Naturwissenschaften (2013) 100:805–809
DOI 10.1007/s00114-013-1077-7

SHORT COMMUNICATION

Scouts behave as streakers in honeybee swarms

Uwe Greggers · Caspar Schöning · Jacqueline Degen · Randolf Menzel

Received: 19 February 2013 / Revised: 17 June 2013 / Accepted: 18 June 2013 / Published online: 28 June 2013

Abstract Harmonic radar tracking was used to record the flights of scout bees during takeoff and initial flight path of two honeybee swarms. One swarm remained intact and performed a full flight to a destination beyond the range of the harmonic radar, while a second swarm disintegrated within the range of the radar and most of the bees returned to the queen. The initial stretch of the full flight is characterized by accelerating speed, whereas the disintegrating swarm flew steadily at low speed. The two scouts in the swarm displaying full flight performed characteristic flight maneuvers. They flew at high speed when traveling in the direction of their destination and slowed down or returned over short stretches at low speed. Scouts in the disintegrating swarm did not exhibit the same kind of characteristic flight performance. Our data support the streaker bee hypothesis proposing that scout bees guide the swarm by traveling at high speed in the direction of the new nest site for short stretches of flight and slowing down when reversing flight direction.

Keywords Honeybee swarm · Nest-site scouts · Harmonic radar tracking · Flight guidance

Introduction

Honeybee colonies reproduce by forming swarms. Usually, the old queen leaves the hive with about 75 % of the worker bees, forming a swarm that temporarily settles nearby before departing to a new nest site (Rangel and Seeley 2012). A new nest site needs to be found by scout bees (Lindauer 1955; von Frisch 1967). These scouts advertise for the respective nest site, taking into account its size, quality, and distance (Seeley 1977). If the scouts find more than one nest site, the decision-making process may last for hours, or sometimes even days, until a quorum is reached (Seeley and Visscher 2004). The intriguing behavioral phenomena of judging nest-site quality, the decision-making process, and the guidance of the swarm towards the new home have been explored most successfully by Seeley and co-workers over the last 35 years (Seeley 2010; Schlegel et al. 2012). Scout bees play a key role in these processes. Lindauer (1955), Gilley (1998), and Beekman et al. (2006) estimated that less than 5 % of the bees in the swarm belong to the group of informed bees, the scouts, when the swarm heads off towards the new nest site, prompting the question of how such a small number of bees can guide a swarm of usually several thousand. Back in 1955, Lindauer had already proposed that scouts guide by flying faster than the other bees in the swarm, signaling to the uninformed bees whom to follow. This proposal is known as the "streaker bee" hypothesis (Beekman et al. 2006), and it stands in contrast to the "subtle guide" hypothesis (Couzin et al. 2005) which suggests that the scouts steer the swarm by simply tending to move in the direction of the new home. The streaker bee hypothesis has gained support from a number of elegant experiments in which the flights of single bees within the swarm were photographed or video-recorded (Beekman et al. 2006; Schultz et al. 2008) during short stretches of the swarm's flight. The analysis of these pictures showed that most of the bees within the swarm fly rather slowly and erratically while a small number of bees perform as streakers, flying faster when directing towards the new nest site. Beekman et al. (2006) and Schultz et al. (2008) concluded that these streakers are the scouts, those bees that had discovered the new nest site and had danced for it before the swarm took off. But since they could not identify the scouts individually within the flying swarm, their conclusion, although compelling, should be considered tentative.

The streaker bee hypothesis would be supported if one could show that the individuals identified as scouts perform as predicted, namely flying at high speed when directing

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-013-1077-7) contains supplementary material, which is available to authorized users.

U. Greggers · C. Schöning · J. Degen · R. Menzel (✉)
Freie Universität Berlin, Berlin, Germany
e-mail: menzel@neurobiologie.fu-berlin.de

towards the new nest site and slower when changing direction. Such data can be collected when scouts within a flying swarm are tracked individually using harmonic radar for flight tracking. These data also allow an estimation of the speed of flight in the whole swarm as it develops after takeoff. Furthermore, one can examine the behavior of scouts in a swarm which has lost its queen, a situation which leads to disintegration of the swarm and initiation of searching flights for the queen. Here, we report the flight behavior of scouts in these two situations. Our results support the streaker hypothesis of swarm guidance.

Methods

Experimental procedures and data collection

The study site was located near Klein Lüben (Brandenburg, Germany, approx. 150 km northwest of Berlin). Artificial swarms of honeybees (*Apis mellifera*) were prepared as described by Seeley (2003). In short, a small colony (about 5,000 bees) was fed by providing sucrose solution inside the hive. The next day, the size of the hive box was reduced and the queen was captured and caged, and 2 days later, the bees were shaken into a box with an ample supply of sucrose solution. The box was kept in the dark for 1–2 days. Then, the bees were shaken onto the ground in front of a vertical wooden post with a flat board nailed to the top to which the caged queen was fixed. The bees quickly assembled around the queen. Sucrose solution was supplied via a container attached to the wooden board. In one swarm, the wings of the queen were clipped in order to cause the swarm to return to the queen after takeoff. Scouts finding a natural nest site were identified by their dances, and some of these scouts were equipped with a radar transponder. The method for building radar transponders, fixing them to the bee and tracking them with the harmonic radar, has already been described in Riley and Smith (2002), Riley et al. (2005), and Menzel et al. (2005, 2011). Due to the fact that the flights of the two transponder-carrying scouts in each swarm crossed from time to time, the signals from the transponders could not be related with certainty to one or the other animal throughout the entire flight track, but along stretches between such cross points. The range of the harmonic radar was 900 m. Since the swarm was set up 650 m away from the radar in a northerly direction and the swarm took off in the same direction away from the radar, the scouts were tracked over a flight distance of about 200 m. Radar tracking allows only for two-dimensional locations. No information is available about height over ground. The spatial resolution of the harmonic radar signal was improved by calculating for each "paint" (the distribution of radar signal) the point of highest signal intensity. This procedure allowed us to localize signals to a 4 m radius.

Results

The two swarms were prepared at an interval of 10 days. Two days after setting up the artificial swarms, all scouts in both swarms reached a quorum and danced predominantly for a nest site about 1,500 m in a northerly direction. Two scouts in each swarm were equipped with transponders immediately after dancing either late on the first day or early on the second day (5 to 7 h before the swarm took off). Thereafter, they did not perform any additional inspection flights, but in some cases continued dancing. The first swarm performed a full flight, whereas the second swarm returned to the starting point after an excursion of about 150 m in a northerly direction, because the queen's wings had been trimmed in an attempt to force the swarm to disintegrate. We hypothesized that under such conditions, the scouts may perform differently.

Figure 1a, b presents the flight tracks of the two scouts in each of the two swarms as recorded with the harmonic radar, and Fig. 1c, d shows the flight speed of these scouts. The flight performance of the scouts in swarm 1 was more directed than that of the scouts in swarm 2. The flights of the scouts in swarm 2 back to the starting site are not shown. The flight speed of the scouts in swarm 1 accelerated whereas that of the scouts in swarm 2 was low and constant. Since we had no separate measure of the movement of the swarms, we fitted a polynomial function to the respective tracks of both scouts in the two swarms. The polynomial of the fit for swarm 1 is close to a parabolic function (Fig. 1c), while that of swarm 2 was close to a linear function (Fig. 1d). These functions were interpreted as the average positions of the respective swarm. The animation of Fig. 2a, b (in the Supplementary Material) allows reading the instantaneous deviations between these functions and the tracks of the individual scout.

The initial flight phase is characterized by multiple loops with little forward movement in both swarms. Then, the scouts in swarm 1 performed faster forward-directed flights interrupted by usually slower and shorter return flights or rather stationary loops. A total of at least four clearly faster forward-directed flight stretches were identified for each scout (Fig. 2a). The distributions of the flight speed of flight components are shown for both scouts in Fig. 2a, b. Forward-directed flight components are faster than backward-directed components. Zero flight speed indicates that the scouts moved within the radius of spatial resolution during the 3-s detection intervals of the harmonic radar. The high frequency of no and very slow movements of scouts indicates that they stay in close contact to the swarm. The scouts in swarm 2 performed only one to two such faster forward-directed flight components and flew in multiple turns with about equal speed in most of the forward- and backward-directed components (compare the animations in the Supplementary Material).

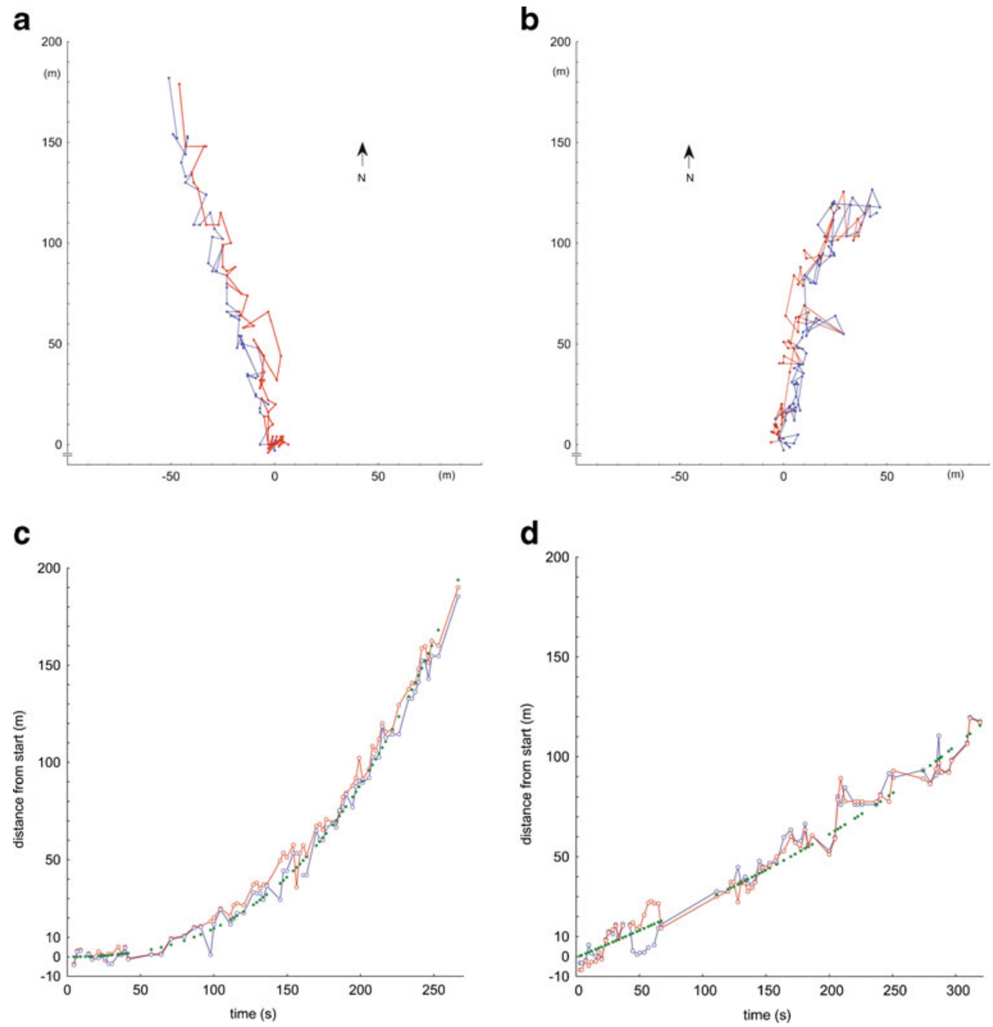

Fig. 1 Flight patterns of the two transponder-equipped scouts in each of the two swarms. Notice that the assignment of the radar signals to one or the other individual scout is arbitrary at those locations where the signals overlap. **a**, **b** Flight trajectories of the two scouts in swarm 1 (**a**) and swarm 2 (**b**) as recorded with the harmonic radar. Each point represents the location of a radar signal. The flight paths in swarm 2 were interrupted due to the disappearance of the scouts behind a small cabin. **c**, **d** Flight speed of the two scouts in each of the two swarms. Swarm 1 (**c**) accelerates its speed. The *dotted line* gives the best fit of a polynomial function for the averaged flight speeds of the two scouts. The speed increases from close to zero to a value of up to 1.6 m/s at the end of the tracks. Swarm 2 (**c**) performed a rather steady and slow movement (.33 m/s) and returned to the starting position where the queen had remained since she could not fly. The *dotted line* indicates the interruption of signal detection

Discussion

Flight tracking with harmonic radar provides advantages but also limitations. One advantage is that an individual bee can be followed over distances of up to 2.6 km, depending on flight direction relative to the radar station. Disadvantages relate to spatial and temporal resolution and to the separation between radar signals if more than one bee is marked with a transponder. Temporal resolution is limited by the rotation of the radar screen (20 rpm), and spatial resolution is limited by the size of the radar paint. Here, we improved spatial resolution to a 4 m radius. No flight advance will be measured if narrow loops are performed within the temporal/spatial resolution of the radar technique. Such narrow loops were frequently seen in the four scouts radar tracked here. Since two bees in each swarm were equipped with a transponder, the individual flight paths could not be separated when their flight trajectories crossed. This limitation prompted us to follow two scouts and not one scout and one non-scout swarm member because we are not able to distinguish between the two flight tracks if they cross. Irrespective of these limitations, scouts of swarm 1 clearly performed several faster forward-directed flights, slower backward-directed flights, and less looping flights with little or no gain of distance within the resolution of our radar technique, whereas those of swarm 2 performed only one or two faster forward-directed flights and many more backward-directed and looping flights.

These results support the streaker bee hypothesis (Beekman et al. 2006; Schultz et al. 2008) and not the subtle guide hypothesis (Couzin et al. 2005), helping us to distinguish between the two hypotheses of swarm flight guidance currently discussed intensively (Couzin et al. 2005; Seeley 2010). According to the streaker bee hypothesis, a small number (2–4 %) of informed bees (scouts) guide the swarm by conspicuous behavior, namely fast streaks of flight components that are directed towards the goal, whereas the subtle guide hypothesis allows for the possibility that informed members of the swarm do not identify themselves by conspicuous behavior. Streaking behavior in bee scouts was observed by Beekman et al. (2006)and Schultz et al. (2008)

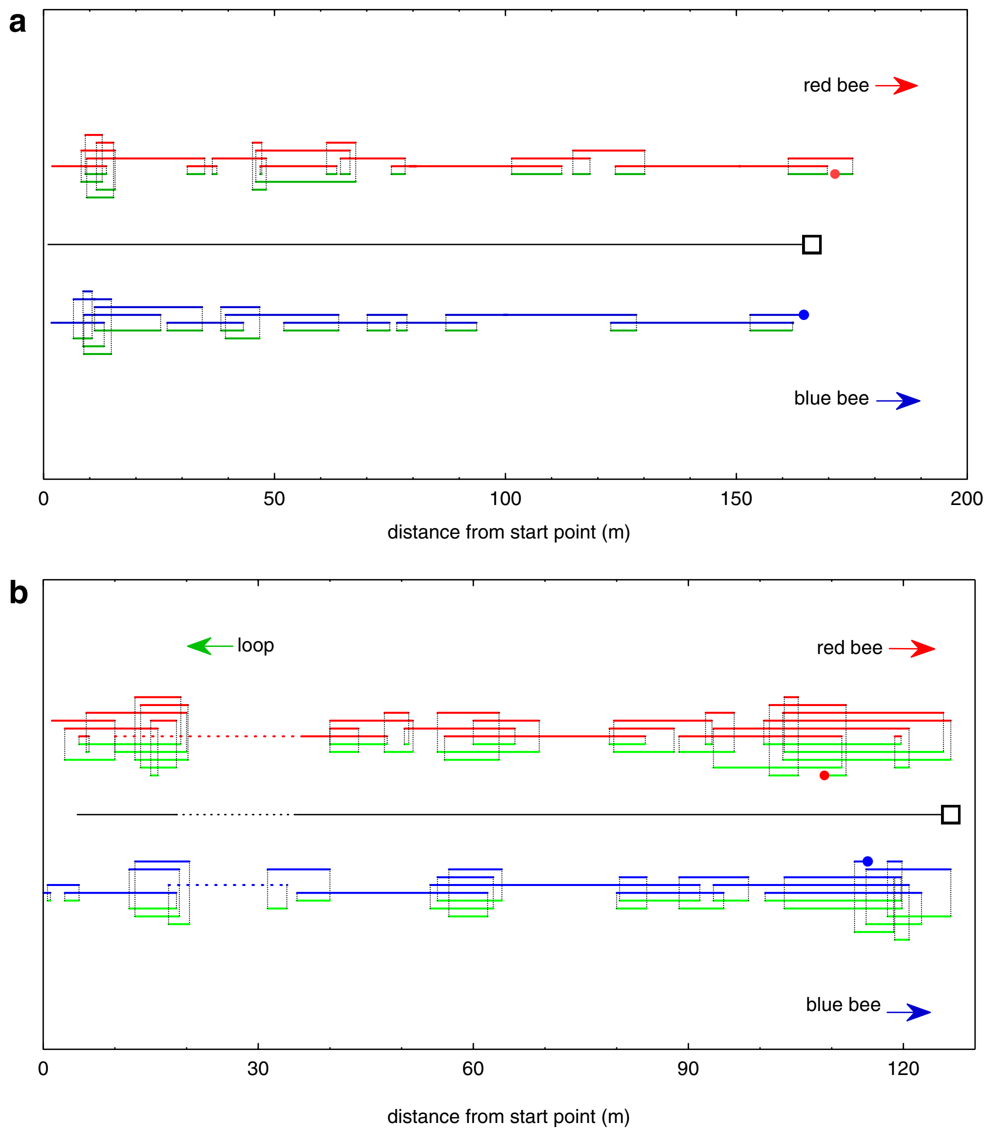

Fig. 2 Flight performance of the two scouts in swarm 1 (**a**) and swarm 2 (**b**). Sequences of forward- and backward-directed flight components of the respective two scouts (*red* and *blue*). The *red and blue lines* indicate forward-directed flight components; the *green lines* represent the backward-directed flight components. These figures are animated in the Supplementary Material

predominantly at the forefront and in the higher levels of the swarm cloud, and it was logical to conclude that they are performed by scouts. Here, we show that streaking behavior is indeed performed by scouts that were identifiable by their dances. The streaking behavior is particularly characteristic if they guide an integrated swarm including the queen. Fast flight streaks require the scout to slow down and/or fly backwards in order not to lose contact to the slowly advancing swarm. We observed both behaviors. The number of streaks performed by individual scouts seems to be small; both of the scouts that we examined in detail in swarm 1 only produced at least four streaks each within the first 200 m of the swarm's flight. As the flight animation shows (Supplementary Material), the streaks of the two scouts may happen at roughly the same time or at different times. It has been assumed in a model calculation of group movement that guiding behavior by informed members would be most effective during the initial phase of movement when most of the animals have not yet taken up a predominant travel direction (Janson et al. 2005). This assumption is not supported by our data. The scouts performed their most obvious streaks at a time when the integrated and fully performing swarm has taken up its travel direction. However, it might well be that the initial streaks are much shorter than those performed later and may be subject to the limitations of temporal–spatial resolution of our radar technique. Indeed, if streakers would make long streaks at a time when the swarm assembles and advances very slowly, they would lose contact with the swarm cloud.

Acknowledgments The study was supported by DFG grant Me 365/34-1, the Dr. Klaus Tschira Stiftung, and the Gemeinnützige Hertie Stiftung. We are most grateful to Prof. W.D. Haass and Dipl.-Ing. B. Fischer for constructing and building the harmonic radar device. We are most grateful to the anonymous reviewers for their most helpful comments.

References

Beekman M, Fathke RL, Seeley TD (2006) How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? Anim Behav 71:161–171

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433(7025):513–516

Gilley DC (1998) The identity of nest-site scouts in honey bee swarms. Apidologie 29:229–240

Janson S, Middendorf M, Beekman M (2005) Honeybee swarms: how do scouts guide a swarm of uninformed bees? Anim Behav 70(349):458

Lindauer M (1955) Schwarmbienen auf Wohnungssuche. Z vergl Physiol 37:263–324

Menzel R, Greggers U, Smith A, Berger S, Brandt R, Brunke S, Bundrock G, Huelse S, Pluempe T, Schaupp F, Schuettler E, Stach S, Stindt J, Stollhoff N, Watzl S (2005) Honeybees navigate according to a map-like spatial memory. Proc Nat Acad Sci USA 102(8):3040–3045

Menzel R, Kirbach A, Haass W-D, Fischer B, Fuchs J, Koblofsky M, Lehmann K, Reiter L, Meyer H, Nguyen H, Jones S, Norton P, Greggers U (2011) A common frame of reference for learned and communicated vectors in honeybee navigation. Curr Biol 21:645–650

Rangel J, Seeley TD (2012) Colony fissioning in honey bees: size and significance of the swarm fraction. Insect Soc 59:453–462

Riley JR, Smith AD (2002) Design considerations for an harmonic radar to investigate the flight of insects at low altitude. Comput Electron Agric 35:151–169

Riley JR, Greggers U, Smith AD, Reynolds DR, Menzel R (2005) The flight paths of honeybees recruited by the waggle dance. Nature 435(7039):205–207

Schlegel T, Visscher PK, Seeley TD (2012) Beeping and piping: characterization of two mechano-acoustic signals used by honey bees in swarming. Naturwissenschaften 99(12):1067–1071

Schultz KM, Passino KM, Seeley TD (2008) The mechanism of flight guidance in honeybee swarms: subtle guides or streaker bees? J Exp Biol 211(Pt 20):3287–3295

Seeley TD (1977) Measurement of nest cavity volume by the honey bee (*Apis mellifera*). Behav Ecol Sociobiol 2:201–227

Seeley TD (2003) Consensus building during nest-site selection in honey bee swarms: the expiration of dissent. Behav Ecol Sociobiol 53(6):417–424

Seeley TD (2010) Honeybee democracy. Princeton University Press, Princeton

Seeley TD, Visscher PK (2004) Quorum sensing during nest-site selection by honeybee swarms. Behav Ecol Sociobiol 56:594–601

von Frisch K (1967) The dance language and orientation of bees. Harvard University Press, Cambridge