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Research article

Self-assemblage formation in a social insect: the protective curtain of a honey bee swarm

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Summary. This paper considers a little-studied topic in the biology of social insects: the formation of self-assemblages. It focuses on the mechanisms whereby the outermost workers in a bivouacked swarm of honey bees, when rained upon, form a water repellent curtain of bees over the swarm cluster. Specifically, we analyzed how the worker bees in the mantle of a swarm cluster adjust their body orientation, wing spread, and inter-individual spacing to form a protective curtain when wetted. When warm and dry, the mantle bees orient their bodies weakly with respect to gravity, do not tuck their heads under adjacent bees, have high variability in wing spread, and space themselves widely. In contrast, when warm and wet, the mantle bees orient uniformly with head upward, tuck their heads beneath the abdomens of bees above, hold their wings together, and press tightly together. This produces a surface that closely resembles a tiled roof. When cool and dry, the mantle bees generally orient their bodies with head upward, press their heads into the interior of the cluster, hold their wings wide apart, and draw close together. We also examined the age distribution of the mantle bees. Older bees are more likely than younger bees to be found in the mantle of a swarm, perhaps because younger bees are more important than older bees to colony survival after swarming and so occupy a more sheltered position in a swarm. Finally, we tested whether swarm clusters that have formed a protective curtain shed water more effectively than ones that have not formed a curtain. We found that this is the case.

Key words: Apis mellifera, curtain, honey bees, self-assemblage, swarming.

Introduction

Recently, Anderson et al. (2002) introduced an important concept for the study of social insects: the self-assemblage. They define a self-assemblage as a “physical structure comprised of individuals that have linked themselves to one another.” For example, when a colony of Japanese honey bees (*Apis cerana*) is attacked by a large predatory hornet (*Vespa mandarina*), four to five hundred bees will form a tight ball around the hornet and will raise the temperature inside the ball sufficiently to kill the hornet (Ono et al., 1987, 1995). The functions of self-assemblages are diverse and include defensive doorway plugs, as in *Colobopsis* ants (Wilson, 1971: pp. 159–160); temporary shelters, as in army ant bivouacs (Schneirla, 1971: p. 58; Franks 1989); pulling chains for predation or nest construction, as in *Azteca* ants (Morais, 1994) and weaver ants (Ledoux, 1950; Hölldobler and Wilson, 1990: pp. 618–629); and rafts to escape flooding, as in fire ants (Morrill, 1974; Jaffe, 1993). Self-assemblages can be viewed as intermediate-level parts in a social insect colony (Anderson and McShea, 2001a, b), just as organs and tissues exist as intermediate-level parts in an organism (McShea and Venit, 2001). An intriguing question about self-assemblages is how they are formed, but so far little attention has been paid to this subject (Anderson et al., 2002). The present study clarifies the mechanisms of formation of one type of self-assemblage: the protective curtain of a honey bee (*Apis mellifera* L.) swarm cluster that appears when the outermost bees become wetted by rain.

A honey bee swarm arises when a group of some 10,000 worker bees and a queen bee leave a hive to start a new colony. Shortly after leaving the hive, the bees assemble in a beard-like cluster that usually hangs from a tree branch. A few hundred scout bees fly from this cluster, locate a suitable nest site, and eventually lead the swarm to its new domicile. The swarm cluster is made up of interconnected, stationary bees with passageways between them that are used by mobile bees traveling between the cluster’s core and its mantle (Heinrich, 1981a). The configuration of bees on the surface (mantle) of a swarm cluster is known to change as a function of weather conditions (see Fig. 1a, b). In cool and dry weather, the mantle bees cluster tightly and point their heads inwards (Heinrich 1981a, 1993). The interior pas-

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sageways are filled, reducing the cluster's porosity and thus the convective heat loss from the swarm. This protects the swarm from low temperatures and reduces the rate at which the bees drawn down their energy reserves to generate heat (Heinrich, 1981b). In contrast, in hot and dry weather, the bees increase their spacing, thereby increasing the volume of the swarm cluster, and form channels within the cluster where fanning may occur (Heinrich, 1981a, b; Camazine et al., 2001).

The most striking configuration of the mantle bees arises in warm and rainy weather. When rained upon, the mantle bees form a distinctive curtain that has a remarkable resemblance to a tiled roof, each bee serving as one tile (see Fig. 1c). Presumably, the formation of this particular self-assemblage provides some degree of waterproofing of the swarm cluster. Pilot observations indicated that we could induce the mantle bees in a swarm cluster to form a protective rain curtain at will, by spraying them with a mist of water from a spray bottle. Given the ease with which we could elicit the formation of this self-assemblage, we decided to study the behaviors underlying its assembly. Our approach was to compare the configurations of the bees on the surface of a swarm cluster before and after being sprayed with water, and between various weather conditions, to see what adjustments these bees make to form a protective curtain. Also, we checked whether a bee's age affects her probability of being involved in curtain formation. Lastly, we tested the hypothesis that forming a protective curtain helps a swarm shed rain.

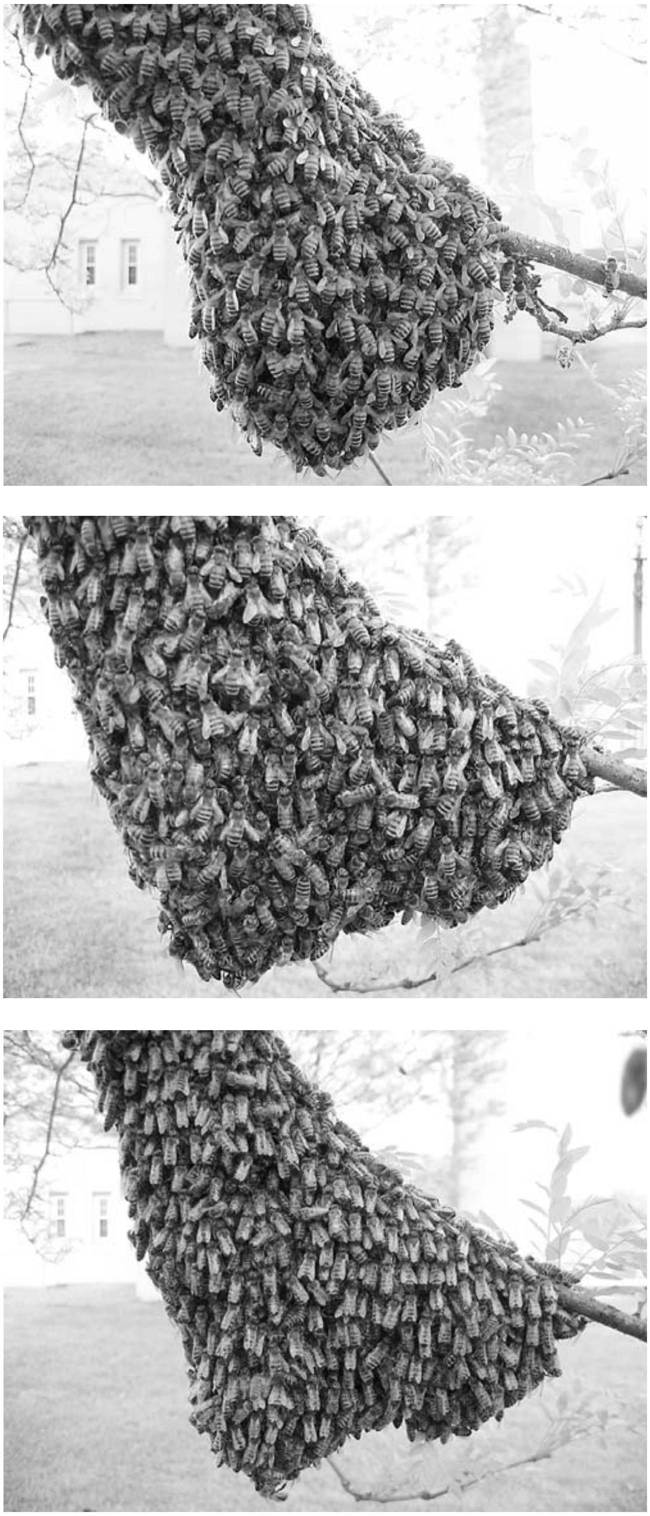

Figure 1. One swarm cluster as it appeared under three distinct environmental conditions occurring on one day. A, morning, cool (11 °C) and dry. B, afternoon, warm (27 °C) and dry. C, afternoon, warm (27 °C) and wet

Methods

Study sites

Ten swarms were studied in two locations. Swarms 1, 6, 7, 8, 9 and 10 were prepared from colonies kept at the Liddell Field Station in Ithaca, New York (42°44N, 76°50′W) and were studied there. Swarms 2, 3, 4, and 5 were prepared from colonies kept in Kittery Point, Maine and were ferried out to the Shoals Marine Laboratory on Appledore Island, Maine (42°58′ N, 70°37′ W) where they were studied (see also Seeley and Visscher, 2003).

Swarm preparation

All of the swarms studied were artificial swarms made from colonies headed by Buckfast queens (a cross of *Apis mellifera mellifera* and *A. m. ligustica*; see Adam, 1987). To prepare a swarm, the source colony's queen was located and placed in a small queen cage (3.2 × 10.0 × 1.6 cm). Then, using a large funnel, we shook 1.0 kg of worker bees (approximately 7,500 bees) off the frames of the source colony's hive and into a swarm cage (15 × 25 × 35 cm), where they were kept with their queen for 2–3 days until abundant wax scales were seen at the bottom of the cage. During this time, the bees were fed *ad libitum* with a sugar solution (1 : 1 by volume, granulated sucrose: liquid water) by brushing it onto the wire-screen sides of the swarm cage. A group of bees treated in this way behaves like a natural swarm once the bees are released (Combs, 1972; Heinrich, 1981a; Seeley and Buhrman, 1999). Next, the swarm cage was opened and the queen (still in her own little cage) was fastened to a swarm mount (see below). The worker bees, mostly still in the cage, were then shaken onto the base of the mount whereupon they clustered around their queen.

Apparatus

To analyze the mechanisms of protective curtain formation, Swarms 1–5 were mounted on a swarm mount (see Fig. 1 in Seeley and Buhrman, 1999) which consists of a vertical wooden board with a central opening in which a queen cage is placed. The worker bees cluster over the queen cage, on one side of the board. The swarm mount has 2 feeder bottles which were kept filled with sugar solution so that the bees on the mount had constant access to food. The video equipment consisted of an S-VHS camera (Panasonic WV-F250B) and docking videocassette recorder (Panasonic AG-7450) equipped with a time-code generator (Panasonic AG-F475). The videotapes were analyzed using a videocassette player with variable speed playback (JVC BR-S525U). Ambient temperature was recorded using a copper-constantan thermocouple probe and a digital thermometer (Bailey Bat-12). This was fixed to the swarm mount, 2 cm below the clustered bees.

Swarms 6 and 7 were mounted on either a windowsill or a tree branch (see below) to study the ages of the bees in protective curtains, and swarms 8–10 were mounted on a horizontal dowel (see below) to study the shedding of water by protective curtains.

Video recording and analysis

A 10 × 15 cm area on the surface of each of Swarms 1–5 was recorded for 30 min during which the first 5 min comprised the warm and dry condition, the next 5 min were the warm and wet condition (achieved by spraying the mantle bees lightly with water from a spray bottle), and the last 20 min were the transition back to the warm and dry condition. Swarm 1 was also recorded under natural rain to check that spraying the mantle with water evoked the same protective curtain formation as is elicited by natural rain. Swarms 2, 3, and 5 were also video recorded for about 5 min each under cool and dry conditions, early in the morning, before their bees were active.

For each swarm, one video frame was chosen for analysis for each of the following conditions: the initial warm ($T > 20\,°C$) and dry condition, the warm ($T > 20\,°C$) and wet (from being sprayed) condition, and every 5 min following the spraying until the end of the 30-min recording session. Also, for the relevant swarms, one frame was analyzed for the cool ($T < 10\,°C$) and dry condition and the natural rain condition.

During playback, each video frame was divided into 25 quadrats with a grid placed on the video monitor. Within each quadrat, one bee whose thorax and wings were clearly visible was chosen for analysis. Whenever there were multiple bees to choose from in a quadrat, the bee closest to the center of the quadrat was chosen as that quadrat's focal bee. If a quadrat had no bee whose thorax and wings were clearly visible, the quadrat was skipped. For the focal bee in each quadrat, the following variables were measured: 1) *body orientation relative to gravity* (the angle between vertical and the midline of the thorax; e.g., head pointing straight up = 0° and straight down = 180°), 2) *head tucking* (whether or not the focal bee had her head tucked beneath an adjacent bee, 3) *wing spread* (the acute angle formed by the leading edge of one forewing and the midline of the thorax; both wing angles were measured and averaged for a single value per focal bee), and 4) *distance between bees* (average distance from the center of the thorax of the focal bee to the centers of the thoraces of the two nearest bees).

Age distribution of mantle bees

Swarms 6 and 7 contained cohorts of labeled, known-age bees. These cohorts were produced by labeling newly emerged bees with age-specific paint marks and then adding them to colonies from which artificial swarms were made, as described above. Newly emerged bees were obtained by removing 2 frames with emerging brood from a hive, shaking all the adult bees from these frames, and placing them overnight in an incubator set at 36 °C. The next day, the adult bees walking on these frames were labeled. In Swarm 6, each cohort contained 50 bees while in Swarm 7 each cohort contained 80 bees. The cohorts were generally spaced 3 days apart, but occasionally the spacing was greater (up to 9 days) due to bad weather. In Swarm 6 there were 9 cohorts spread over 37 days and in Swarm 7 there were 11 cohorts spread over 31 days. The total number of bees (labeled and unlabeled) was smaller in Swarm 6 than in Swarm 7. The former was from a colony in a 2-frame (observation) hive whereas the latter was made from a colony in a 5-frame hive.

Swarm 6 was mounted on a windowsill whereas Swarm 7 was mounted on a tree branch. While each swarm was clustered, we scanned its mantle 1–3 times daily for 3 days (Swarm 6) or 2–3 times daily for 4 days (Swarm 7) for known-age bees, counting the number of such bees. All observations were made under warm and dry conditions. Using these counts, we calculated the average number of bees in each cohort that were visible in the mantle at any one time. Finally, each swarm was transferred to a hive and killed, and the number of bees present in each age cohort was determined. These numbers enabled us to calculate for each age cohort the mean percentage of the bees in the mantle at any one time.

Test for improved rain shedding

We conducted the following test to see whether forming a protective curtain helps a swarm shed rain. Swarms 8–10 were placed separately in the center of a 90-cm-long, 2.54-cm-diameter, horizontally mounted dowel that was supported at each end. This was accomplished by wiring the cage containing each swarm's queen atop the center point of the dowel. Each swarm formed a symmetrical cluster such that the two sides of its cluster were indistinguishable to us. Next, for each swarm, we chose at random one side of the swarm cluster and sprayed onto it 830 mg of water using a spray bottle that delivered a fine mist. This induced the formation of a rain curtain on the sprayed side of the cluster but left the unsprayed side unaffected. Next, we dribbled 5000 mg of water onto each side of the cluster, doing one side at a time. Each time, we collected with dry paper towels spread beneath the swarm the water that was shed. The paper towels were weighed before and after the dribbling of the water, to measure the amount of water that was shed from each side of each swarm.

Statistics

Rayleigh's test was used to determine if a circular distribution of body orientations was significantly different from random and a parametric two-sample test was used to determine if two mean vectors (from two circular distributions) were significantly different, both as described by Batschelet (1965, pp. 28–33). Student's t-test was used to compare the means of two continuous variables (percentage of bees with head tucked, angle of wing spread, and distance between bees). Two-tailed tests were used unless we expected the difference between two means to be in a certain direction, e.g. the mean distance between mantle bees would be smaller in cool weather relative to warm weather. To determine the significance of the regression coefficients in the study of the ages of mantle bees, i.e., to test whether these coefficients were non-zero, we used t-tests, as described by Sokal and Rohlf (1981, pp. 469–477).

Results

Absence of turnover in mantle bees during curtain formation

The mantle bees stayed in place in the cluster during the formation of a rain curtain. In swarms 1–4, we followed 25 randomly chosen bees in the video recording from 1 min before to 1 min after spraying the swarm with water, hence throughout the period of curtain formation, which takes only a few seconds (see Figs 2 and 3). In each swarm, all 25 bees stayed in place in the mantle throughout this period, and all 25 bees made the adjustments in body orientation, wing spread, and inter-bee spacing described below.

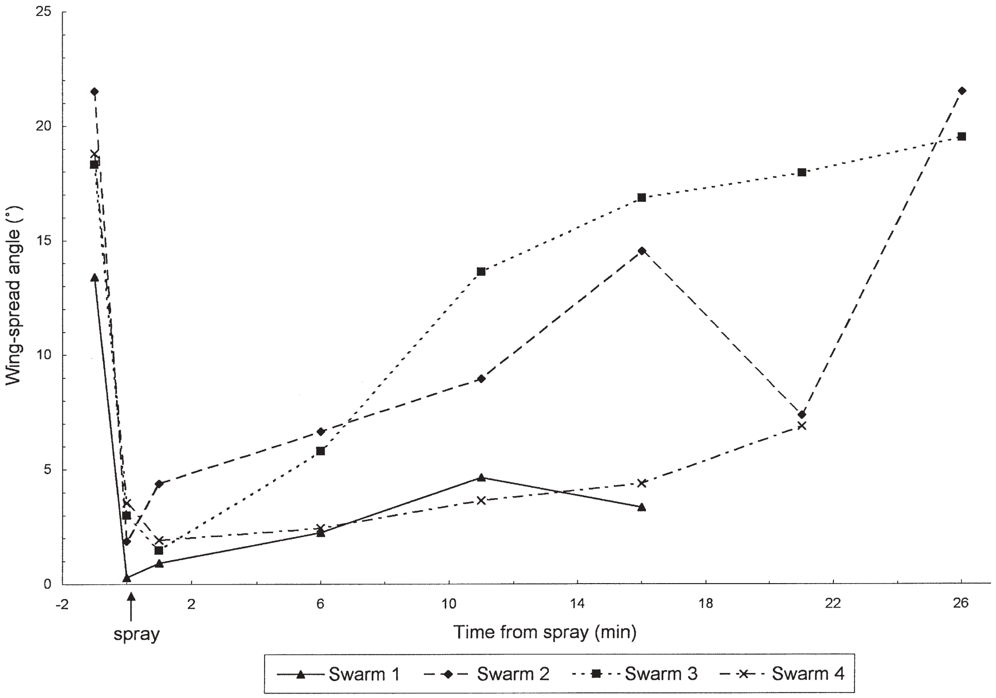

Figure 2. Mean wing-spread angle of mantle bees as a function of time before and after being sprayed by water at time = 0. Wing-spread angle is the angle formed by the leading edge of one wing and the midline of the thorax. Data from 4 swarms

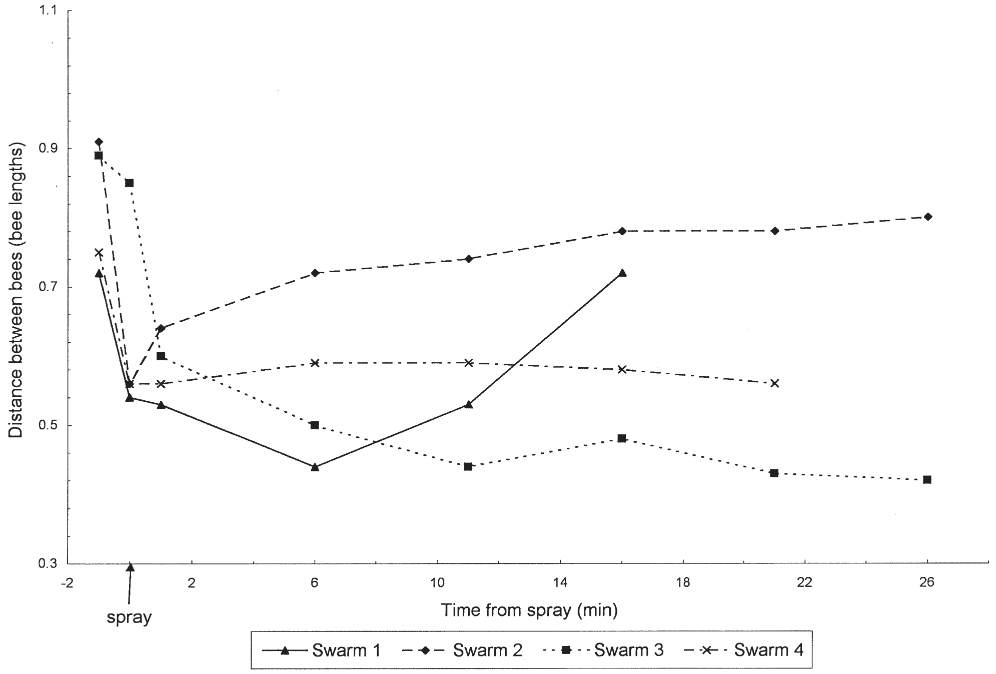

Figure 3. Mean distance between bees as a function of time before and after being sprayed by water at time = 0. Data from 4 swarms

Body orientation relative to gravity

Under warm and dry conditions, the mantle bees generally oriented themselves with head pointing up. The mean vector bearings for Swarms 1–4 were close to 0° (straight up): 338°, 2°, 3°, and 5° (see Table 1). For all swarms except Swarm 1, the distribution of body angles was significantly different from random (Rayleigh's test, $P < 0.01$ for each swarm). However, in each swarm there was much scatter around the mean vector bearing; the length of the mean vector ranged from 0.31 to 0.66, where a value of 0.00 would denote a uniform circular distribution of body angles and a value of 1.00 would denote a perfect alignment of body angles.

Under warm and wet conditions, the mantle bees adjusted the orientation of their bodies relative to vertical so that essentially every bee was oriented with head pointing straight

Table 1. Comparisons, for several variables, of mantle bees under different weather conditions

Variable	Swarm	Weather conditions			
		Warm & dry	Warm & wet	Cool & dry	Natural rain
Body orientation (mean vector bearing and length)	1	338°, 0.31	359°, 0.99	–	358°, 0.94
	2	2°, 0.66	359°, 0.99	356°, 0.87	–
	3	3°, 0.57	1°, 0.92	19°, 0.70	–
	4	5°, 0.59	358°, 0.96	–	–
	5	–	–	0°, 0.90	–
Head tucking' (% of bees)	1	0	45	–	24
	2	8	42	44	–
	3	16	48	20	–
	4	21	63	–	–
	5	–	–	28	–
Wing spread angle (mean ± SD)	1	13° ± 17°	1° ± 1°	–	13° ± 16°
	2	22° ± 18°	2° ± 5°	36° ± 9°	–
	3	18° ± 16°	3° ± 5°	27° ± 18°	–
	4	19° ± 18°	4° ± 5°	–	–
	5	–	–	26° ± 15°	–
Distance between bees (in bee lengths, mean ± SD)	1	0.7 ± 0.2	0.5 ± 0.1	–	0.5 ± 0.2
	2	0.9 ± 0.3	0.6 ± 0.1	0.7 ± 0.1	–
	3	0.9 ± 0.2	0.6 ± 0.1	0.7 ± 0.1	–
	4	0.8 ± 0.2	0.6 ± 0.1	–	–
	5	–	–	0.7 ± 0.1	

up. The mean vector bearings for Swarms 1–4, when sprayed with water, ranged from 358° to 1° and, strikingly, the mean vector lengths were all nearly 1.00, ranging from 0.92 to 0.99. Likewise, when Swarm 1 was observed under natural rain, the mean vector bearing and length were 358° and 0.94. In each swarm, the distribution of body angles differed significantly from random (Rayleigh's test, $P < 0.01$).

Under cool and dry conditions, the mantle bees showed a pattern of body orientation intermediate to the previous two conditions. As before, the bearing of the mean vector was approximately 0° (356° to 19°), but the length of the mean vector ranged from 0.70 to 0.90, indicating a level of alignment higher than when warm and dry but lower than when warm and wet. In each swarm, the distribution of body angles differed significantly from random (Rayleigh's test, $P < 0.01$ for each swarm).

Head tucking

Under warm and dry conditions, few of the mantle bees tucked their heads beneath the bodies of adjacent bees. The percentages of bees with heads tucked in Swarms 1–4 ranged from 0 to 21%, with the mean percentage just 11% (see Table 1). For all 4 swarms, these percentages rose markedly when the mantle bees were sprayed with water, for then the percentages of mantle bees with heads tucked ranged from 42 to 63%, with the mean percentage 47%. The difference between these two mean percentages (for warm and dry vs. warm and wet conditions) of mantle bees with head tucked is highly significant (2-sided t-test of binomial probabilities, $P < 0.001$). In addition, because the mantle bees under warm and wet conditions were almost perfectly aligned, with each bee standing with her head pointing up, every time a mantle bee tucked her head beneath an adjacent bee it was almost always a case of tucking her head beneath the abdomen of a bee directly above. Curiously, when the mantle bees in Swarm 1 experienced natural rain, a relatively small percentage of them, just 24%, tucked their heads. The lower percentage for the natural rain than for our artificial spraying may have arisen because fewer bees were wetted by the rain, which was light, than by our spraying, which was thorough.

Under cool and dry conditions, the percentages of bees with heads tucked were intermediate to the other two conditions. The percentages ranged from 20–44%, with a mean of 31% which is significantly higher than the mean for the warm and dry condition (2-sided t-test of binomial probabilities, $P < 0.05$), but is not significantly lower than the mean for the warm and wet condition ($P > 0.25$).

Wing spread

Under warm and dry conditions, the mantle bees generally held their wings apart. The mean wing-spread angles for Swarms 1–4 ranged from 13° to 22° and the standard deviations ranged from 16° to 18°, indicating considerable variation around the means (see Table 1).

Under warm and wet conditions, the mantle bees adjusted the positions of their wings so that essentially every bee pulled her wings tightly together, thus covering her abdomen. Consequently, the mean wing-spread angles of mantle bees that had been sprayed ranged only from 1° to 4°, and the standard deviations were small, only 1–5°. For all 4 swarms, the wing-spread angle decreased significantly (2-sided t-test, P< 0.001) when the bees were sprayed with water. When the mantle bees in Swarm 1 experienced natural rain, they drew their wings together less tightly than when they were sprayed with water (see Table 1). As with the head tucking, this difference probably arose because fewer bees were wetted by the rain than by our spraying.

Under cool and dry conditions, the mantle bees adopted yet a different pattern of wing spread: they spread their wings widely so that each bee's wings tended to partially cover the adjacent bees. The mean wing-spread angles of the 3 swarms studied under cool and dry conditions ranged from 26° to 36°, which were all greater than the wing-spread angle recorded under warm and dry conditions or warm and wet conditions. Statistical analyses (2-sided t-tests) revealed that in Swarm 2 the mean wing-spread angle was significantly greater under cool and dry conditions relative to either warm and dry ($P < 0.01$) or warm and wet ($P < 0.01$) conditions. In Swarm 3, the mean wing-spread angle was significantly greater under cool and dry conditions relative to warm and wet conditions ($P < 0.01$) but not relative to warm and dry conditions ($P > 0.05$).

Figure 2 shows how the mantle bees in Swarms 1–4 abruptly reduced their wing spreads when they were sprayed with water (transition from warm and dry condition to warm and wet) and how they slowly resumed their original wing spreads in the 25-min period following the spraying.

Distance between bees

Under warm and dry conditions, the mantle bees kept themselves relatively widely spaced. The mean distance between the thorax centers of adjacent bees in Swarms 1–4 was 0.7 to 0.9 bee lengths, and the standard deviations ranged from 0.2 to 0.3 bee lengths, indicating considerable variation around the means (see Table 1).

Under warm and wet conditions, the mantle bees pressed together, thereby reducing both the mean and the variance in their spacing. The mean separations became only 0.5 to 0.6 bee lengths, and the standard deviations fell to just 0.1 bee lengths. For all 4 swarms, the spacing of the mantle bees decreased significantly (1-sided t-test, $P < 0.01$ for each swarm) when they were sprayed with water. The mantle bees of Swarm 1 that experienced natural rain showed a pattern of tight spacing similar (2-sided t-test, $P > 0.60$) to that of the mantle bees that were sprayed with water.

Under cool and dry conditions, the bees reduced their spacing, but not as much as under the warm and wet condition. Statistical analyses revealed that in Swarm 2 the mean distance between thoraces was significantly less under cool and dry conditions relative to warm and dry conditions (1-sided t-test, $P < 0.01$) but not relative to warm and wet (1-sided t-test, $P > 0.50$) conditions, likewise in Swarm 3, the mean distance between thoraces was significantly less under cool and dry conditions relative to warm and wet conditions (1-sided t-test, $P < 0.01$) but not relative to warm and dry conditions (1-sided t-test, $P > 0.50$).

Figure 3 shows how the mantle bees in Swarms 1–4 rapidly reduced their spacing when they were sprayed with water (transition from warm and dry condition to warm and wet). It also shows how in swarms 1 and 2, though not in Swarms 3 and 4, the mantle bees returned to their original spacing during the 25-min period following the spraying.

Age distributions of mantle bees

The percentages of marked bees of various ages that were seen in the mantle of Swarms 6 and 7 are shown in Fig. 4. For both swarms, younger bees had a lower likelihood of appearing in the mantle than the older bees. Statistical analysis revealed that for both swarms the slope of the regression line fitted to the data was positive and was significantly different from zero (Swarm 6, $P < 0.02$; Swarm 7, $P < 0.01$). The percentages of the known-age bees found in the mantle, for each age, were noticeably higher in Swarm 6 than in Swarm 7, probably because the population of Swarm 6 was less than half that of Swarm 7 (see Methods).

Rain shedding

In Swarms 8–10, we compared the amount of water that was shed from the two sides of a swarm cluster, one that had and one that had not formed a protective curtain. The average weight of water collected beneath a swarm when 5000 mg of water was dribbled on it was 4553 ± 282 mg for the side with a protective curtain and 2798 ± 374 mg for the side without a protective curtain (1-sided, paired t-test, $P < 0.01$).

Discussion

In their seminal review of self-assemblages in insect societies, Anderson et al. (2002) point out that almost nothing is known about the proximate mechanisms by which these collective structures form. They also state that the study of these mechanisms is the most important avenue of future research on self-assemblages. We have shed a little light on this intriguing subject by making detailed behavioral observations on the workers in honey bee swarms that form a water repellent curtain when it starts to rain.

It has long been known that a honey bee swarm cluster is covered by a dense mantle of tightly interconnected bees, some 1–3 bees thick, which provides protection for the more loosely arranged bees inside the cluster (Meyer, 1956). Also, it was previously reported that the mantle bees are generally the older bees in a swarm whereas those in the core are mainly the younger bees (Meyer, 1956), a finding that is confirmed by our results (Fig. 4). Heinrich (1981a) has pointed out that younger bees have the lowest metabolic rates and the least ability to thermoregulate, and this may explain why they position themselves in the core; they achieve optimum temperatures by seeking the site with the highest temperature and where they are warmed passively. It may also benefit the

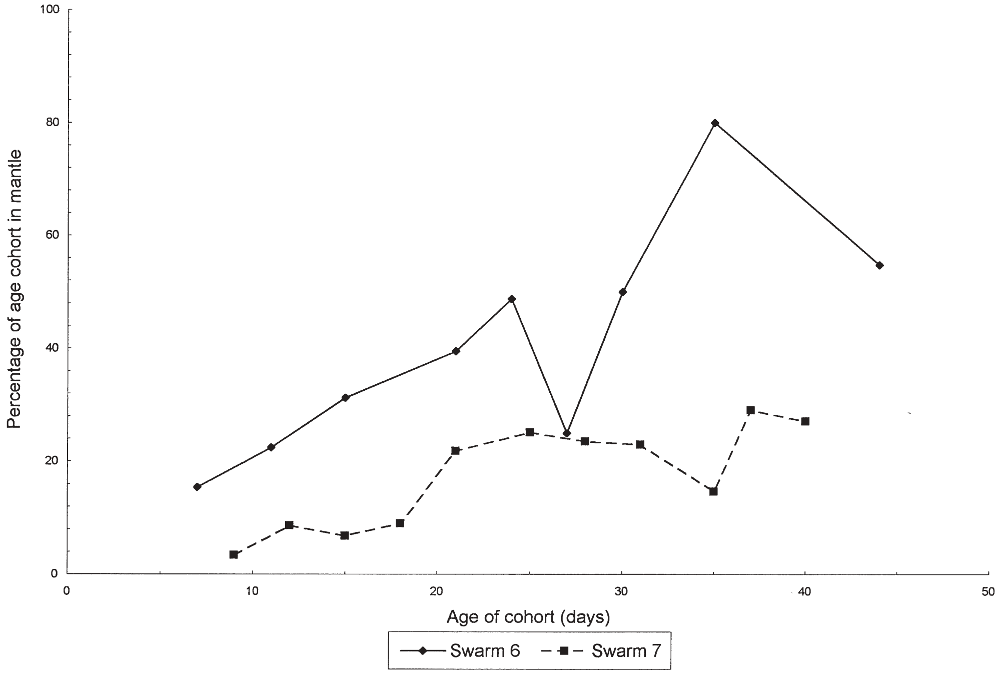

Figure 4. Percentages of bees in different age cohorts that were observed in the mantle of their swarm. In swarm 6, there were 9 cohorts, ranging in age from 7 to 44 days. In swarm 7, there were 11 cohorts, ranging in age from 9 to 40 days

economy of a swarm to have the younger bees at the core. Relative to older bees, younger bees have greater potential life spans and thus higher potential contributions to the fledgling colony. Therefore, if bees in the core of the swarm are safer than those in the mantle, then the arrangement of younger bees in the core helps a swarm maximize the total labor output of its constituent workers. It would be interesting to compare, in terms of colony founding success, swarms with the typical age distribution and swarms whose age distributions are skewed in favor of younger bees or older bees. Winston (1987) has suggested that younger bees are disproportionately represented in swarms because they are more valuable than older bees in providing the labor needed for colony founding. Interestingly, in the bivouac clusters of army ants (*Eciton* spp.), the outermost layer of workers is also not a random sample of a colony's members. Instead, the outside of a bivouac consists mainly of larger workers, perhaps because they are more effective as guards and less prone to desiccation than smaller workers (Schneirla, 1971).

It was also already well known that a honey bee swarm cluster is an adaptable, dynamic structure that changes in response to external conditions. Our results for the two conditions of warm/dry and cool/dry confirm what has been reported already by Heinrich (1981a). During hot weather, the spacing of the bees (in both mantle and core) increases and channels form through which air circulates, sometimes aided by fanning bees. Conversely, during cold weather, the bees cluster more tightly, by aligning their bodies and reducing their spacing, and they spread their wings. These adjustments reduce the porosity of the swarm cluster and presumably minimize its heat loss by convection.

What our study reveals for the first time is exactly how the mantle bees adjust themselves in response to the start of rain to form a cover for the swarm cluster that is effective at shedding water. Evidently, the mantle bees make these adjustments in response to the sensation of water; they are made immediately upon being wetted and gradually disappear as the water evaporates (Figs 2 and 3). It also seems likely that the mantle bees do not need to actively communicate with each other when forming the protective curtain, for each bee can make the necessary adjustments simply in response to the sensation of water on herself, hence without signals from her swarm mates. Heinrich (1981a) presents evidence that the adjustments that swarm bees make for thermoregulation also do not involve communication, but instead arise from each individual responding independently to her immediate environment. Our most important finding is that the mantle bees do not make a few large adjustments (i.e., change position in the cluster, produce recruitment signals, etc.) to form a water repellent cover; instead, they make several small adjustments. These include: (1) rotating the body so that it is oriented head upwards, (2) tucking the head under the abdomen of the individual above, (3) pulling the wings tightly together over the abdomen, and (4) pressing together and so reducing the space between bees. The overall result is a collective structure that closely resembles a tiled roof (Fig. 1c) and that is remarkably effective at shedding whatever water rains down on the cluster. It will be interesting to see if future investigations of adaptive tuning in self-assemblages that are dynamic structures – such as the pulling chains of leaf-cutting ants and the bivouacs of army ants – reveal that they rely on individuals making a few dramatic switches in behavior or whether they too operate by individuals making many subtle adjustments in behavior.

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