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SHORT COMMUNICATION

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Thorough warm-up before take-off in honey bee swarms

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Abstract In a bivouacked swarm of honey bees, most individuals are quiescent while a small minority (the scouts) are active in choosing the swarm's future nest site. This study explores the way in which the members of a swarm warm their flight muscles for take-off when the swarm eventually decamps. An infrared camera was used to measure the thoracic (flight muscle) temperatures of individual bees on the surface of a swarm cluster. These are generally the coolest bees in a swarm. The warming of the surface-layer bees occurred mainly in the last 10 min before take-off. By the time a take-off began, 100% of the bees had their flight muscles heated to at least 35°C, which is sufficient to support rapid flight. Take-offs began only a few seconds after all the surface-layer bees had their flight muscles warmed to at least 35°C, but exactly how take-offs are triggered remains a mystery.

Introduction

After leaving its parental nest, a honey bee swarm usually spends a few days hanging from a tree branch in a beard-like cluster while its scout bees select a suitable nesting cavity (Lindauer 1955; Seeley and Buhrman 1999). During this time, the vast majority of the 10,000 or so bees in a swarm remain quiescent to conserve the swarm's energy reserve: the 30–40 mg of rich sugar solution carried inside each bee (Combs 1972). As was shown by Heinrich (1981), the bees in the core of a cluster maintain a 30–40°C microclimate, by trapping the metabolic heat produced by the resting bees and by adjusting the cluster's porosity to control its rate of heat loss. Meanwhile, the outermost bees in a cluster maintain themselves above a relatively low set-point of 15°C (Heinrich 1981), thus minimizing their energy expenditure for heat production but at the same time keeping their flight muscles warm enough to generate heat by shivering (Esch 1988).

This is comparable to the distribution of temperatures of bees in a hive, where workers in the core (the sealed brood area) maintain high thoracic temperatures to warm the pupae while workers in the periphery maintain lower temperatures (Esch 1960; Bujok et al. 2002; M. Kleinhenz et al., unpublished).

Once the scout bees in a swarm have chosen a home site, the swarm decamps in a dazzling display of coordinated group behavior. All the bees in the swarm cluster launch into flight in about 60 s, form a cloud of swirling bees, and begin moving off together, with the scouts somehow guiding all the others to their new dwelling place (Seeley et al. 1979, reviewed by Dyer 2000). Given that a worker bee needs a flight muscle temperature of at least 33–35°C for rapid flight (Esch 1976; Heinrich 1979), it is not surprising that several investigators have reported that during the 10–30 min before take-off the temperature gradient in a swarm cluster becomes abolished such that the bees in the cluster's mantle become as warm as those at its core (Heinrich 1981; Seeley and Tautz 2001). The warming of the mantle bees is evidently stimulated by mechanical piping signals produced by scout bees running over and through these bees (Seeley and Tautz 2001), and is a result of the bees generating heat by shivering (Esch et al. 1991). In this paper, we describe how the bees in a swarm cluster warm themselves in preparation for take-off.

Materials and methods

The main investigations were carried out at the University of Würzburg in June 2002. Two artificial swarms of *Apis mellifera carnica*, each consisting of a mated queen and 1.0 kg of worker bees (approximately 7,500 individuals), were prepared using the

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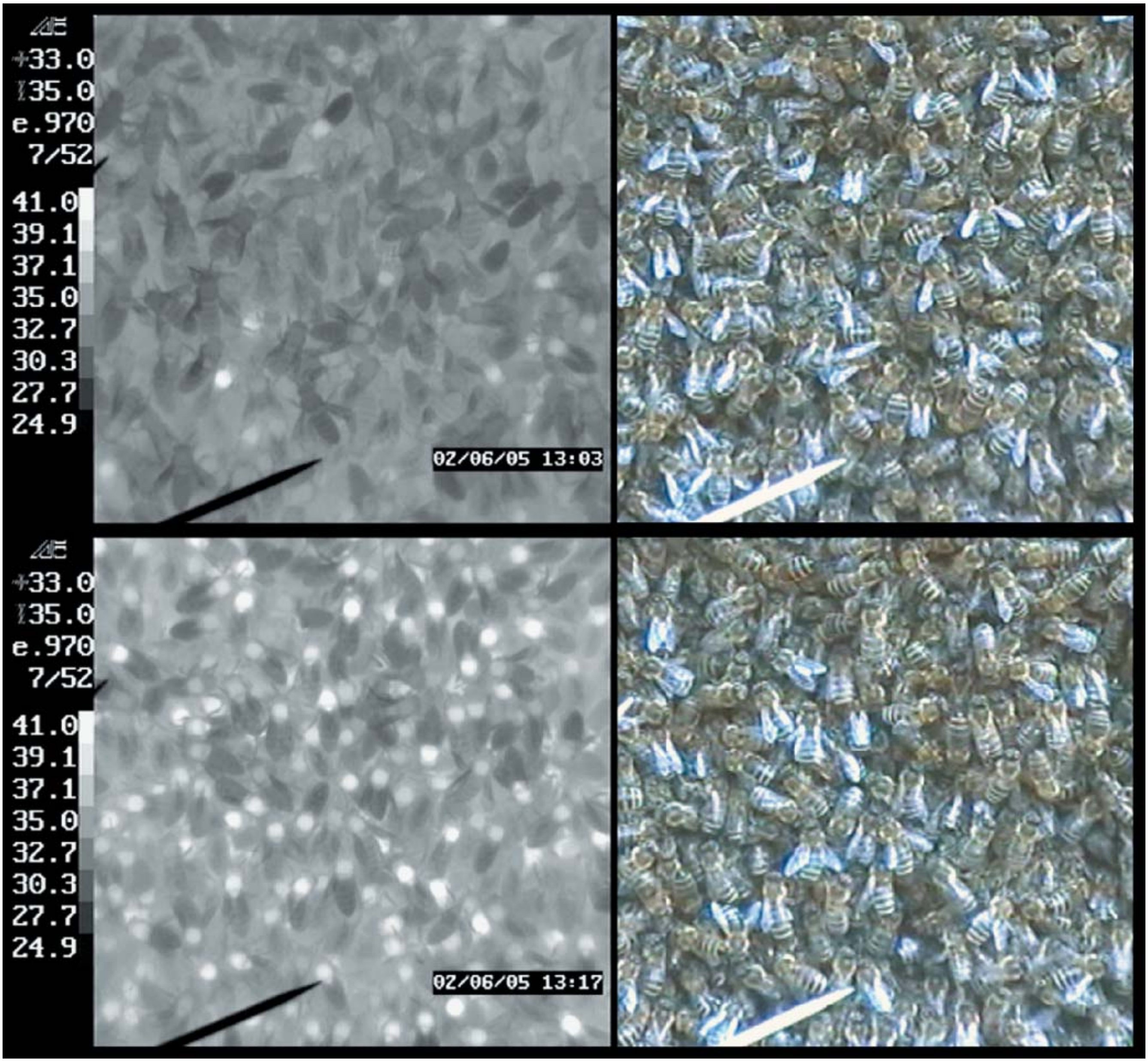

Fig. 1 Bees on the surface of a honey bee swarm when viewed with infrared video camera (*left*) and standard video camera (*right*). The top pair of images was made 15 min before the start of take-off; the bottom pair was made only 1 min before the start of take-off. Although the standard camera images taken at different times do not appear different, the infrared camera images do. Shortly before take-off, but not 14 min earlier, the thoraces of all bees on the swarm's surface glowed with a temperature ≥35°C

standard method of placing a queen in a small cage, hanging this inside a larger cage holding the workers, and feeding the confined bees copiously with sugar syrup for several days, until wax scales drop from the workers, indicating that they are primed for setting up a new domicile (details in Seeley and Tautz 2001). Both swarms were prepared on 31 May. On 4 June, swarm 1 was placed on a swarm mount of the design described previously (see Fig. 1; Seeley and Buhrman 1999). This swarm performed two take-offs, one on 5 June and another on 8 June. Immediately after its second take-off, swarm 1 was transferred to a hive and swarm 2 was placed on the swarm mount. It performed a take-off on 9 June. In both cases, the swarm's queen was kept caged on the swarm mount so that the swarm would return after taking off.

We made thermographic measurements of the bees composing the outer surface of the swarm cluster during the final 30 min before each take-off. The bees within a 10×10 cm area were recorded simultaneously with a camcorder and an infrared videocamera [Radiance PM1/1.5.1b, Raytheon Amber; wavelength range = 3.5–5.6 μm, emissivity value = 0.97, suitable for the bee thorax (Stabentheiner and Schmaranzer 1987), accuracy = ±0.7°C]. Single frames from the infrared videocamera recordings were captured by a computer every 30 s. The thorax surface temperature of each discernible bee was calculated from each single frame using camera-specific software (Ambertherm 1.28) and the temperature scale of the infrared images. No measurements were possible if a bee's thorax was shielded by other bees. The swarm board and the thermographic camera were shielded from direct sunlight to avoid disturbance of the temperature measurements. Control measurements with thermistors (Almemo 2290-8; Ahlborn, Holzkirchen, Germany, accuracy = ±0.1°C) on dead and artificially heated bees (thorax temperatures from 18 to 32°C; *n*=12) that were placed at the edge of the swarm board confirmed the accuracy of the thermographic measurements in the range stated above.

We used a thermistor probe to measure the ambient temperature. This probe was placed on the swarm mount, within 5 cm of the bottom edge of the swarm cluster.

Additional work was conducted at Cornell University in June and July 2002, in order to determine the time required by bees in a swarm cluster to complete a take-off. Five artificial swarms of *Apis mellifera ligustica* were prepared and placed on a swarm mount as described above, and their take-off times were measured. We did so by measuring the time interval from when bees began to take flight to when fewer than ten bees remained on the swarm mount. The lingering bees remained on the queen cage, apparently attempting to stimulate the caged queen to take flight. Hence it seemed appropriate not to take them into account when measuring take-off times. The time needed for take-off was measured twice for each swarm, during two separate take-offs. All values are the mean ± SD.

Results

During the final 30 min preceding each take-off, we observed the usual set of events (not presented in detail in this work, see Seeley and Buhrman 1999; Seeley and Tautz 2001): the waggle dancing by the scout bees became unanimous, with all dances denoting the chosen nest site; the piping by the workers went from a pattern of faint, occasional signals to one of loud, continuous signals; the temperature in the swarm cluster's mantle rose to match that in its core; and during the final minute the bees in the cluster began to crawl about instead of hanging quietly. The images from the infrared videocamera revealed yet another dramatic dynamic: shortly before take-off, the thoraces of all the bees composing the surface layer of the swarm cluster began to "glow", indicating unusual warmth (Fig. 1).

The warm-up pattern by the bees in the surface layer of each swarm is shown in Fig. 2. We see that initially, in both swarms, the mean thoracic temperature was less than 32°C and that less than 10% of these bees had a thoracic temperature ≥35°C, and hence were ready for take-off and rapid flight. The video records indicated that the few individuals with such hot thoraces were ones that either had recently landed on the swarm cluster or were about to fly off it. Presumably they were scout bees. We also see that the mean temperature of the surface-layer bees rose slowly but steadily during the final 30 min before take-off. Likewise, the percentage of surface-layer bees with

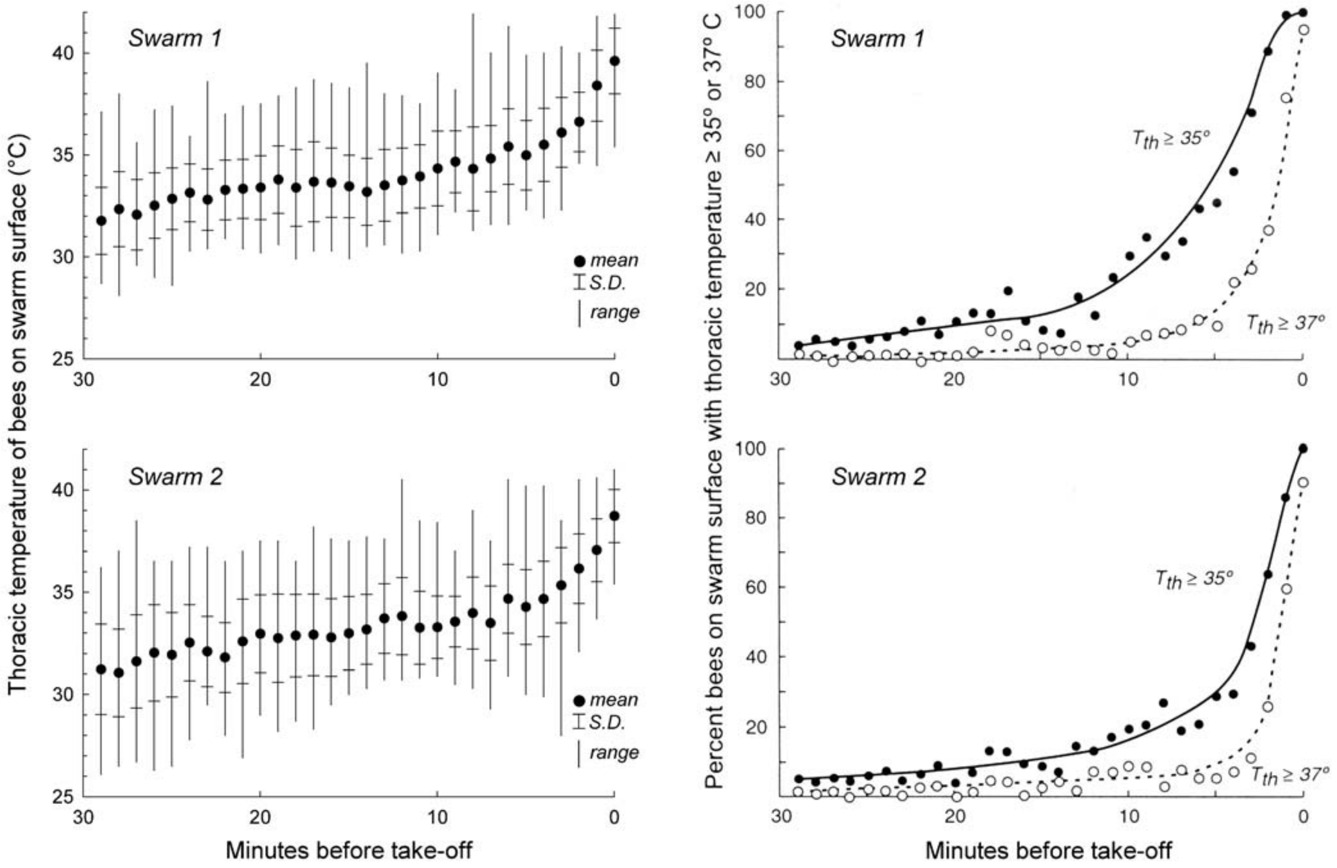

Fig. 2 Two time courses of thoracic temperature increase for bees on the surface of a swarm. Every minute, for 30 min before the start of take-off, we determined the thoracic temperature of every bee visible in a 10×10 cm infrared image (see Fig. 1), i.e., 75±12 bees per image. *Left:* The plot for each minute shows the mean ± 1 SD and the range of the thoracic temperatures. *Right:* The plot for each minute shows what percentage of the bees had a thorax temperature ≥35°C or ≥37°C. For a worker bee, a thoracic temperature of 35°C is needed to support rapid flight. The ambient temperature was 21.5–22.2°C for swarm 1 and 20.6–22.6°C for swarm 2

thorax warmed sufficiently for flight rose slowly but remained low, less than 20%, until 10 min before take-off, when this percentage began to rise faster and faster. Ultimately, when take-off began, the mean thoracic temperature was 39.6°C (swarm 1) or 38.7°C (swarm 2). Also, fully 100% of the surface-layer bees had a thoracic temperature of at least 35°C, and nearly 90% had a thoracic temperature even greater than 37°C. Moreover, in both cases, the thoracic temperature of the queen, measured as soon as she was exposed (in her cage) by the departing workers, was over 40°C: namely 40.7°C and 41.1°C.

To determine whether the rapid rise in number of hot bees in the surface layer of a swarm cluster is produced by interior bees moving out to the surface or by surface-layer bees warming themselves in place, we followed hot, surface-layer bees back in time on the video records. In the final minute before liftoff, there is much movement by the surface bees, so we examined bees starting at a point 1 min before take-off. We traced the histories of 25 surface-layer bees with a thoracic temperature >39°C on swarm 1, and found that only two of these bees had crawled out of the interior of the swarm cluster (8±8 s earlier). Of the other 23 bees, two had recently landed on the swarm surface (6±4 s earlier), seven had crawled across the swarm's surface from a location outside the camera's field of view (7±4 s earlier), and 14 had warmed themselves on the surface of the swarm from a temperature <35°C (34±23 s earlier). These 14 individuals were scattered over the videocamera's field of view; hence there was no sign of there being special nodes of warming bees in the surface layer. We noticed too that most of the hot, surface-layer bees had cool (<30°C) abdomens (see Fig. 1), as would be expected if they had warmed their thoraces while standing in the cool, outermost layer of the swarm cluster but not if they had recently emerged from the hot core of the cluster. It seems clear, therefore, that the rapid rise in number of hot bees in the surface layer of a swarm cluster comes about mainly by surface-layer bees warming themselves in place.

Once a swarm had begun its take-off, the process went quickly to completion. Swarms needed only 68±13 s (range 46–90 s, n=10) to become airborne.

Discussion

Prior studies of thermoregulation in honey bee swarms, which have been based on temperature measurements of the air between bees, have revealed that in the final few minutes before a take-off there is a marked rise to 34–38°C in a swarm's mantle temperature (Heinrich 1981; Seeley and Tautz 2001). The temperature measurements of this study are in good agreement with those of the earlier studies. However, because the present measurements are of the thoracic temperatures of individual bees, they show more clearly and directly than before just how thoroughly the bees in a swarm's mantle warm their flight muscles in preparation for take-off. We see that even though the warming of the surface-layer bees occurs mainly in the last 10 min before take-off, by the time take-off starts 100% of these bees have their flight muscles well warmed for rapid flight. [Strictly speaking, our thermographic measurements indicate the *thorax surface* temperatures of the bees, not their *flight muscle* temperatures. Although it is true that in moving air, where there is forced convection, a bee's thorax surface temperature tends to be 1–1.5°C cooler than its flight muscle temperature (Feller and Nachtigall 1989), because the bees we examined were warming themselves in still air, our measurements of the bees' thorax surface temperatures accurately indicate their flight muscle temperatures (Esch 1960).]

Because we used an infrared camera to make our temperature measurements, our results (Figs. 1 and 2) provide direct information about only the bees in the surface layer of a swarm cluster. Nevertheless, it seems reasonable to infer that by the time the outermost bees were suitably warm for rapid flight, the inner bees were too. Three lines of evidence support this inference. First, the early work of Heinrich (1981) showed that the temperature of a swarm's core is generally 30–40°C, hence the body temperatures of the core bees are almost always at temperatures suitable for flight. Second, the images from our infrared camera showed that as a swarm approached the start of take-off, the interior bees began to shine brightly before the surface bees did, looking like hot coals glowing beneath a layer of cool ashes. And third, we observed that almost immediately after a take-off began (i.e., when the surface-layer bees had taken flight), the inner bees began to take flight. Indeed, it is because there is little delay between outer and inner bees taking flight that the time needed for an entire swarm to become airborne is only about 60 s.

One of the more striking features of our results is the way that the swarms' take-offs began only a few seconds after 100% of the surface-layer bees had warmed their flight muscles to at least 35°C. It seems, therefore, that having all the surface bees suitably hot is part of the trigger mechanism for take-off. But how exactly does this trigger mechanism work? Does each individual on a swarm's surface monitor the thoracic temperatures of her neighbors and launch into flight once she senses that she and her neighbors are all sufficiently hot? Do certain individuals (scout bees?) scurry over the swarm's surface, assessing the thoracic temperatures of the bees there, and release a take-off signal when they sense that every bee is good and hot? The solution to this particular mystery of honey bee swarms must await further study.

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