8 m/s towards 103°. The light wind, moving almost perpendicular to the travel directions of the bees (180° to the feeder and 0° to the hive), only slightly influenced our measurements of the bees' flight speeds.

DISCUSSION

At the heart of this study is the question, how does an informed minority of scouts guide a honeybee swarm as it flies to its new home? We addressed two possible answers to this question, the olfaction hypothesis and the vision hypothesis. It seems doubtful that the olfaction hypothesis is correct, because if it were, then the small treatment swarms should have been unable to fly directly and quickly to the bait hive. The treatment swarms, like the control swarms, flew directly to the bait hive and did so with flight speed patterns and flight times nearly identical to those of the control swarms (Fig. 4, Table 2). Furthermore, the sizes and densities of the two types of swarm showed no differences.

Given the absence of flight differences between the two types of swarm, one might wonder whether the Nasanov glands of bees in the treatment swarms were thoroughly

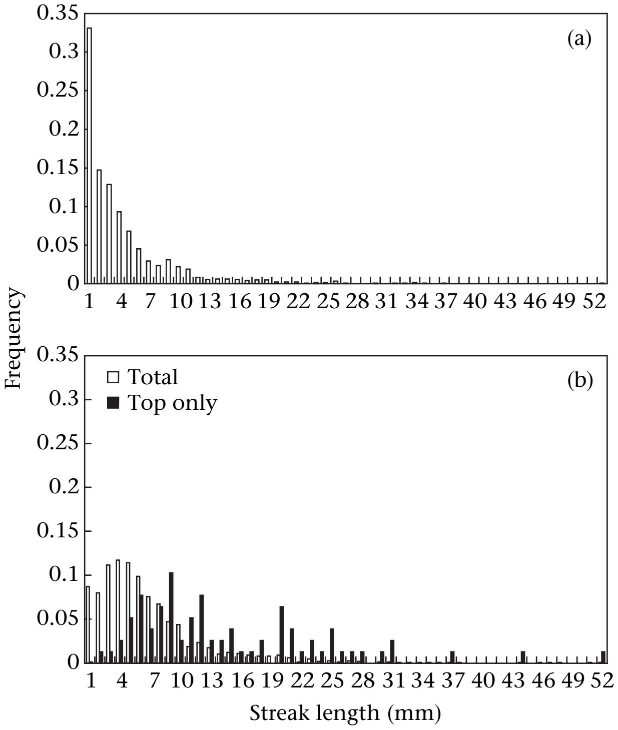

Figure 6. Frequency distributions of lengths of the streaks in the photographs shown in the Supplementary Material when these photographs were enlarged to 600 × 900 mm based on (a) photo S2a in the Supplementary Material ($N = 1333$) and (b) photo S2b in the Supplementary Material. Two distributions are shown in (b), one for all the streaks in the photograph ($N = 1553$) and one for only the streaks in the top half of the photograph ($N = 78$). For both (a) and (b) the conversion factor between streak length and flight speed is 1 mm = 0.3 m/s. Streaks longer than 35 mm probably arose through the overlap of two shorter streaks, because they imply impossibly high flight speeds.

sealed. Three pieces of evidence indicate that they were. (1) We needed to assist the bees from the treatment swarms to form a cluster around the queen on the swarm mount by using a Nasanov lure. (2) When we sampled bees from the treatment swarms shortly after they occupied the bait hive, only a few (0.8–1.6%) of the bees had broken seals. (3) The mean entry time of the treatment swarms was much longer than that of the control swarms (Table 2) apart from treatment swarm 3, when the bait hive was not swapped for a clean one, suggesting that the odour from the artificial Nasanov lure assisted the swarm to move in quickly. We would expect slow entry times if the Nasanov glands were sealed in the treatment swarms, because scout bees normally use the Nasanov gland pheromone to help locate the new entrance opening (e.g. specific knothole or crack), once the swarm has reached its destination (Seeley et al. 1979). Treatment swarms were able to move into the bait hive without extraordinary delay, even though only about 1% of their bees could release Nasanov pheromone. This finding suggests that the visual cue of scout bees massed at the entrance (see Fig. S1 in the Supplementary Material) is important for indicating entrance location when a swarm reaches its new home.

Unlike the olfaction hypothesis, the vision hypothesis remains viable. Ideally, we would have tested the vision hypothesis with an experiment analogous to what we did for the olfaction hypothesis, by comparing swarms in which the scouts could and could not produce visual signals by streaking. Nevertheless, two pieces of evidence strongly support the vision hypothesis. The first is that the peak flight speeds of swarms (2–3 m/s) were well below the peak flight speeds of individual bees (9–10 m/s; Figs 2, 3, 8). This result shows that it is possible for scout bees to streak through a flying swarm. The second piece of evidence shows that some bees do streak through swarms. The photographic analysis indicates that in large swarm 2, both when it was starting its flight and when it was well under way, a minority of the bees were flying at maximum speed (>9 m/s = streak length > 30 mm) in the direction of the swarm's destination, and a majority were flying either more slowly or not in the direction of the swarm's flight, or both (Figs 6, 8). Our photographic analysis does not yield an undistorted distribution of the flight speeds of bees in a swarm, because it measures for each bee the component of her velocity vector that is in the plane of the photograph. Thus, the flight speed of any bee that was flying in or out of this plane was underestimated. The most extreme underestimation would arise for a bee flying perpendicular to the plane of the photograph (directly towards or away from the camera); such a bee would have a streak length of 0 and we would have measured her flight speed as 0. Therefore, the flight speed distributions shown in Fig. 6 are skewed to the left. Nevertheless, the existence of the long (>30 mm) streaks in these photographs indicates unambiguously that bees were streaking through the swarm. Furthermore, these long streaks represent bees flying near the maximum flight speed, so we are confident that the bees producing these long streaks were flying in the plane of the photograph, and hence were aligned with the direction of the swarm's flight (to produce such long streaks without flying in the plane of the photograph, these bees would need to have flown faster than the maximum flight speed of bees). We conclude, therefore, that our photographic analysis documents the existence of bees streaking through the swarm in the direction of the swarm's movement.

Besides enabling us to evaluate the two key hypotheses about the mechanism of swarm guidance by scout bees, our results provide insights about swarms that can guide future investigations. One is the finding that the fast-flying bees, the streakers, appear to be most common in the upper region of a swarm (Fig. 6b). For humans, and probably also for bees, streakers are much more easily seen against bright sky than dark ground or vegetation, so by flying above most of the bees in a swarm, streakers may facilitate the transfer of their direction information to the other bees.

A second general finding about the guidance of swarms is a clearer picture of how a swarm slows itself at the end of its flight. One possibility is that the scout bees drop out of the swarm cloud, land at the nest site, and release Nasanov pheromone to attract the other bees to the endpoint of their trip (Janson et al. 2005). Observations on real swarms (Seeley et al. 1979) are consistent with

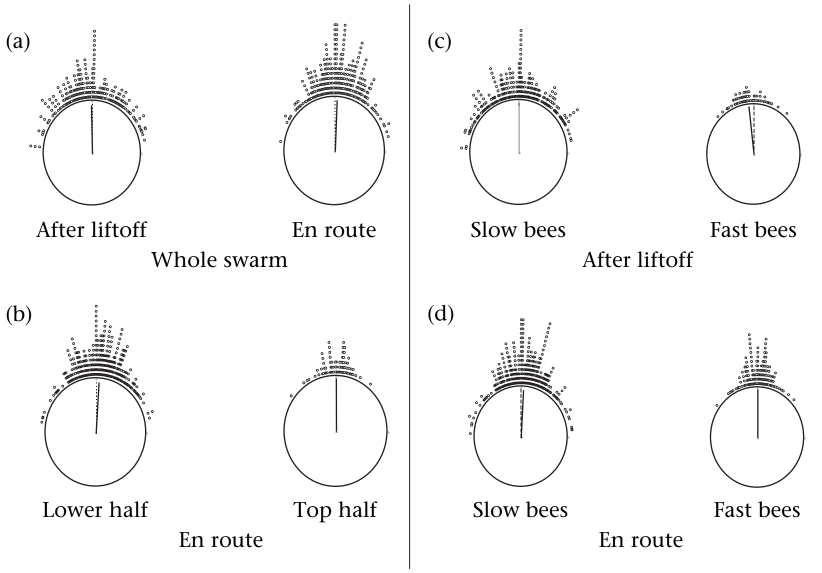

Figure 7. Circular distributions of the angles of the streaks in photographs S2a, b (Supplementary Material). A horizontal streak, produced by a bee flying directly towards the bait hive, is denoted by a dot in the direction of the dashed line (0°). Solid line: mean vector bearing (MVB). When the number of data points exceeded 350, a random sample of 350 data points was chosen to draw the plots. (a) Comparison between just after liftoff (MVB = 358.8, MVB length = 0.91) and while en route (MVB = 2.2, MVB length = 0.94), for the whole swarm. (b) Comparison between the top (MVB = 359.9, MVB length = 0.97) and bottom (MVB = 3.6, MVB length = 0.93) halves of the photograph of the swarm en route. (c, d) Comparisons between streaks shorter than 15 mm (Slow bees) and longer than 15 mm (Fast bees). (c) Slow bees: MVB = 359.4, MVB length = 0.90; Fast bees: MVB = 353.5, MVB length = 0.97. (d) Slow bees: MVB = 2.8, MVB length = 0.93; Fast bees: MVB = 0.0, MVB length = 0.97.

this possibility, but we found a gap of 2–4 min between when the front of a swarm stopped at the tree holding the bait hive and when many bees were landing at the entrance and scenting (Fig. 5). Thus the braking process seems to involve something other than the scout bees removing themselves from the swarm and flying ahead towards the new nest site. Supporting evidence is that swarms consistently began to slow themselves 30 m or more before reaching the bait hive (Figs 2, 4). Scouts are evidently able to cause the swarm to slow down well before they leave the swarm cloud to pinpoint the entrance opening of the new nest site. A possible mechanism by which this can be achieved is by simply slowing down without leaving the swarm (Janson et al. 2005).

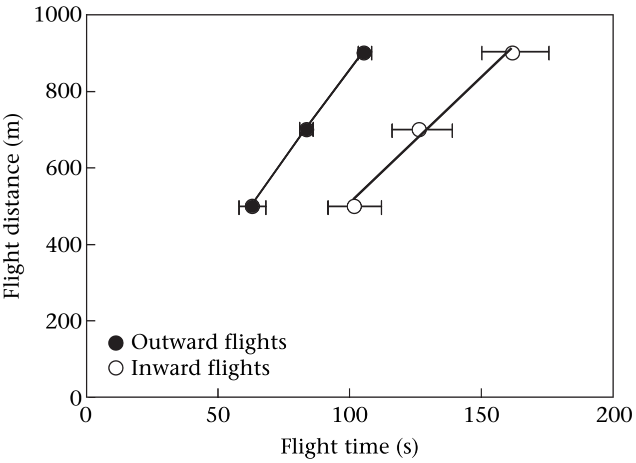

Figure 8. Regression lines showing the maximum flight speed for individual bees when empty (Outward flights) and after having foraged at a feeder (Inward flights) at 500, 700 and 900 m from the hive. The data points are the mean ± SD of 20 bees.

Another general finding is that the density of bees in a flying swarm is usually in the range of 20–60 bees/m^3, which implies that the average distance between bees is about 25–35 cm. This result relates to the theoretical study of swarm guidance by Janson et al. (2005). To test the vision hypothesis, Janson et al. assumed that scouts guide a swarm by flying repeatedly, slightly faster than uninformed bees, through the swarm's centre in the direction of their new home. Janson et al. then incorporated this assumption into a computer model of a flying swarm and ran simulated flights of their in silico swarms. In this model, the bees react to their nearest neighbours so that they avoid those that are too close while being attracted to other bees when the distance between neighbouring bees increases (these behavioural rules are general rules used in models of group movement). Swarm guidance is achieved by the bees aligning their movements with those of the bees within their neighbourhood. The scouts, by initially flying faster than uninformed bees, have more influence on the directional movement of the uninformed bees when the swarm has not yet started to move, thereby steering the swarm into the direction of the new home (as soon as the swarm has reached its maximum speed, the influence of the scouts is greatly reduced). In real swarms, however, the density of bees appears to be low, suggesting that an individual bee has relatively few neighbours to which it reacts. Furthermore, scouts in real swarms appear to be located mostly in the upper part of the swarm (and hence do not fly through the centre of the swarm as in the simulation model), which probably increases their visibility. By increasing their visibility the scouts increase the number of bees whose behaviour is influenced (i.e. increasing the number of bees in their neighbourhood), and doing this may have a similar effect as when the scouts fly through the centre of a swarm cloud.

Finally, a second recent theoretical paper has shown that the movement of an animal group can be guided by a few informed individuals without these individuals providing explicit guidance signals and even without anyone in the group knowing which individuals possess information about travel direction (Couzin et al. 2005). Couzin et al. presented a model of a moving group in which each individual attempts to maintain a personal space by turning away from neighbours within a certain range, and at the same time each individual attempts to move in a preferred direction, if it has one. In this model, only the informed members of the group have a preferred direction, and their tendency to go in this direction steers the group. Couzin et al. found that the proportion of informed individuals needed for accurate directional guidance of the group is potentially small, less than 10%. This theoretical study offers a variant of the vision hypothesis for the mechanism of swarm guidance in honeybees, in which the scouts do not produce a visual signal (i.e. streaking) to steer a swarm, but instead simply tend to fly in the direction of the chosen nest site. We call this the 'subtle guide' version of the vision hypothesis. A logical next step in the study of honeybee swarm guidance would be to test experimentally the streaker bee and subtle guide forms of the vision hypothesis. It will be interesting to see if natural selection has or has not favoured the use of signals by the informed minority of scouts as they guide a honeybee swarm to its new home.

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SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2005.04.009

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