

THE MECHANISMS AND ENERGETICS OF HONEYBEE SWARM TEMPERATURE REGULATION

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SUMMARY

1. Free (active) honeybee swarms regulated their core temperature (T_c) generally within 1 °C of 35 °C. They maintained the same temperature around freshly built honeycomb, and in the brood nest of the hive, from ambient temperatures of between at least 1 and 25 °C. Captive (inactive) swarms in the laboratory often allowed T_c to decline below 35 °C.

2. The temperature of the swarm mantle (T_m) varied with the general activity of the swarm as well as with ambient temperature (T_A), but in captive swarms (and sometimes at night in free swarms), T_m was generally held above 17 °C, even at $T_A < 5$ °C.

3. Within the swarm, temperatures varied between 36 °C, an upper temperature set-point, and 17 °C, a lower temperature set-point.

4. Before swarm take-off, all temperature gradients in the swarm were abolished and T_m equalled T_c .

5. The regulated T_c and T_m were unrelated to size and passive cooling rates in swarms ranging from 1000 to 30000 bees.

6. The weight-specific metabolic rate of swarms was correlated with T_A and T_c , but relatively little affected by swarm size.

7. Bees on the mantle experiencing low temperatures pushed inward, thus contracting the mantle, diminishing the mantle porosity, and filling interior passageways. As a result, their own rate of heat loss, as well as that from the swarm core, decreased.

8. In large tightly clumped swarms, even at $T_A < 5$ °C, the resting metabolic rate of the bees in the swarm core was more than sufficient to maintain T_c at 35 °C or above. The active thermoregulatory metabolism was due to the bees on the swarm mantle.

9. There was little physical exchange of bees between core and mantle at low (< 5 °C) T_A . In addition, there was no apparent chemical or acoustic communication between the bees in the swarm mantle that are subjected to the changes of the thermal environments and the bees in the swarm interior that constantly experience 35 °C regardless of T_A .

10. The data are summarized in a model of T_c control indicating a primary role of the mantle bees in controlling heat production and heat loss.

11. The possible ecological significance of swarm temperature regulation is discussed.

INTRODUCTION

Temperature measurements in bee hives date back centuries, and much has been written about thermoregulation in the honeybee (cf. Seeley & Heinrich, 1980). The brood nest, for example, is maintained at 34.5 ± 0.3 °C (Himmer, 1927), while the brood-less parts of the hive fluctuate between 24 and 34 °C (particularly in the winter). Hive thermoregulation at high ambient temperatures involves a complex, highly integrated social response (Lindauer, 1955).

A swarm, the cohort of about half the hive's workers with a queen that leaves the hive and clusters as a group, typically hangs from the branch of a tree for several hours to several days. It leaves after scouts have discovered and agreed on a new suitable domicile where combs will be built and brood rearing started anew.

To my knowledge, the only published data on swarm temperatures and temperature regulation are those of Büdel (1958) and Nagy & Stallone (1976). Büdel observed a fall in temperature from the core of the swarm cluster to the swarm mantle. Nagy and Stallone observed another swarm for one day and found that its core temperature (T_c) remained near 34 °C at ambient temperature (T_A) from 4–15.4 °C. The swarm had elevated internal CO₂ concentrations at low T_A , and it was concluded that T_c was regulated exclusively by regulation of heat production.

I here report on the first in-depth study of swarm temperatures that demonstrate swarm temperature regulation. Mechanisms and energetics are evaluated from detailed observations of 14 swarms.

METHODS

Except where indicated, all of the data in this study were derived from 14 swarms from the San Francisco Bay area that had left the hive during May and June and were subsequently captured before they had taken up a new residence. Swarm clusters stayed intact throughout the time they were used. Several, where indicated, were experimentally altered in size.

Captive swarms were maintained, manipulated and measured in a respirometry vessel consisting of a commercial plexiglass cylinder (i.d. = 29 cm, L = 43 cm) that was closed at both ends with a grease seal on removable plexiglass plates. Free swarms were, for the most part, maintained outdoors on a window ledge outside the laboratory. Both captive and subsequently freed swarms were attached to plexiglass plate that also served as a lid for the respirometry vessel. A circular area of the lid was honeycombed with 3 mm diam. holes for ventilation, as a foothold for the attachment of the swarm clusters, and for openings to insert thermocouple probes, tubing, and electrical wires. A 4 cm wide strip of gauze netting was hung from the lid to the floor of the respirometer to allow bees to crawl up from the floor and form their cluster under the lid.

A second lid of solid plexiglass was sealed with petroleum jelly over the lid with holes to which the swarm was attached, when it was necessary to provide an air-tight system during measurements of swarm metabolism. Air from the closed system (volume = 28.5 l minus volume of bees) was circulated out of the bee-chamber (through tygon tubing with a peristaltic pump) and through a Beckman E2 par2

magnetic oxygen analyser. The oxygen content of the air was measured to $\pm 0.01\%$ accuracy for 15–20 min durations to determine oxygen consumption rate. All O_2 volumes were corrected to STP. Unless indicated otherwise, the first measurements were taken a half day after the cluster was formed. Subsequent measurements were taken for up to 5 days as ambient temperature about the bees was varied by adjusting the temperature of the room.

Swarming honeybee workers initially carry on the average 50% their body weight of food reserves in their honeystomach (Combs, 1972*a*). The amount of these food reserves, however, varies greatly with the age of the swarm, so that swarm weight is not an appropriate basis on which to base swarm metabolism. Nevertheless, for comparative purposes, it is necessary to convert metabolism to a per weight basis. I compromised by killing each swarm after each set of respiratory measurements and counting the bees it contained. (A pile of 100 bees was individually counted, and then the swarm was divided into estimated groups of 100 bees in continual visual comparison to the pile of singly-counted bees.) The metabolism is based on bee numbers, but for convenience it is given in terms of weight, using 115 mg as a standard bee weight. The metabolism per individual bee can be back-calculated, using any other appropriate bee weight. A bee weighing 115 mg, for example, is one carrying a medium-sized load of food reserves, while an 'empty' European honeybee worker weighs 93 mg (Otis, Winston & Taylor, 1980).

Ambient temperature (T_A) was measured within 5 cm of the side of the swarms. In the captive swarms T_A in the respiratory vessel was varied in a Forma temperature-controlled walk-in room. A period of at least 2 h was allowed for equilibration at each temperature used. The swarm temperatures were measured with a stiff thermocouple probe (with a cm scale inscribed on it) that was inserted in 1 cm increments into the swarm through the holes in the lid to which the swarm was attached. In some instances the swarm was also lifted out of the respirometer (with the lid) to make lateral probes into the swarm. Each two-dimensional swarm temperature profile was an average derived from approximately 100 measurements. The measurements were taken in several planes through the swarm, and the temperature isotherms were not as uniform and spherical through all planes of the swarm as the Figs. (1, 15, 20), that represent an average in several planes, might suggest. Temperature measurements at the swarm mantle, or periphery, tended to be highly subject to large differences at low ambient temperature (due to the large temperature gradient over a small distance). Mantle temperature (T_m) was therefore defined as that measured directly underneath the outermost bees of the cluster. The probing of the cluster for temperature with the thermocouple attached to a cm scale also served to measure swarm dimensions. Temperatures were also recorded from thermocouples using a Honeywell multichannel potentiometric recorder. The temperature from each thermocouple was read every 7–13 s, depending on the number of channels being simultaneously used. 'Continuous' measurements of swarms ranged from several hours to several days. All temperatures were standardized to a U.S. Bureau of Standards thermometer.

Thoracic temperatures (T_{Th}) of bees on the swarm mantle were taken by plucking bees by the wings or legs and within 1–2 s inserting a 40-gauge thermocouple, threaded to the tip of a hypodermic syringe (o.d. = 0.5 mm), and reading temperature

to 0.5°C from an Omega Engineering portable thermocouple thermometer. Continuous measurements of bees were taken, using the Honeywell potentiometric recorder, from 46-gauge cotton-insulated thermocouples inserted about 1–2 mm into the dorsum of the thorax and glued in place with a small drop of warm beeswax–resin mixture. Probes were inserted while the bee was lightly anaesthetized (several seconds) with carbon dioxide. The thermocouple leads were held above the bee during temperature measurements to reduce or prevent tension of the wire on the bee, and to prevent it from tangling or otherwise hampering its movements.

Experimental manipulation of swarms was generally done at low ambient temperatures, reducing the numbers of bees taking flight and leaving the clusters. Swarms were divided by gradually pulling them apart, or by providing two hold-fasts for them to crawl up on after they had been shaken to the bottom of the vessel.

In one swarm the core was enclosed in a cylinder of fine screening while the rest of the swarm enveloped this cluster. To achieve this configuration the empty cylinder was first attached to the lid of the container, and allowed to dangle to within approximately 3 cm of the floor. The bees were then placed (shaken) into the bottom of the container. They immediately commenced to crawl upward inside and outside the cylinder, until the cluster was formed at the top, underneath the lid.

Sound recordings inside swarms were made from a microphone that was used as a perch about which a swarm was built. Additionally, other recordings were made from a microphone held directly against the outside of the swarm. A small (6 cm diam.) speaker that was used to play back the sounds recorded on tape was also incorporated into the swarm centre, along with thermocouples that continuously recorded swarm temperatures on the Honeywell Multichannel Potentiometric recorder.

Honeystomach contents were obtained by tearing away the posterior portion of the abdomen, isolating the honeystomach, and taking up the contents in $10\ \mu\text{m}$ or $20\ \mu\text{l}$ Drummond 'Microcap' capillary tubes. Volume of the capillary tubes was measured to the nearest mm, and the sugar solution was transferred to a Bellingham and Stanley refractometer to measure sucrose equivalents of sugar concentration.

RESULTS

(A) *Swarm temperatures*

Swarms of bees dumped into the respirometer started to form a cluster within minutes. They crawled up the gauze strip suspended from the middle of the cover, and massed along this gauze under the cover. Almost all of the bees joined the cluster, and except at high T_A , few bees attempted to leave it.

Settled swarms had steep temperature gradients from centre to outside at low T_A (Fig. 1). The highest temperatures were encountered near the geometrical centre of the swarm, and in small swarms the high temperature was usually localized in a relatively small area of the swarm volume. Small clusters of only 2000 bees maintained a small core area at up to 36°C at T_A of 2°C for at least a day.

When a swarm, particularly a small one, was maintained at 5°C for several days, bees were hanging in seeming lifeless chains from the tightly contracted cluster. These bees eventually dropped from the cluster. They were incapable of either movement

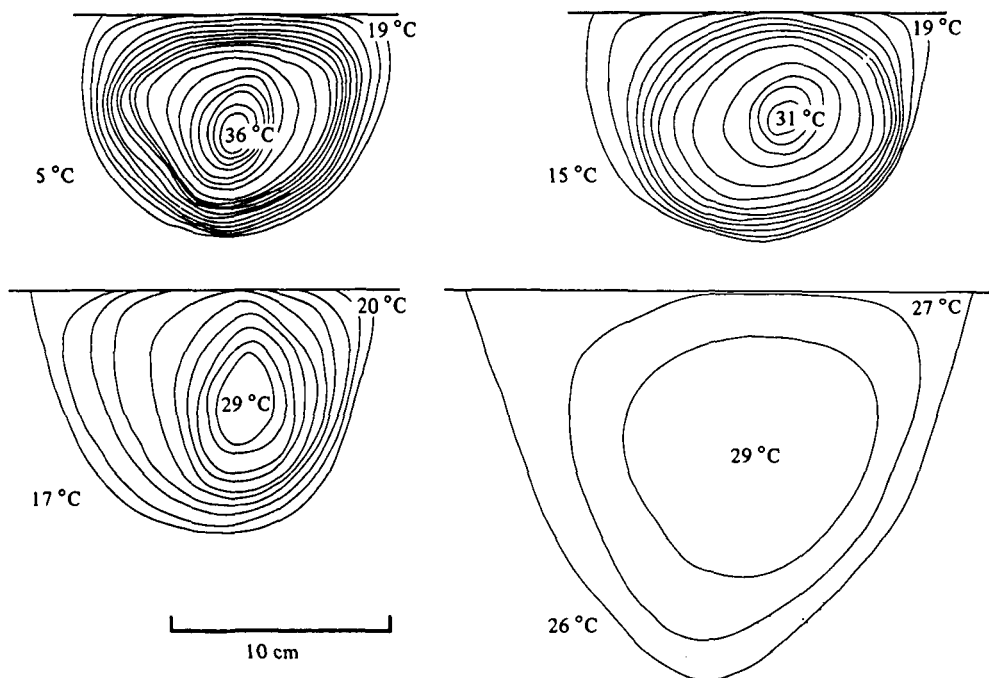


Fig. 1. Internal temperatures and 1 °C isotherms of a captive swarm of 5284 bees at four different ambient temperatures.

stinging. However, even those bees cooled to 1 °C revived when warmed to room temperature. There was at first a preponderance of drones among the bees that dropped out of the cluster when it was maintained at low T_A for prolonged periods of time. Most (but not all) of the workers that dropped out had empty honeystomachs. When the empty workers revived (after being taken out of the cold room) they were able to walk but unable to fly until they were fed sugar or honey. After feeding they resumed flight in seconds.

No systematic measurements were made of the length of time that swarms maintained a high core temperature as a function of swarm size at low T_A . But swarm clusters of 2000–3000 bees had bees dropping out after one night at < 5 °C, while those of ≥ 6000 bees did not. Nevertheless, larger swarms kept at ≤ 5 °C for prolonged periods of time also had bees dropping out from the swarm periphery, even when core temperature exceeded 38 °C.

There was a tendency for some swarms (Fig. 1) to have higher core temperatures at lower than high T_A ; swarms sometimes reduced core temperature at $T_A = 11$ –22 °C (Fig. 2). In both small and large swarms T_c tended to reach an upper ceiling near 35–38 °C (Fig. 2). Large captive swarms often maintained higher T_c than small swarms, and in one instance a large quietly resting swarm achieved a T_c of 46.5 °C (at $T_A = 2$ °C), approximately 10 °C above the temperature normally maintained at both lower and higher T_A (Fig. 2).

The behaviour of the bees at the swarm periphery varied markedly with temperature. At T_A of 13–18 °C the bees appeared to be quiet and undisturbed, but at T_A

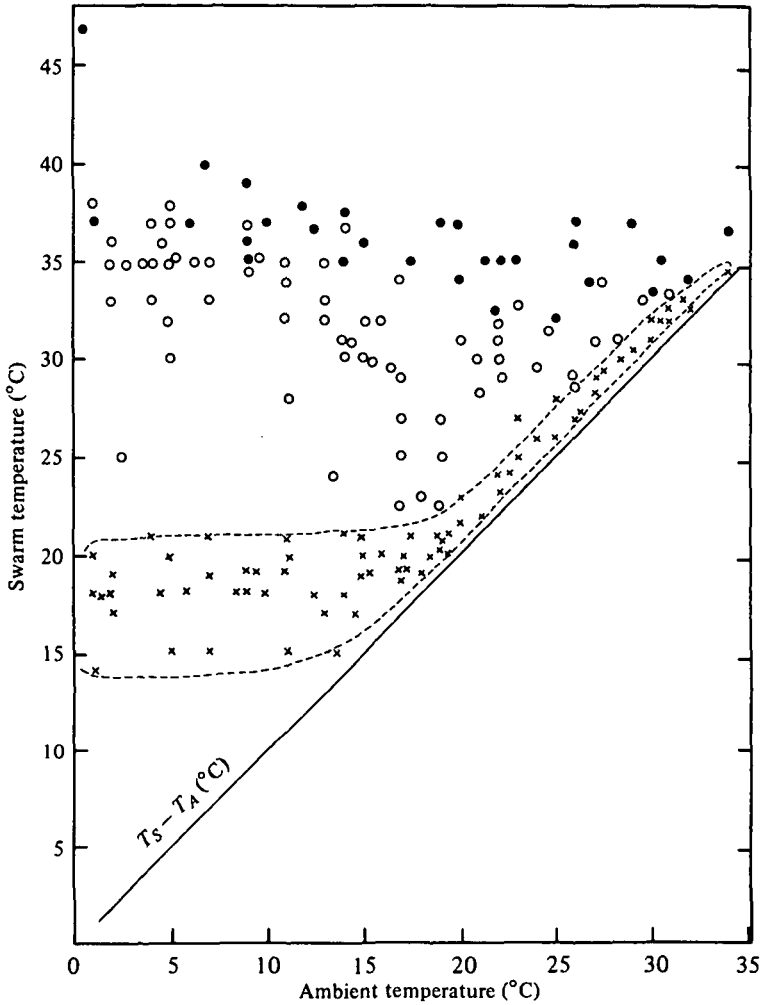


Fig. 2. Core (circles) and mantle (crosses) temperatures of captive swarms in the laboratory as a function of ambient temperature. Open circles: swarms of 2000-10000 bees. Filled circles: swarms of 15000-17000 bees.

$< 10^{\circ}\text{C}$ the peripheral bees were buzzing lightly with their wings held at an angle laterally. (Bees out of the cluster also shiver, but they then keep the wings folded dorsally over the abdomen, and they do not buzz or move their wings under these circumstances.) At $T_A > 25^{\circ}\text{C}$ some of the bees were leaving the cluster, flying against the walls of the respirometer containing the swarm, and many bees of and on the swarm mantle were moving.

Temperatures of the swarm mantle were relatively independent of T_A from 1 to 15°C , being regulated on the average near $18\text{--}19^{\circ}\text{C}$ (Fig. 2). At $T_A > 17^{\circ}\text{C}$, the temperature of the swarm mantle passively followed T_A , averaging approximately 1.5°C above it.

Free swarms showed interesting variations from the above observations. Free swarms usually had more activity of bees on the swarm periphery in the daytime; bees were continuously leaving the swarm and returning to it. The temperature of the

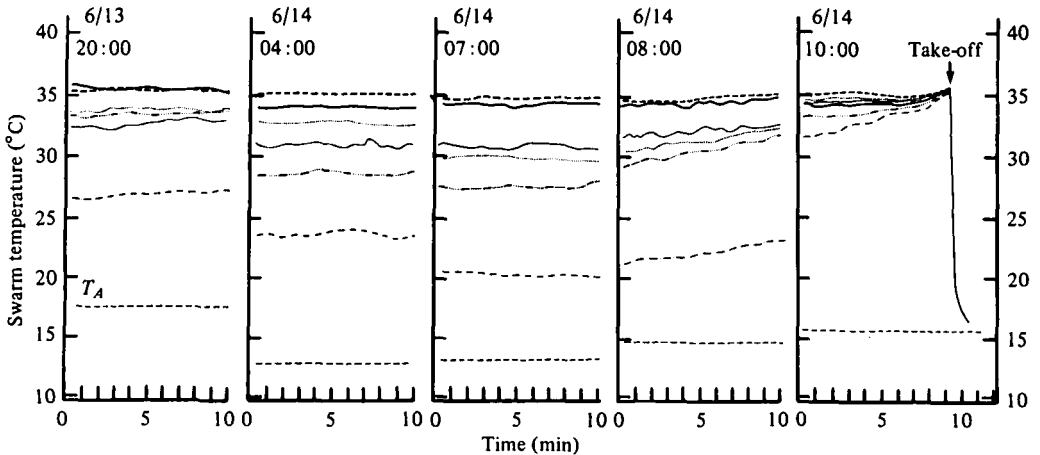


Fig. 3. Sections of a continuous record of temperatures in a free swarm until 10.10 h, at swarm take-off, showing regulation of T_c at 35 °C, drifting of mantle temperature, and abolishing of temperature gradients before take-off. —, swarm centre at 20 cm depth. --, swarm centre at 10 cm depth. — · —, mantle. ·····, half way between centre and mantle at 15 cm depth. ·····, half way between centre and mantle at 10 cm depth. The swarm contained 28000 bees.

mantle in free swarms at 15–18 °C, for example, was 26–27.5 °C, significantly ($P < 0.05$) above the apparent minimum maintenance level in T_m of captive swarms. (Bees enter cold torpor when cooled to below 15 °C.) Furthermore, presumably because the T_m of free swarms was usually well above the minimum temperature necessary for the bee's arousal, it could fluctuate more widely. Mantle temperature varied diurnally, from near 20 °C at night at 13 °C as in captive swarms, to over 30 °C at 16–23 °C in the daytime (Figs. 3, 4).

Core temperatures of free swarms were, both at night and in the daytime, regulated relatively precisely near 35 °C over the range of T_A from 13–24 °C (Figs. 3, 4). Over this range of T_A core temperature was independent of swarm size; swarms of 600–3400 g of bees maintained the identical temperature as that recorded within the capped brood, and in the passageways between capped brood, of an active hive (Fig. 4). Core temperature is thus not simply a passive phenomenon resulting from heating and cooling characteristics; T_c is actively regulated.

Although the temperature of the swarm mantle in free swarms fluctuated diurnally, the bees nevertheless exert considerable control on T_m . As in the laboratory (Fig. 2), bees of free swarms always maintained T_m above the minimum for rapid arousal, and before take-off nearly all temperature gradients were abolished (Figs. 3, 5). Take-off in two 'normal' swarms, one weighing 600 g and one weighing 3400 g occurred in both when T_c and T_m were 35 °C. Take-off is a sudden event, occurring over a matter of seconds.

It is doubtful that swarm temperature, as such, is a signal for take-off. First, the bees may maintain elevated T_m for an extended period of time without taking off. For example, two large and one medium-sized swarms were mixed to create a 'super' swarm of at least 30000 bees. Bees of this large cluster appeared to be agitated, and core temperature approached and stayed at 38 °C for several hours, 3 °C higher than

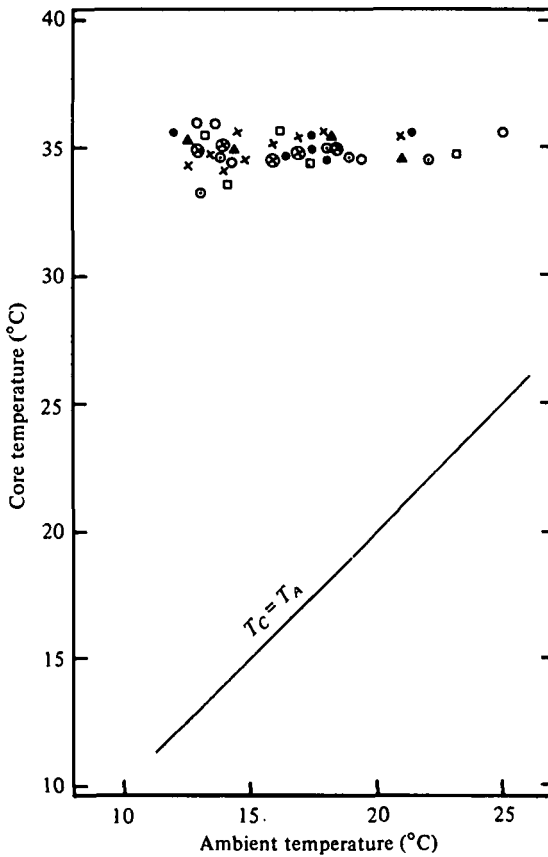


Fig. 4. Temperatures recorded from the brood nest of a hive (●), and the stabilized core temperatures of free swarms of various sizes (×, 275 g; ⊙, 600 g; □, 1200 g; ⊗, 1300 g; ○, 1900 g and ▲, 3400 g) over a range of ambient temperature (< 15 °C, at night. > 15 °C, in daytime).

the relatively precisely regulated temperature of all of the other observed free swarms. In the composite swarm, temperature of the mantle soon exceeded 35 °C (Fig. 5), and the bees maintained temperatures near 38 °C for approximately 6 h. When the composite swarm left enmasse T_m had achieved 38 °C, the same as T_c . No directional dances of any of the bees were seen on this swarm before it left, and if flew < 100 m before re-aggregating and settling on a tree. The next morning at 14 °C its T_c was 35 °C and T_m was 30 °C, as in other free swarms. (The swarm later divided.)

In summary, T_c are normally regulated at the same temperature as brood nest temperature. However, except prior to take-off, temperature of the swarm mantle is regulated at an approximately 16 °C lower temperature set-point, and allowed to fluctuate above the set-point.

The captive swarms that allowed T_c to decline below 35 °C were not necessarily low on food reserves. For example, in one 3-day-old swarm (of approximately 16000 bees that consistently kept T_c at near 29–31 °C and T_m near 20 °C for 2 days at T_A of 19 °C) the honey stomach contents of 21 of 23 bees examined were distended with 10–45 μ l of concentrated (> 70%) honey, comparable to that of freshly swarmed

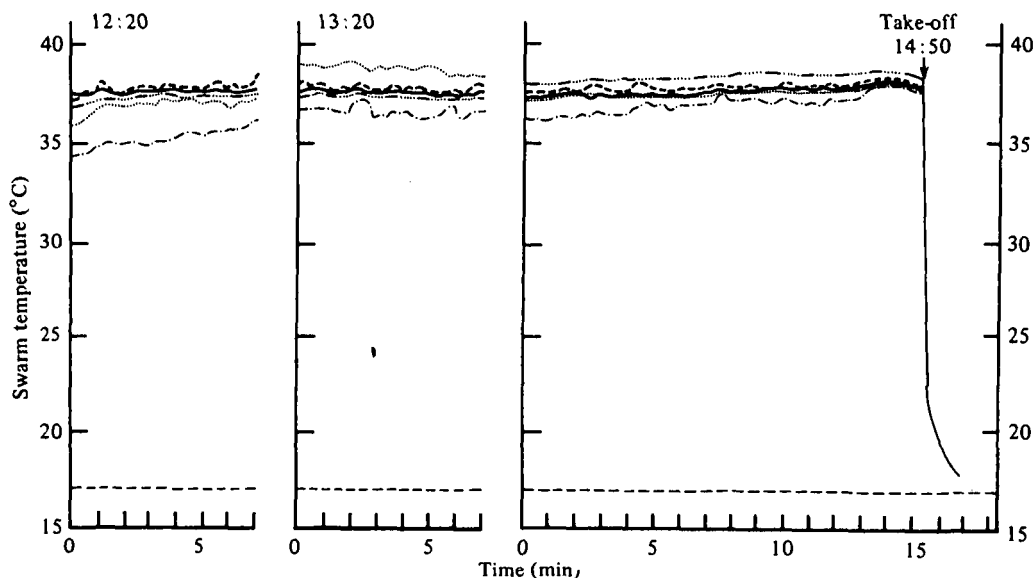


Fig. 5. Sections of continuously recorded swarm temperatures until 14.50 h, at swarm take-off —, swarm centre at 12 cm depth. ---, swarm centre at 8 cm depth. ·····, mantle. - · - · - ·, half-way between centre and mantle at 12 cm depth. - - - - -, half-way between centre and mantle at 8 cm depth. The swarm contained approximately 30 000 bees that had been mixed together from three separate swarms at 08.30 h.

bees (Combs, 1972*a b*; Otis *et al.* 1980). Only two out of the 23 bees had empty honeystomachs. The swarm's hypothermia was thus not due to a depletion of food reserves.

A free swarm of only 2400 bees maintained at T_c of 35 ± 1 °C, both day and night, even at 13 °C during the first 3 days after swarming. Two swarms (of 3000 and 20000 bees) had core and mantle temperatures continuously monitored for 4 and 10 day, respectively. The swarms were free and eventually began to build combs in the centre of the cluster. Both swarms had distinctive diurnal temperature cycles of both T_c and T_m . In the larger swarm T_c at night ($T_A = 13$ –14 °C) usually declined from 35.5 to 33.0 °C, while T_m declined to 22–25 °C, from above 30 °C in the daytime when T_A ranged from 15 to 20 °C. On four successive nights at $T_A = 14$ –15 °C core temperatures declined to 31, 26, 27 and 31 °C. Corresponding mantle temperatures were 19, 21.5, 21.0 °C and 20.5 °C. In the mornings core temperatures rose to 34–35 °C, to be followed by increasing T_m that sometimes reached nearly the same temperatures as the core, particularly when dancers were active on the swarm exterior. When there was little apparent activity on the swarm exterior, the T_m declined. The bees of at least the smaller swarm had exhausted their original honey reserves from their old hive, since no bees (in a sample of 22) contained concentrated sugar (honey) in their honeycrop. Six of the 22 bees had empty honeystomachs, and the remaining 16 had dilute sugar solution as in nectar ($\bar{x} = 33\%$, range 21–55%). Volume of honeystomach reserves ranged widely, from 0–39 μ l ($\bar{x} = 10.2$ μ l). Sugar reserves in the honeystomachs averaged 3.6 mg (0–21 mg, S.E. = 1.1). It appears, therefore, that this swarm was relatively low on food resources, and had resorted to foraging and energy economy

in temperature regulation for immediate survival, rather than committing all of time and energy resources to searching for a new hive.

One 4-day-old swarm that was set free on the windowsill (after being used for experiments in the laboratory) took off 6 days later. It left behind a newly formed honeycomb (16 × 17 cm) containing some pollen but no honey. The bees had presumably taken the honey with them. (Another swarm under similar conditions that was killed after several days had also built a similarly-sized comb, but this comb was filled with honey.)

Bees in the hive maintained the same temperature in the brood nest as the swarm bees did in the swarm core. But bees out of the hive behaved differently when placed into the respirometer. Bees out of a small hive (population = 11 100 bees) placed into the respirometer at 5 °C, unlike the swarm bees, did not form a tight, quiet cluster. After a few hours some of these bees formed a loose cluster with a core temperature of 36 °C, but most of the bees continued to mill around without joining this cluster. The T_A inside the respirometer rose to 26 °C. (The T_A inside the respirometer at 5 °C containing swarms generally rose only to 7–9 °C.) The next morning all of these bees from the hive were prostrate and motionless on the bottom of the respirometer. The honeystomachs of 50 randomly chosen of these prostrate individuals were empty.

Free swarms that started to build combs inside their suspended cluster, and in which T_c were continuously recorded, had T_c identical to those of freshly emerged swarms. However, when placed into a respirometer, such 'hive-swarms' behaved differently than freshly emerged swarms. In two of such 'hive-swarms' that were deprived of their comb and placed into the respirometer, the animals remained active, heated the inside of the respirometer to 30 °C at external T_A of 5 °C, and lay in heaps after one day. As in the hive bees, the honeystomachs of 50 of these prostrate bees that were examined were empty.

(B) *Passive heat flow*

Heating and cooling characteristics of groups of dead bees cannot be used to indicate the actual heat flow rates through live swarms, but they can provide comparative estimates of heat production rates in various portions of live swarms.

As shown in the following experiment, different parts of a swarm cool at different rates, and passive heat flow is slow. A clump of 7000 bees was held together in gauze and heated until T_c reached 27 °C and T_m was 36 °C. The bees were then placed at 0 °C to observe the cooling rates in relatively still air (Fig. 6). The temperature of the mantle declined rapidly, creating a temperature gradient both toward the inside and the outside. Core temperature continued to *increase* for 1 h, when temperatures near the periphery of the cluster were still 20 °C above ambient (Fig. 6). These measurements suggest that any heat produced in the centre of a swarm cluster would require relatively long durations before it could passively affect the periphery.

In a second experiment, the same dead bees were spread, heated to 44 °C and mixed, and a new artificial cluster created with uniform temperature throughout. When placed at 3 °C the cluster core did not cool to 22 °C until 140 min, when T_m was 9 °C (Fig. 7), roughly mimicking the temperature gradients observed in live swarms, except for the specific magnitude of T_c and T_m .

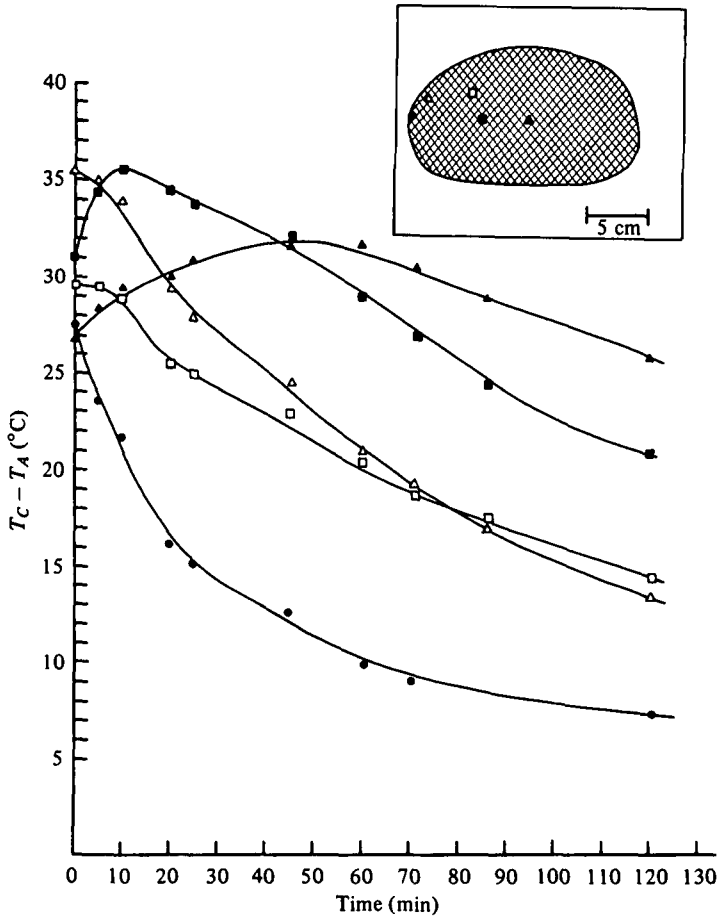


Fig. 6. Temperature changes in a cluster of 7000 dead bees (770 g) after it was heated to near 36 °C (on the outside) and then placed at near 0 °C. Key at upper right indicates approximate shape and size of the cluster, as well as the positions of the thermocouple probes that correspond with the respective temperature changes indicated.

The rate at which heat is lost passively from a cluster of bees is obviously a function of its size. Since swarms regulated the same core temperature regardless of their size, the passive cooling rates of differently-sized dead swarms gives a relative measure of the physiological-behavioural adjustments that the bees must make in their thermoregulatory response.

Cooling rates of the cores were made from dead bee clumps (held together by light gauze) ranging in size from 1000 to 30000 bees, similar to the variation in the bee numbers in the live swarms that were observed. The capacity of these bee clumps to maintain passively an elevated T_c was, as expected, dramatically a function of group size. Cooling rates over this size range, at a temperature gradient of 24 °C from core to ambient, ranged from 0.0269 °C min⁻¹ °C⁻¹ (1000 bees) to 0.0013 °C min⁻¹ °C⁻¹ (30000 bees), more than a 20-fold difference (Fig. 8). Thus, the large swarms potentially need at least 20 times less metabolic effort to maintain the core heated, or a corresponding greater effort to keep it cooled (depending on which mechanism is more important) than the small ones.

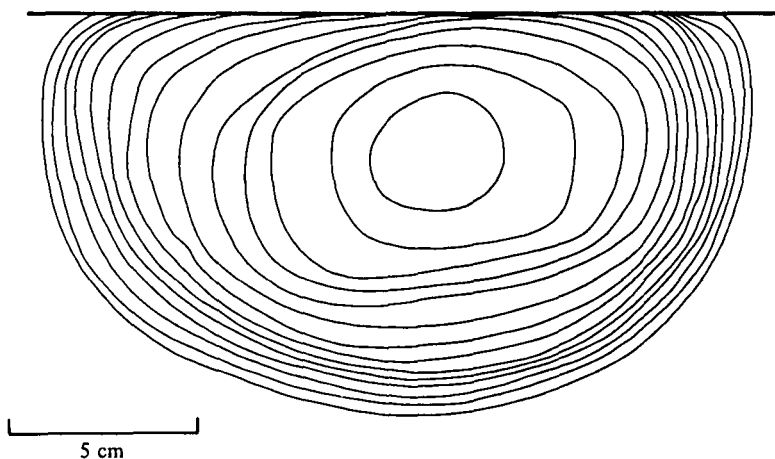


Fig. 7. Temperature isotherms in a clump of 7000 dead bees after they had been heated uniformly throughout to 44°C , and then allowed to cool at $T_A = 3^{\circ}\text{C}$. Core temperature after 140 min was 22°C (this figure). Each line represents at 1°C temperature isotherm.

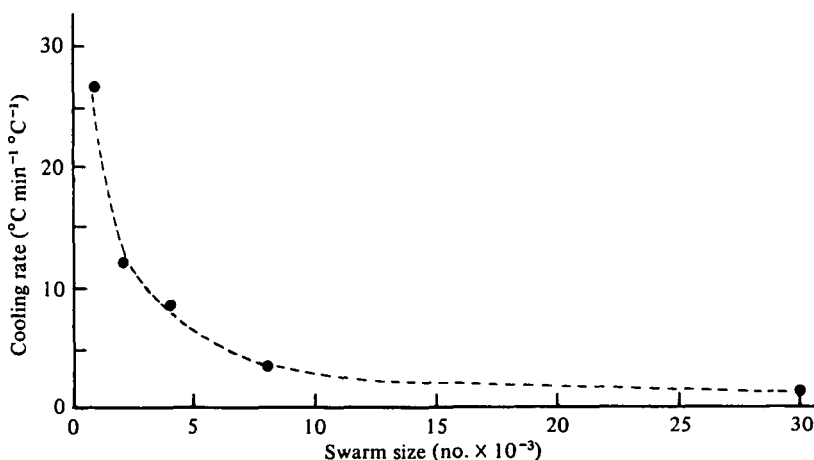


Fig. 8. Passive cooling rates of differently-sized clusters of bees as a function of cluster size.

(C) *Swarm metabolism*

The metabolic rate of swarms ranged widely as a function of several variables. When the bees were active and in the process of settling into a cluster their metabolic rate was much higher than later after the swarm was settled. Even 2 hr after the swarm cluster was formed, the rate of oxygen consumption per unit weight of bees was several-fold greater than a half day later.

Two swarms that had been fed dilute honey through the plexiglass lid to which they were attached exhibited erratic and high rates of oxygen consumption, even one day after feeding. Their oxygen consumption rates (eight measurements) varied between 1.5 and $5.0 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ without any recognizable pattern with regard to T_A at T_A from 9 to 33°C .

Swarms that were given at least 8 h to come to rest showed a pattern of oxyg

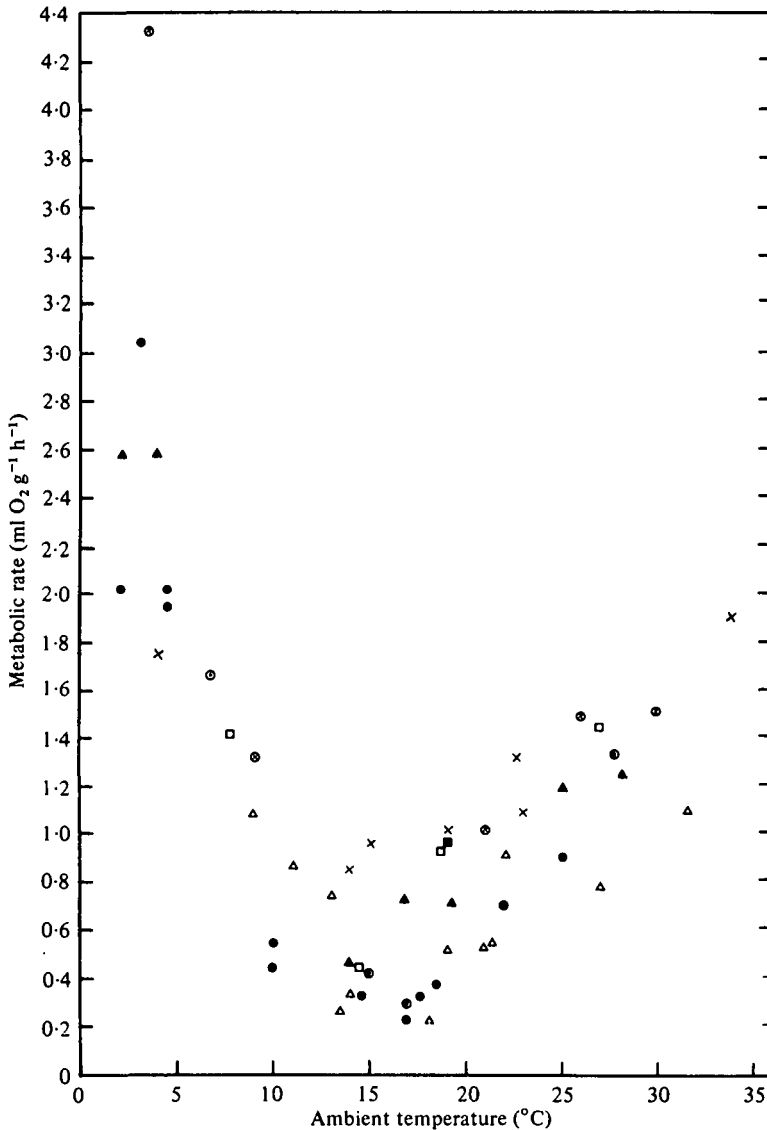


Fig. 9. Metabolic rates of eight different swarms with different numbers of bees ($\square$, 1800; $\blacksquare$, 4900; $\bullet$, 5280; $\blacktriangle$, 5650; $\odot$, 8200; $\triangle$, 10 000; $\otimes$, 15 300 and $\times$, 16 600) as a function of ambient temperature. All of these swarms had been at rest for at least 8 h. None had been fed. All had been maintained in the temperature-controlled room.

consumption related to ambient temperature. At T_A of $\leq 5^\circ\text{C}$ the metabolic rate ranged from approximately $1.8\text{--}4.3\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$, declining to $0.3\text{--}1.0\text{ ml}$ at $10\text{--}23^\circ\text{C}$, and increasing again to near 1.5 ml at T_A near 30°C (Fig. 9). Some of the elevated metabolism recorded at the higher T_A , however, was probably an artifact due to bees that had left the swarm cluster and were flying against the walls of the respirometer. For example, if in a swarm of 15 000 bees 100 individuals were flying, a swarm metabolism of $1.35\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ would have given an apparent value of $1.85\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ given the measured metabolic rate of individual bees in free flight (Heinrich,

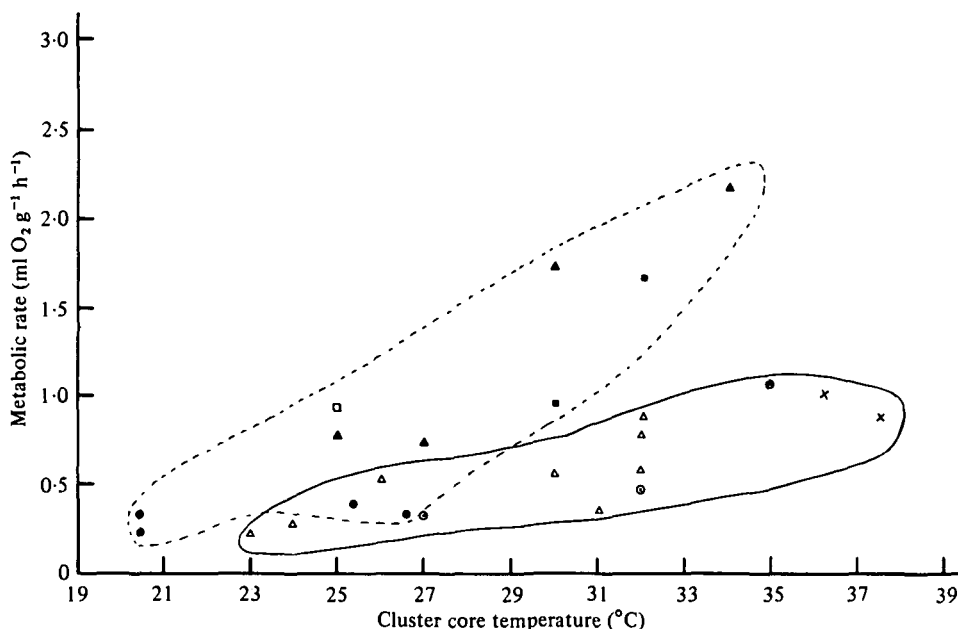


Fig. 10. Metabolic rates of seven different swarms (symbols same as in Fig. 9) at T_A of 12–21 °C as a function of cluster core temperature during the oxygen consumption measurements. Data here included of some swarms after they had been fed. Upper lines enclose data from swarms with up to 5600 bees. Lower lines enclose data from swarms with 8200–16600 bees.

1980). At $T_A < 10$ °C the bees on the swarm periphery were vibrating their wings (the wings looked 'fuzzy') and buzzing. The wings appeared in focus to the unaided vision at T_A near 15–20 °C, when the bees then seemed to be quiet and at rest.

Surprisingly, in swarms ranging from 1800 to 16600 bees that had approximately eight times different cooling rates (Fig. 8), there was little or no apparent tendency for the small groups to have a higher metabolic rate than the larger ones. To the contrary, at low, medium as well as high T_A , some of the highest weight specific metabolic rates were recorded from large swarms (Fig. 9) having higher T_c (Fig. 2). Such results would be expected if metabolic rate were in large part determined by resting metabolism, rather than by energy expended for thermoregulation.

It appears that T_c has a larger effect on swarm metabolism than cooling rate that varies with swarm size, particularly near the thermal neutral zone where the bees did not have to expend energy for thermoregulation. For example, at T_A between 12 and 21 °C, where the metabolic rate varied from 0.23–1.2 ml O_2 g⁻¹ h⁻¹, the high values were observed in large swarms, which usually maintained higher core temperatures in this range of T_A than smaller swarms (Fig. 2). These data thus suggest that any possible effects of swarm size on metabolic rate are masked by a greater effect of swarm temperature. Nevertheless, when metabolic rate is plotted as a function of swarm core temperature (Fig. 10), there is a tendency for small swarms, at any given core temperature, to have a greater metabolic rate than large swarms. For example, at a T_c of 35 °C the metabolic rate of swarms of 2000–6000 bees averaged 2 ml O_2 g⁻¹ h⁻¹, while the metabolic rate of swarms of 15000–16000 bees averaged 1 ml O_2 g⁻¹ h⁻¹. These results suggest a small amount of compensatory metabolism for thermo-

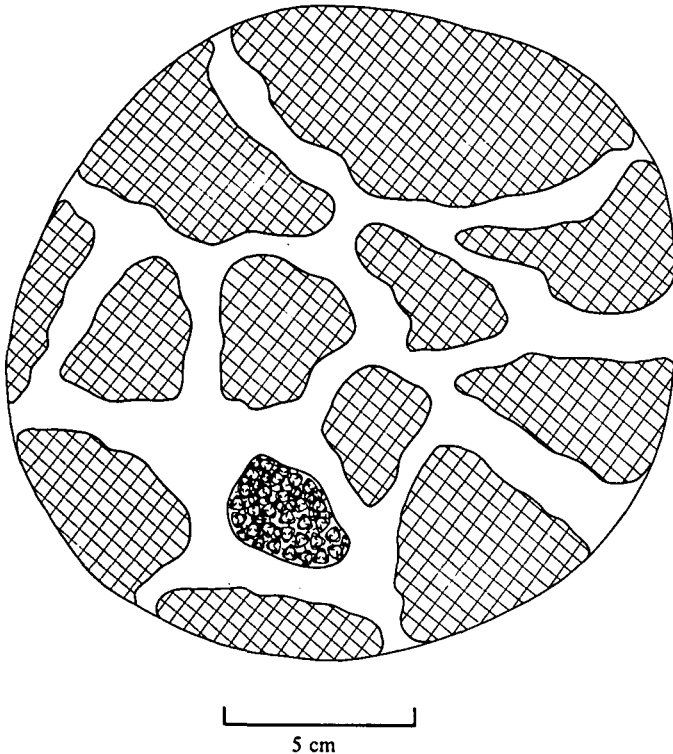


Fig. 11. View into a swarm of 8000 bees at $T_A = 24^\circ\text{C}$ through the plexiglass to which it was attached, showing curtains of stationary bees (cross-hatching) and open passageways through the swarm used by active bees. The heads of the bees pointing upward are depicted in one of the curtains.

regulation, but if thermoregulation is accomplished by the regulation of heat production then they are several-fold lower in magnitude than predicted from the passive cooling curves of dead swarms.

Metabolic rate, however, could vary over an order of magnitude at a given core temperature. For example, in one swarm of 1200 g at 15°C , the metabolic rate increased 13-fold within seconds after carbon dioxide was released through a pipette into the swarm cluster.

(D) *Control of heat loss*

The rate of heat loss from the swarm interior should be a function of its relative surface area, porosity of the mantle, and convection currents within the swarm. The bees varied all three of these parameters as a function of temperature, thus demonstrating a considerable capacity and sophistication of heat loss regulation.

The transparent plexiglass respirometer cover to which the swarms were attached in the laboratory allowed a direct view into the swarm interior. At high T_A numerous passageways were visible within the top of the swarm between hanging clusters of immobile bees that had their heads pointing upward (Fig. 11).

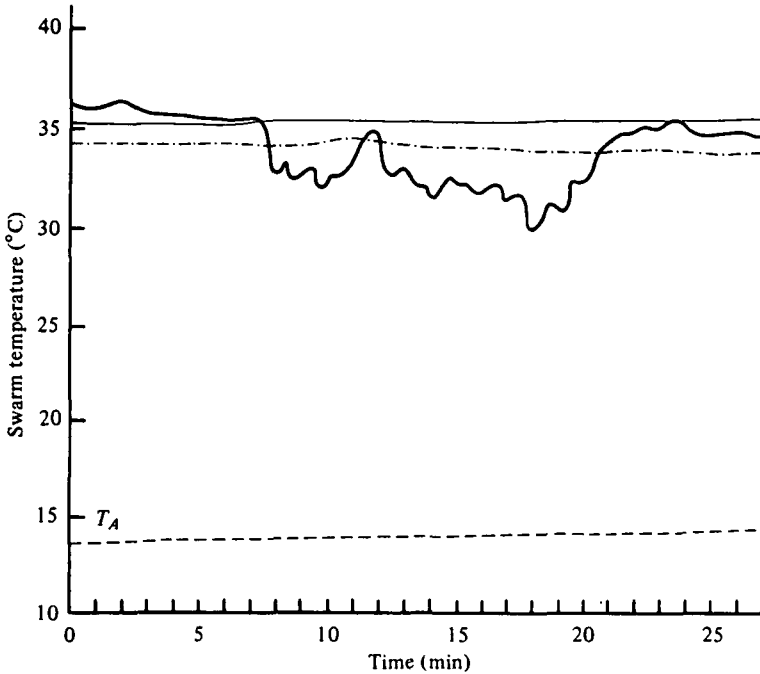


Fig. 12. Typical rapid, short-term swarm core temperature changes observed in a free swarm of 10000 bees. —, swarm centre. ---, swarm mantle. — · —, half-way between core and mantle.

The enlargement of the cluster at high T_A by loosening the mantle and enlarging it not only must increase the rate of passive heat loss, it also should provide the opportunity for active ventilation of the swarm interior along these passageways.

In one swarm with a T_c of 34 °C (10 cm down into the swarm), the temperature within the bee clusters near the surface (at 1.5 cm depth) was 28.5 °C. However, the temperature within the passageways visible through the plexiglass at the same depth fluctuated widely over 2 °C, averaging 30.2 °C ($N = 10$). These observations suggest that heat was rising in gusts through the swarm.

Erratic and rapid temperature fluctuations were also often recorded from thermocouples inserted deeply (10 or more cm) into the interior of free swarms (Fig. 12). These rapid temperature changes from the swarm interior were decreases, or cooling, and they were far more rapid than could be accounted for by passive cooling (Fig. 8). Core temperatures sometimes dipped temporarily lower than those recorded from near the swarm periphery (Fig. 12). Since these erratic temperature reductions in an otherwise hot area of the swarm were observed primarily near the swarm centre, rather than at the periphery where there were fewer passageways, they were probably due to the inadvertent placement of the thermocouples into passageways where cool air was being circulated from the outside. The passageways are conduits for heat from the swarm interior to the outside.

It could be experimentally demonstrated that the bees can rapidly release heat from the swarm. As indicated previously, the bees responded to an experimental influx of CO_2 into the swarm interior with at least a 13-fold immediate increase in heat production, as determined by the increased rate of oxygen consumption. Similarly

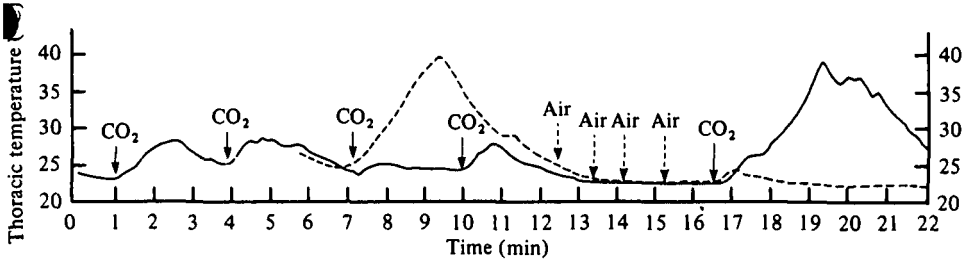


Fig. 13. Thoracic temperature changes, and two full pre-flight warm-up curves of two bees. The bees were run simultaneously (at $T_A = 20^\circ\text{C}$), and the arrows indicate whether both or just one bee was subjected to puffs of air or CO_2 .

individual bees with low T_{Th} subjected to brief puffs of CO_2 showed increases of T_{Th} (Fig. 13). When the bees were well-fed but torpid they aroused fully, warming up from $23\text{--}40^\circ\text{C}$ or more at rates of $7.3\text{--}8.0^\circ\text{C}/\text{min}$. Bees with nearly empty honeystomach showed only a small and transient increase of T_{Th} . Bees subjected to puffs of air did not show the increases of T_{Th} .

Carbon dioxide also affected whole swarms. Thermocouples were inserted into the swarm interior to record an anticipated potential explosive rise in core temperature following CO_2 injection. However, the results of this experiment showed that despite the elevated heat production, core temperature was usually maintained relatively stable. When CO_2 was pumped into a large swarm at $100\text{ ml}/\text{min}$, there were no obvious effects. However, at pumping rates of $200\text{ ml}/\text{min}$ the bees responded. Responses were very variable (see Fig. 14). Different experiments showed decreases in T_c , no change in T_c , and increases of T_c . In all instances, however, large volumes of CO_2 pumped into the swarm caused the swarm to release large amounts of heat, as shown by the rise in T_A near the swarm. Swarms expanded within minutes, mimicking the behaviour observed during overheating. Possibly low CO_2 concentrations at low T_A affect heat production without opening the swarm mantle, while high CO_2 concentrations invariably result in mantle opening, and heat loss. The precise interactions between these variables at different T_A were not here investigated.

The hanging clusters of bees in the swarm interior were interconnected with the immobile bees that made up the swarm exterior, or mantle. The passageways within the cluster opened to the exterior in numerous places, and bees travelled freely in, out and within the swarm along these passageways. As T_A was lowered the passages near the swarm periphery became filled with bees, while those in the centre remained open. As T_A was lowered further, the swarm mantle gradually became thicker, until even the passageways became packed full of immobile bees. At $T_A < 5^\circ\text{C}$ there were no more passageways visible from the top of the plexiglass; the whole top of the swarm was a solid wall of bee heads butting against the plexiglass.

Whether or not there were passageways present below this wall was not determined in the present study; however, since the swarms greatly contracted at low T_A (Fig. 1) it is evident that space within the cluster must become more and more limited as T_A is lowered.

The swarms not only decreased their surface area at low T_A , they also changed their shape and mantle porosity. At high T_A the bees spread laterally along the top of the cluster on the plexiglass cover, and the bees dangled down in a long 'beard'. As

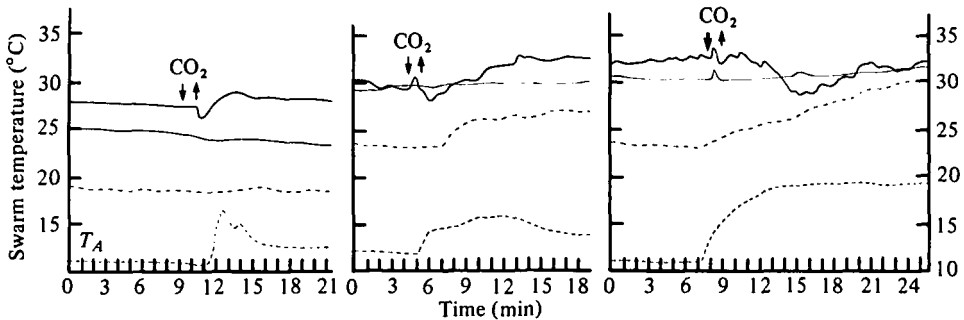


Fig. 14. Temperature changes of the swarm cluster and swarm mantle following the introduction of CO_2 into the swarm centre (see Methods). Arrows indicate the time of CO_2 introduction and the relative amount of CO_2 . The bees of swarm no. 5 (left) were relatively immobile. Designations of lines as in Fig. 12.

T_A was lowered this beard was resorbed as the bees crawled upward filling the passageways within the swarm cluster. Similarly, the bees from the swarm periphery and at the top, pointed their heads inward, as if trying to push into the swarm (Fig. 15). As a result of the bees' attempts to push headfirst into the interior of the swarm cluster from the outside, the swarm not only contracted in size, but the 'pores' of the swarm mantle became plugged and the swarm mantle became denser as well as thicker.

The bees on the swarm periphery should immediately feel any change in T_A , and their response can affect core temperature. When a tightly clustered swarm of 20000 bees with a high core temperature (30°C) was taken from 10°C in the cold room to the higher temperature outdoors (at 20°C), the mantle expanded while T_c declined 3°C in 10 min. (The mantle temperature increased). Within a half hour, however, T_c began to increase again and then reached the 35°C typical of free swarms. In the second trial (Fig. 16), the swarm was taken from 1°C to the relatively warm outdoors at 16°C . Instead of increasing, T_c again declined (from $37\text{--}34^\circ\text{C}$ in 15 min) and then stabilized between $34\text{--}35^\circ\text{C}$. The rapid T_c declines were presumably due to an increase in heat loss as the bees in the swarm mantle loosened up and reduced their role as insulators.

In the reverse experiment a swarm that had been maintained at high T_A (26°C) was suddenly (inside 2 min) put into the cold room at 1°C . In these bees T_c declined only 2°C in 65 min, from $29\text{--}27^\circ\text{C}$. The T_m declined from $27\text{--}17^\circ\text{C}$ in 50 min, but then its temperature rose to 20°C in the next 15 min, indicating that it is regulated and not a passive function of T_A . Since T_c in this example had declined slightly, rather than having increased, the temperature increase of the bees on the swarm periphery was due to their metabolism. Indirectly the bees on the swarm periphery were also affecting T_c , since by their heat production they were reducing the outward temperature gradient, and hence the rate of heat loss of the swarm exterior.

A second swarm transferred from high T_A to low T_A behaved similarly. This second (free) swarm, consisting of approximately 20000 bees, had a T_c of 36°C and a T_m of 25.5°C at $T_A = 16.5^\circ\text{C}$. When placed to the low T_A of 1°C , T_m rose from $25.5\text{--}28^\circ\text{C}$ within 7 m (Fig. 16), while T_c declined from $36\text{--}31^\circ\text{C}$ in 40 m and then gradually increased back to 33°C .

The above data show that the bees on the swarm periphery respond to the sudden

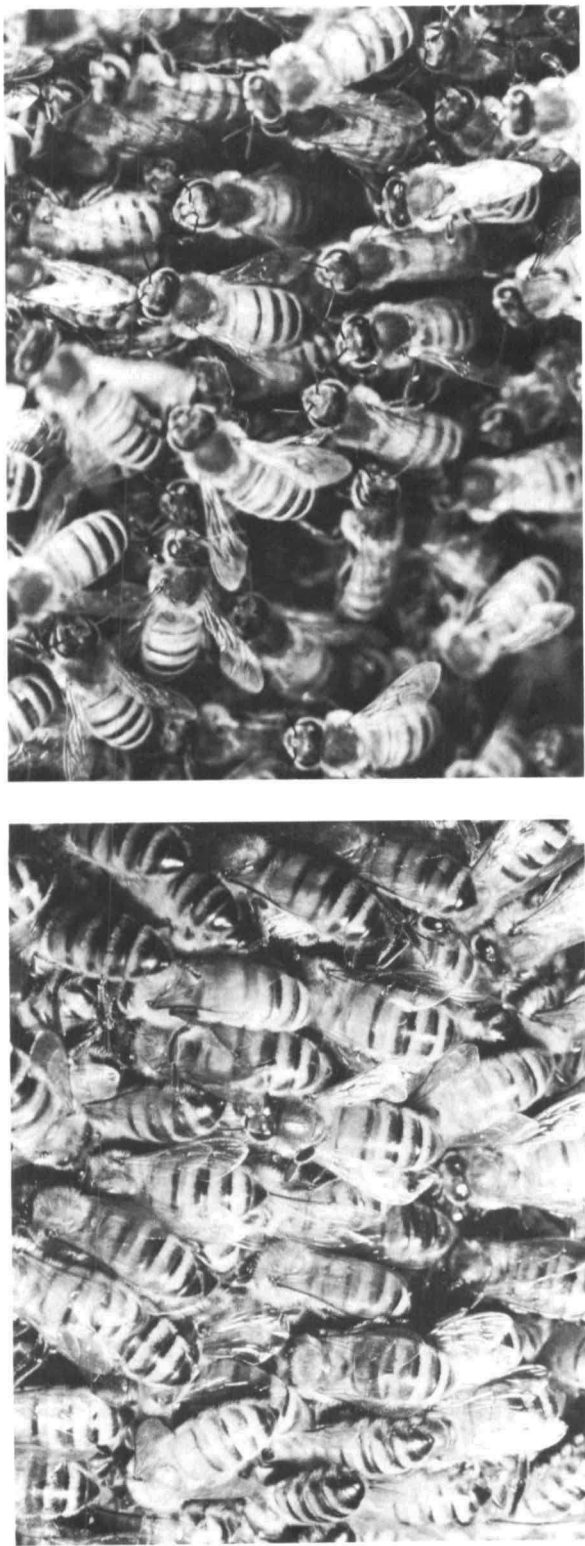


Fig. 15. Photographs of the swarm mantle at $T_A = 3^\circ\text{C}$ (left) and at $T_A = 25^\circ\text{C}$ (right) showing orientation of bees and relative mantle porosity.

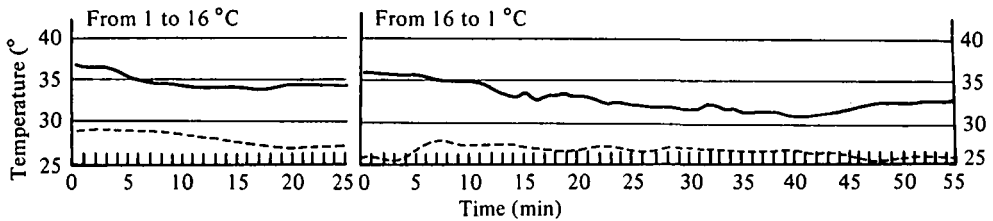


Fig. 16. Changes of core (—) and mantle (---) temperature of a swarm of approximately 20000 bees that had been equilibrated to 1 °C in the laboratory and then placed (within 2 min) outdoors to 16 °C (left) and vice versa (right). Note the immediate decline of T_c as the swarm is placed to the higher T_A , and the delayed response in T_c increase after initial cooling with an immediate T_m increase in the reverse experiment.

cold they experienced by heat production; they resist cooling. However, they do not cause sudden cluster contraction to retard heat loss. After 30 min at 0 °C the cluster is visibly smaller, but at 60 min the cluster is still contracting, and contraction is not yet completed.

(E) 'Co-ordination' of swarm thermoregulation

Swarm temperature, as indicated above, is regulated by a complex interplay involving regulation of heat production and control of heat loss. However, the temperature is not regulated uniformly throughout the swarm. The core and mantle are usually regulated at different temperatures, and the activity of bees in one part of the swarm cluster affects the temperature of bees in another part. Is the complex swarm response governed by a central directive, analogous to a control centre as in the central nervous system of an animal? Does swarm thermoregulation involve a complex social response, as hive thermoregulation at high T_A (Lindauer, 1954), or are the responses of the individual bees sufficiently intricate and diverse to result in the seemingly coordinated pattern of response? The following experiments were designed to test a number of possible alternative mechanisms that could be involved in the observed swarm thermoregulatory responses.

(a) *The queen.* The queen plays a large role in swarm cohesiveness, but it is doubtful that she has a direct role in thermoregulation, as such. A swarm weighing 602 g was gently pulled apart to create two groups of bees, one weighing 236 g and the other weighing 366 g. Both groups maintained core and mantle temperatures of 35–36 °C and 19 °C, respectively, like those of the parent cluster. The bees were killed and examined; only one of the experimental daughter clusters contained a queen. The presence of a queen was thus not necessary to achieve the high temperature in the centre of the swarm cluster.

(b) *Exchange of bees between swarm core and periphery.* The observation that T_c were sometimes higher at low than at high T_A could conceivably suggest that bees in the interior 'knew' that it was cold outside and were producing heat to counteract the heat loss on the exterior. Did bees travel between the swarm core and mantle to test external T_A ? This possibility seems unlikely, as indicated by the following experiments.

To determine if, or at what rate, bees from the mantle of the swarm change places with those in the swarm interior, bees that were part of the swarm exterior were

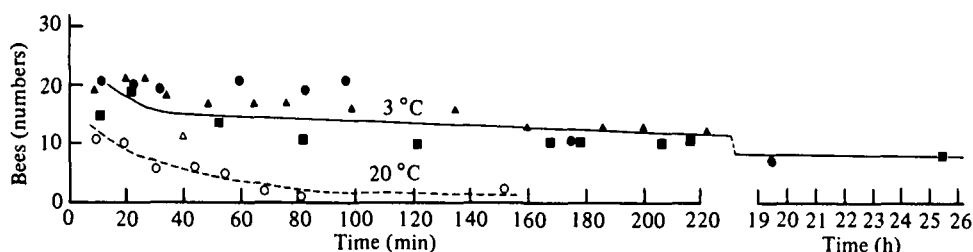


Fig. 17. Numbers of marked bees seen on the mantle of a captive swarm as a function of time after being paint-marked while on the swarm mantle. Different filled symbols indicate experiments at 3 °C, and open circles indicate one experiment at 20 °C. Swarm size was 16 600 bees, except for Δ 5200 bees).

marked by lightly daubing their wings *in situ* with quick-drying enamel paint (Pactra 'namel from Pactra Industries, Inc., Los Angeles, CA 90028).

In one set of four experiments at 3 °C with 50 paint-marked bees each, the numbers of marked individuals were subsequently counted. The marking procedure appeared to agitate the bees for several minutes in the localized swarm area of the marking. Relevant observations therefore only proceeded 10 or more minutes later, when the bees appeared to have again come to rest.

More than half of the marked bees disappeared from the surface of the swarm during the few minutes that they were agitated, but after 10 min most of the remaining marked bees remained in place. For example, in one swarm of 16 600 bees at 3 °C there were on the average 15 bees out of a batch of 50 marked ones visible after 40 min, and at 200 min there were still 12 remaining on the swarm surface. Approximately eight remained after one day (Fig. 17). At 20 °C, on the other hand, the bees of the same swarm were visibly active on the swarm surface, and most of the 50 marked bees had entered the swarm in 80 min (Fig. 17).

The 'slow' disappearance of marked bees from the swarm mantle is not due to the reaching of an equilibrium of bees entering and returning. First, the bees disappeared primarily during the marking disturbance, and not under the more normal conditions a few minutes later when they had come to rest. In order to determine how many bees could be counted on the swarm surface when all bees were randomly distributed throughout the swarm, I destroyed the swarm cluster (by shaking it apart) containing 150 marked bees (from three experiments). When the swarm reformed there were 13 marked bees visible on the mantle. This is an average of 4.3 bees for each of the experiments with 50 bees each, in contrast to the eight per experiment observed after one day (Fig. 17). Thus, the bees were not yet in equilibrium after 1 day, or the paint-marked bees previously observed on the swarm mantle had a preference for the mantle and had returned to it. The latter supposition was tested in another experiment. For example, after the 13 of the 150 marked bees were removed, one would predict that, if the remaining marked 137 bees moved randomly, 11.9 would eventually be seen on the surface. On the other hand, if the 13 bees that were removed from the surface constitute a large portion of a surface-loving cohort, then there should be fewer than 12 appearing at the surface in subsequent swarm reshuffling. When the swarm was scrambled a second time (by shaking it and letting it reform) it had only seven marked bees on the surface, rather than the 11.9 predicted in random mixing. In addition, the bees that stayed on the mantle at low T_A remained for the most part in relatively precise locations, engaging in little lateral motion (Fig. 18).

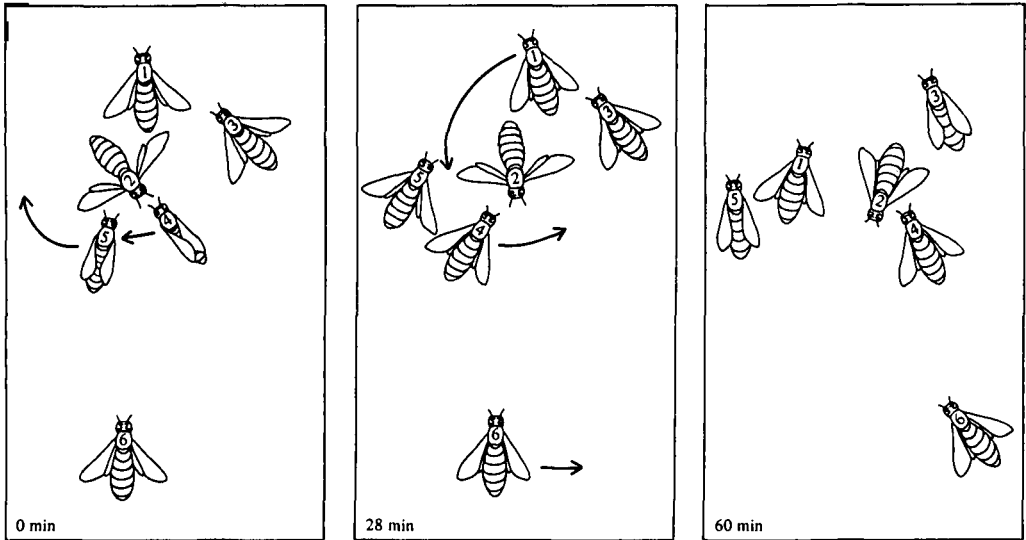


Fig. 18. Movements of six individually paint-marked bees were identified by arbitrary numbers on a captive swarm of 16600 bees at 3 °C over a 60 min period. From photographs.

(c) *Physical isolation within the swarm.* Exchange of bees between core and mantle is not necessary to maintain a high T_c at low T_A . When bees filling the interior of a swarm were physically prevented from contacting the swarm mantle (see Methods) the swarm core was maintained at 37 °C at T_A of 4 °C (Fig. 19), near the same upper T_c observed in swarms where bees had free access between the core and the periphery that experiences the fluctuations in ambient temperature (Fig. 2).

(d) *Sound communication?* Do the bees in the swarm core produce heat in response to sounds produced by the bees on the swarm periphery that are shivering at low T_A ? A swarm was allowed to form around a small speaker, and the taped recordings of bees from the mantle of a swarm cluster held at 3 °C, as well as sounds from a microphone placed in the centre of this cluster, were played into the interior of a swarm with a T_c of 30 °C at $T_A = 20$ °C. There was no noticeable response in either case in the temperatures continuously recorded in the centre of the swarm near the speaker when these bee sounds (as well as recordings of African 'killer' bees attacking a microphone) were broadcast in the centre of the swarm with sufficient volume to be conspicuously audible through the swarm to a person standing near it.

(e) *Gas exchange between swarms.* Gas was exchanged from the core of one swarm to that of another in order to determine if low concentrations of a pheromone or some other chemical are involved in stimulating bees to produce heat in the swarm interior in response to external thermal conditions. One swarm was held in a cold room at 4 °C, where it maintained a T_c of 26–28 °C during the experiment. Another swarm, with $T_c = 28$ –30 °C, was maintained outside the cold room at an ambient temperature of 20 °C. A tygon tube connected the centres of the two swarms, and a peristaltic pump was used to exchange gas (at 70 ml/min) between the two swarm cores. This exchange, either from the 4 °C swarm to the 20 °C, or vice versa, resulted in no observable T_c change, suggesting that CO₂, or other chemical agents, are probably not involved as major factors affecting the normal dynamics of swarm temperature regulation.

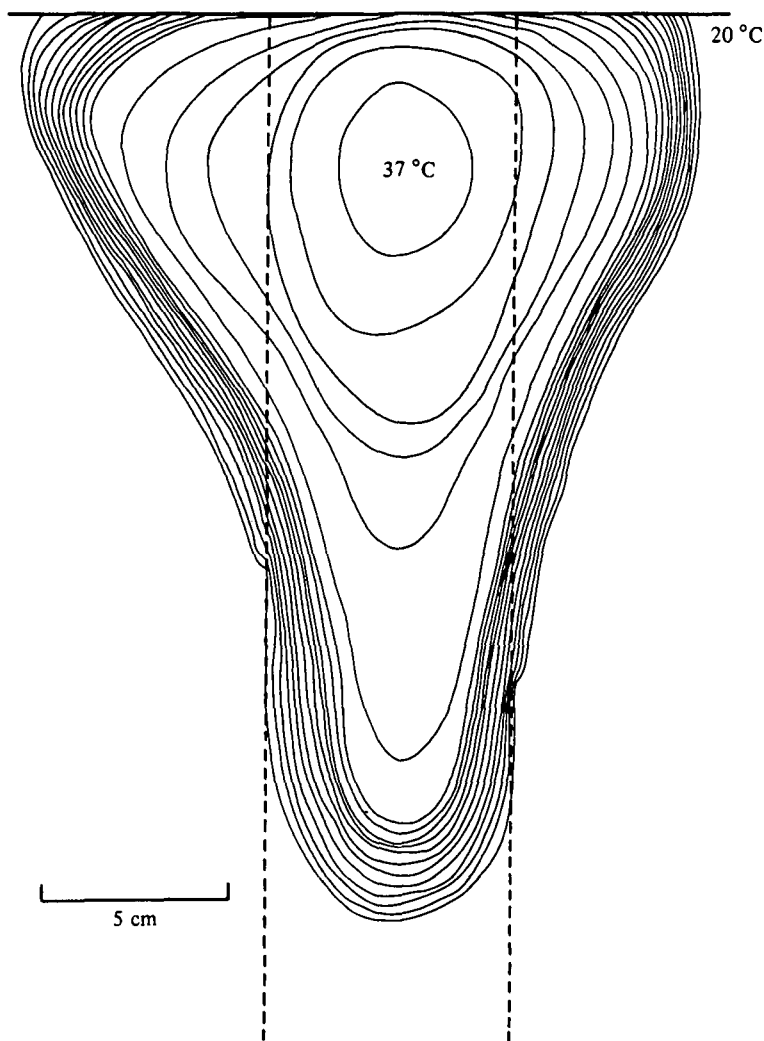


Fig. 19. Temperature isotherms (1 °C) in a swarm of 8000 bees that is partially built in a gauze cylinder attached to the plexiglass foothold of the swarm. $T_A = 4$ °C.

(F) *Thermoregulation of bees on the swarm mantle*

The bees on the swarm mantle, at least in 'inactive' captive swarms, are incapable of immediate flight at $T_A < 20$ °C. When the swarm is distributed (by blowing on it, touching it, or vibrating it), the bees on the swarm mantle raise their abdomens and expose their stingers. If the disturbance is great enough, active, flight-ready, bees emerge from the swarm interior, walk actively about on the swarm surface, and sometimes attack. At $T_A > 25$ °C a slight disturbance on the swarm exterior brings many active bees to the swarm surface. In addition, at high T_A bees that are stationary and attached to each other in the mantle may also disengage and walk.

At least at T_A of 16 °C or less, there was no overlap in thoracic temperature between the bees that made up the swarm mantle and those that walked over them. When bees were pulled from the mantle to measure their T_{Th} , other bees came to the swarm

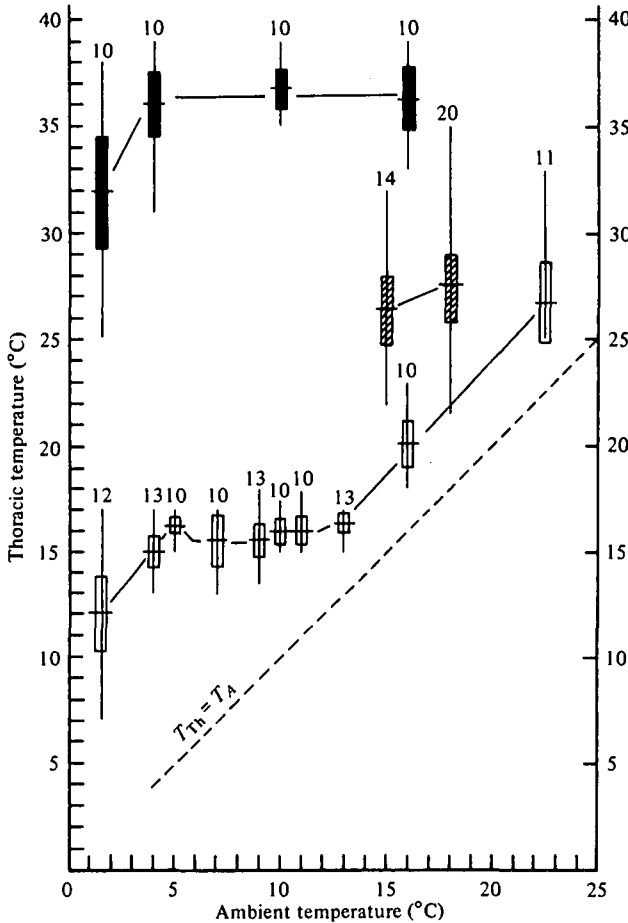


Fig. 20. Thoracic temperatures of bees on the swarm mantle, either attached to each other to form the mantle (open bars) or walking on top of the mantle (closed bars). The two hatched bars represent data of stationary bees from free swarms. The other data are from captive swarms. Two standard errors and the range are indicated on each side of the mean. Numbers indicate sample size.

exterior, whose T_{Th} were also measured. The T_{Th} of bees composing the swarm mantle was, on the average, 15–16 °C independent of T_A over the range of T_A from 4–13 °C (Fig. 20). Above 13 °C their T_{Th} was no longer stabilized and averaged 4 °C above T_A .

The T_{Th} of bees walking on the swarm mantle was also stabilized over a similar range of T_A , but it was regulated near 36 °C, (21 °C higher than that of bees constituting the mantle of the swarm). In general, the T_{Th} of the bees walking on the swarm was similar to T_e , while the T_{Th} of the bees of the swarm mantle was the same as T_m or several °C lower.

Mantle bees of free (active) swarms had significantly ($P < 0.05$) higher T_{Th} than those of captive swarms, but their T_{Th} were usually still significantly lower ($P < 0.05$) than those of bees that came to the swarm surface when the swarm was disturbed (Fig. 20).

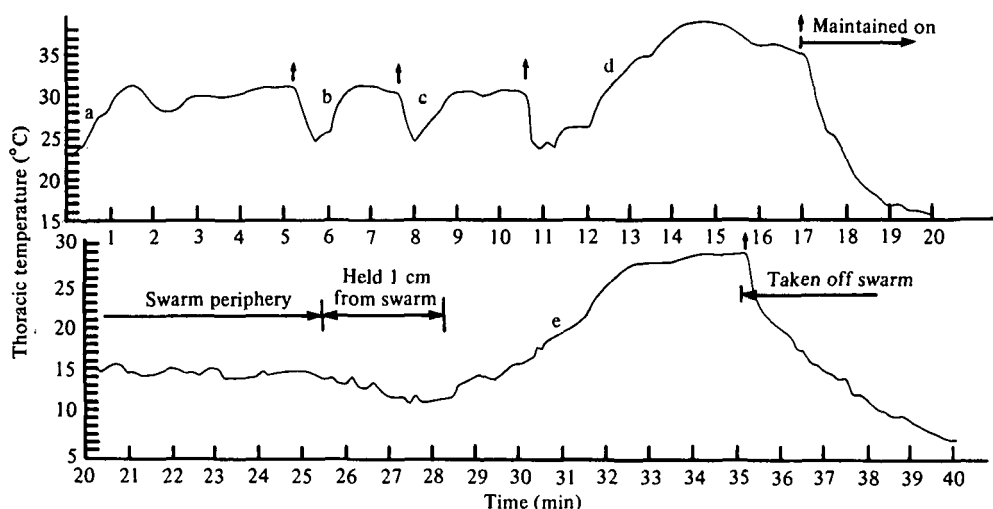


Fig. 21. Thoracic temperature of a bee from the swarm mantle that was returned to the swarm mantle, allowed to enter the swarm (a-e) and pulled back out to the swarm mantle (arrows), maintained on the swarm mantle, held 1 cm from the mantle, and taken off the swarm to T_A of 4 °C.

The surface temperature of the swarm cluster also increased prior to swarm take-off, when all of the bees presumably had high T_{Th} . However, high T_m of free swarms were also observed in the daytime without subsequent swarm take-off. Episodes of elevated T_m appeared to be correlated with dance activity on the swarm exterior. Mantle temperatures were always considerably lower than T_c when the bees on the swarm mantle showed little motion.

At low T_A the bees on the swarm mantle maintained their T_{Th} above 15 °C, which is high enough to avoid cold torpor so that they can quickly warm up, either by way of their own endothermic heat production, or by crawling into the swarm interior. For example, a 46-gauge wire thermocouple probe was used as a 'leash' while measuring the T_{Th} of a bee on the swarm mantle at T_A of 4 °C. The temperature of the bee could be lowered or raised by pulling the animal out of the swarm cluster or allowing it to burrow back into the cluster. When the tether was allowed to be loose the bee (probably agitated, and attempting to escape?) immediately crawled back into the swarm and was warmed to 30 °C. When the bee was allowed to crawl on the outside of the swarm, with the tether being held taut so that the insect could not enter the swarm, its T_{Th} was maintained at 15 °C (Fig. 21) like that of other bees on the swarm periphery (Fig. 20). The bee with its $T_{Th} = 15$ °C was still able to crawl into the swarm cluster, through layers of tightly packed bees, and achieve a T_{Th} of at least 28.5 °C within several minutes (Fig. 21). When taken completely off the swarm, the bee quickly entered cold torpor. As indicated previously, however, undisturbed bees on the swarm mantle normally remained for many hours, and possibly for several days, without attempting to crawl into the swarm interior to get warmed up (Figs. 17, 18).

Individual bees taken from a swarm mantle (Fig. 22) or from a hive entrance and tethered by similar light thermocouple leads displayed no apparent differences in

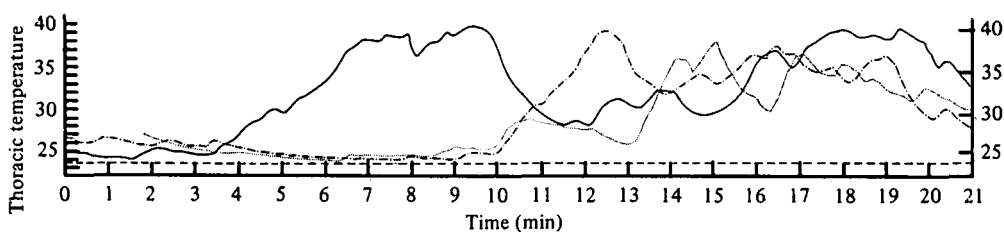


Fig. 22. Thoracic temperature of three bees at 24 °C, that had been stationary with a low T_{Th} on the mantle of a swarm at 3 °C several minutes before.

endothermically elevated T_{Th} . In both groups of bees endothermy was largely a function of feeding; the bees became torpid when their honeystomach was empty, and they warmed up within seconds after they were offered sugar water. In both groups of bees T_{Th} varied greatly from one individual to the next, tending to fluctuate widely without being regulated at any specific set-point so long as the bees were walking about. None of these endothermic bees buzzed during warm-up, and also unlike the bees on the swarm mantle, these bees maintained their wings folded over the abdomen except when attempting to fly.

DISCUSSION

When a 'prime' swarm, consisting of approximately half of a colony's 50000 or so inhabitants, leaves the hive with the old queen, the bees cluster typically in an unprotected place for 1–2 days before finding and occupying a new hive (see Lindauer, 1955). 'After swarms', which sometimes leave the colony after prime swarms, are composed of fewer bees. They contain one or more virgin queens, and they carry less food reserves (Otis *et al.* 1980). Prime and after swarms were not distinguished in this study, in part because observations on any one of the 14 swarms studied were short-term, so that depletion of food reserves was probably not a major factor in thermoregulatory energetics.

A honeybee swarm is not a random aggregation of independent individuals. It has a specific physical organization, and some of its activities are integrated by complex communication. The physical structure of the swarm consists of a mantle of bees in several layers, connected to each other in chains (Meyer, 1956). These 'Hüllbienen' are for the most part 18–26 days old. Inside the swarm cluster are more hanging chains of primarily younger bees, the 'Innenbienen', that are connected in various places to the mantle. Large spaces within the swarm interior allow the bees to move freely. Meyer (1956) also reports that the bees enter and leave the swarm by a flight hole in the mantle, the 'Flugloch'. In the present study, however, I observed (at $T_A = 14$ –20 °C) bees leaving and returning to four free swarms without making use of a flight hole.

Meyer (1956) reported that approximately two-thirds of the bees on the exterior change places with those on the interior every 10 min. I did not observe such rapid exchange of bees between the swarm mantle and the interior in captive swarms (Figs. 17, 18), except when they were disturbed or at high T_A . However, data from marked bees confirmed the previous observations that the outside bees tended to be a

different subset from those in the interior. At high T_A the bees on the swarm exterior were moving about, while at low T_A they tended to be locked into stationary positions (Fig. 18). However, since there was usually more activity on the mantle of free than in captive swarms, this may have been accompanied by a concomitant greater exchange of bees. Presumably Meyer (1956) observed her free swarms at $T_A > 17^\circ\text{C}$. My data on captive swarms indicate, however, that the exchange of bees between exterior and interior does not have a thermoregulatory function, since the same T_c were maintained regardless of the activity, or temperature, on or of the swarm mantle (Figs. 3, 5).

Ultimately, the functional unity of a swarm is achieved not by physical configurations among the component bees, but by the communication among them. As elegantly demonstrated by Lindauer (1954), the communication system allows the bees of a hive to thermoregulate at high T_A , and in a swarm the communication system is used to come to a consensus on the best possible available future nest site (Lindauer, 1955). Mechanisms of communication allow the swarm consisting of 30000 or more bees to leave their cluster in seconds and fly as a unit to their chosen nest site. It would seem that communication could also be involved in coordinating activities between bees at the swarm core, where the highest temperatures are generated, and at the swarm mantle, the only place where bees experience the changes at the ambient thermal environment.

(A) *Mechanisms of thermoregulation*

The data of the present study confirm the previous observations that core temperature is regulated relatively precisely (Nagy & Stallone, 1976), and that temperatures in other parts of the swarm cluster may vary widely (Büdel, 1958). Regulated cluster-core temperatures were nearly identical at $35\text{--}36^\circ\text{C}$, with those recorded in the brood nest (Figs. 2, 4) and they were within approximately 2°C of those in bees during and just before vigorous and continuous flight activity at near optimum T_A for flight (Heinrich, 1979). These data suggest that 36°C is a preferred body temperature of active bees as well as that most suitable for the development of their brood (Himmer, 1927). It is not immediately clear why $35\text{--}36^\circ\text{C}$ is also a preferred temperature of the centre in the broodless cluster with relatively inactive bees (see below). It has previously been supposed that the bees have different temperature set-points for the brood-less areas of the nest. But perhaps it is more correct to presume that, within given energy constraints, the bees maintain temperatures near $35\text{--}36^\circ\text{C}$ whenever they find it feasible to do so by clustering, and that the pheromones that are associated with brood thermoregulation at 36°C (Koeniger, 1978), are aggregation pheromones that induce clustering and not thermoregulation, *per se*. Clustering results in the accumulation of heat, which is followed by thermoregulation.

If $35\text{--}36^\circ\text{C}$ are 'preferred' temperatures of the bees, it begs the question why generally only the bees in the centre of the swarm cluster achieve it. I speculate that like the preferred activity temperatures, which are near the maximum tolerable (see Heinrich, 1977), the 'preferred' swarm core temperatures are also close to an upper set-point. If so, then it provides an explanation for the tolerance without apparent attempt at thermoregulation, of most of the bees other than those of the swarm core

■ lower temperatures. The evidence for the above hypothesis comes mostly from the observation that core bees of large swarms regulate the rate of heat loss from the swarm core, rather than regulating the rate of heat production. The core bees tend to be the younger bees (Meyer, 1955) that have the lowest metabolic rates and the least ability to thermoregulate (Allen, 1955). Young bees achieve optimum temperatures primarily by behavioural thermoregulation, seeking areas of high T_A where they are warmed passively (Allen, 1955).

Individual bees by themselves do not stabilize their T_{Th} by endogenous heat production at any one specific setpoint when not in flight (Figs. 21, 22). They expend heat for thermoregulation, but as individuals their capacity to thermoregulate is energetically prohibitive for more than a few minutes at a time. In a large cluster, however, the bees near the centre are necessarily heated by their own *resting* metabolism, particularly if the bees on the swarm mantle are tightly packed to retard the rate of heat loss from the centre. By crowding, however, the bees on the mantle are presumably first of all affecting their own body temperatures by conserving the heat that they produce. Free & Spencer-Booth (1958) have shown that in groups of 10–200 bees, the larger groups have the highest core temperatures. The bees cluster, reducing their rates of food consumption due to elevated metabolism. Presumably the results of the small bee clusters can be extrapolated to the present study. However, in swarms of 1000–16000 individuals, the majority of the individuals are surrounded by other bees and thus not experiencing the extereal T_A .

In large clusters, heat loss rather than heat production begins to predominate as a necessary regulatory mechanism. For example, in a dense cluster of 30000 bees, the bees in the core have a cooling rate of $0.001315\text{ }^{\circ}\text{C min}^{-1}\text{ }^{\circ}\text{C}^{-1}$ (see Fig. 8). This corresponds to a passive cooling rate of $30 \times 0.001315\text{ }^{\circ}\text{C min}^{-1}\text{ }^{\circ}\text{C}^{-1} = 0.0395\text{ }^{\circ}\text{C min}^{-1}$ if the swarm were to maintain $T_c = 35\text{ }^{\circ}\text{C}$ at $T_A = 5\text{ }^{\circ}\text{C}$. A bee weighing 115 mg (with a specific heat = $0.8\text{ cal g}^{-1}\text{ }^{\circ}\text{C}^{-1}$) in the centre of the cluster and cooling only passively, would need to expend $0.0395\text{ }^{\circ}\text{C min}^{-1} \times 0.115\text{ g} \times 0.8\text{ cal g}^{-1}\text{ }^{\circ}\text{C}^{-1} = 0.0036\text{ cal min}^{-1}$, or $1.88\text{ cal g}^{-1}\text{ h}^{-1}$, or consume $1.88/4.8 = 0.39\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ to produce sufficient heat to oppose this cooling in order to stabilize T_c at $35\text{ }^{\circ}\text{C}$. How does such a calculated metabolic rate compare to measured metabolism?

The resting metabolism (when there is no electrical activity from the flight muscles) in bumblebees with $T_{Th} = 35\text{ }^{\circ}\text{C}$ is $12.5\text{ ml O}_2\text{ g thorax}^{-1}\text{ h}^{-1}$ (Fig. 1, Kammer & Heinrich, 1974). If the ratio between thoracic and body weight (2.95), and the rate of metabolism, is similar in the honeybees, then resting metabolism at $T_{Th} = 35\text{ }^{\circ}\text{C}$ is $4.24\text{ ml O}_2\text{ g}^{-1}\text{ body weight h}^{-1}$, corresponding to an $4.24/0.39 = 10.9$ times *lower* energy expenditure than that estimated above to be necessary to maintain T_c at $35\text{ }^{\circ}\text{C}$. Thus, the bees in the core of a large swarm should have a greater potential problem getting rid of excess heat, rather than having to produce heat specifically to maintain T_c at $35\text{ }^{\circ}\text{C}$, even at $T_A = 5\text{ }^{\circ}\text{C}$. Undoubtedly live bee clusters are not as dense as the clusters of dead bees used for the calculations of passive heat loss and heat production, so that the measured cooling rates (and estimated resting metabolic rates) represent lower limits.

Other calculations like those above show that in a small swarm cluster of 1000 bees, each bee in the core requires a minimum oxygen consumption rate of $8.06\text{ ml g}^{-1}\text{ h}^{-1}$ ■ or T_c to be maintained at $35\text{ }^{\circ}\text{C}$ at $T_A = 5\text{ }^{\circ}\text{C}$. Such an oxygen consumption rate is

roughly equivalent to the resting metabolism of bumblebees at that T_{Th} . Thus, swarm clusters with less than 1000 bees even the core bees would have to expend some energy in shivering to maintain T_c at 35 °C, at least at T_A near 5 °C.

Regulation of heat loss is accomplished by ventilatory currents in the swarm interior (see Fig. 12). At high T_A the swarm mantle (Fig. 15) as well as the swarm interior (Fig. 11) becomes porous, as the tightly-packed bees from the swarm interior come to the outside, creating space in the centre for ventilation to occur. As a consequence of this behaviour the whole swarm cluster responds, so that heat is released from the core.

The bees on the swarm mantle experience the direct effects of the thermal environment. However, they are affected by, and in turn affect, the thermoregulatory responses of the bees in the swarm interior. When T_c is high the bees on the mantle will also receive heat from the core, replacing heat they lose to the environment, and thus *retarding their cooling rate and reducing their burden of heat production for thermoregulation*. This burden could be reduced to the extent that they can tolerate lower body temperatures. Indeed, since excess heat that must be dissipated is passively produced in the swarm interior, it should be advantageous for the mantle bees to refrain from heat production so that the temperature gradient within the swarm is outward, and outward heat flow is facilitated. If the temperature of the swarm were maintained uniform throughout, there would be no possibility for passive conductive heat flow from the swarm core to the swarm mantle. In a cluster of 7000 bees the cooling rate of the bees on the swarm exterior at $T_m - T_A = 14$ °C was 0.20 °C min⁻¹ (Fig. 6). This indicates that those bees on the swarm periphery must have a metabolic rate of 2.0 ml O₂ g⁻¹ h⁻¹ in order to stabilize their T_{Th} at 19 °C at a T_A of 5 °C (Fig. 2). This rate of metabolism is well above that of resting bees with such a low T_{Th} (Kammer & Heinrich, 1974), confirming the visual observations that the bees on the swarm periphery shiver at low T_A .

The question arises whether the bees on the swarm periphery shiver to maintain a high temperature (35 °C) in the centre of the swarm, or whether they attempt to regulate their own T_{Th} at 19–20 °C. The data are consistent with the model that while 36 °C represents the upper temperature set-point that the core bees must guard not to exceed, approximately 15 °C represents the lower set-point that the mantle bees must guard not to fall below. Bees can survive at a T_{Th} of 5 °C, and recover after 40 h (Free & Spencer-Booth, 1960), but they cannot maintain contact and responsiveness with the rest of the swarm when T_{Th} falls much below 15 °C. The T_{Th} of bees within the swarm fluctuates widely, depending on the circumstances, between these lower and upper set-points, and there is no evidence that bees in one part of the swarm know what the temperature is in another, and modify their behaviour accordingly for swarm temperature regulation as a whole.

The data suggests, instead, that the bees on the swarm mantle, which are the older bees (Meyer, 1956), the ones with a preference for lower T_A and a greater ability to thermoregulate (Allen, 1955), play the major role in affecting swarm temperature. First, by shivering they regulate their own, and hence swarm mantle temperature (Fig. 23). Secondly by huddling and pushing inward at low T_A they affect swarm size, porosity, and internal convection currents and hence core cooling. The mantle bees

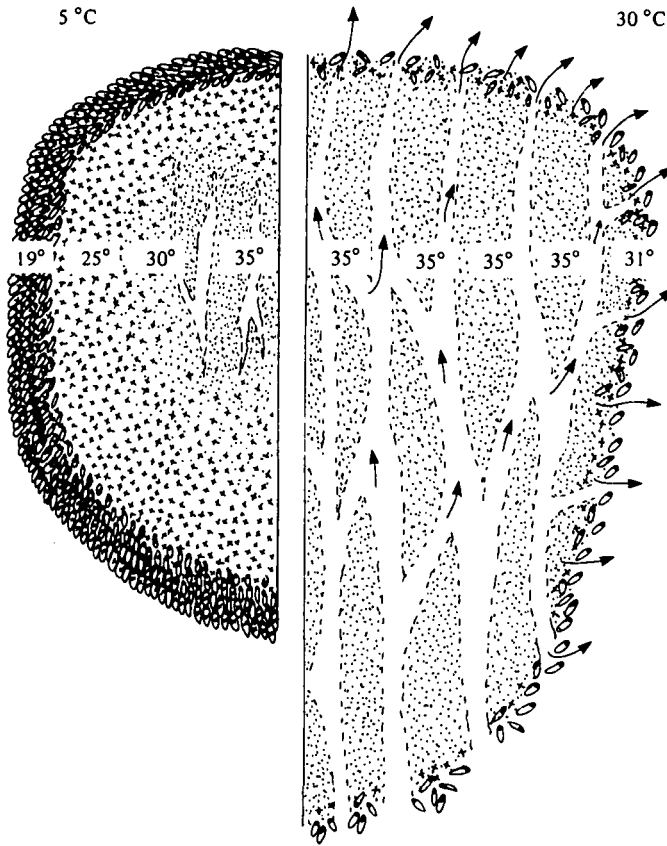


Fig. 23. Diagrammatic model summarizing thermoregulation of the swarm cluster at low T_A (left) and high T_A (right), indicating positions of bees, channels for ventilation, heat loss (arrows) and areas of active (crosses) and resting metabolism (dots), and approximate temperatures.

regulate core temperature indirectly by retaining heat, but if they are too effective in retarding heat flow, then the core bees can usually dissipate the excess by forced convection. In one instance a large swarm achieved a T_c of 46°C at $T_A = 2^\circ\text{C}$ (Fig. 2), and in numerous individual swarms there was a tendency for T_c to increase at lower T_A . The reasons for this are unclear. Possibly the mantle bees sometimes huddle so tightly at low T_A , crowding into the interior, until no more channels remain for convective cooling of the core bees.

The above model conflicts with that of Nagy & Stallone (1976), who from observations of one swarm for one day, concluded that swarms did not vary their rate of heat loss. They measured CO_2 concentrations of 0.5% inside the cluster at T_A of 15°C , and CO_2 concentration increased approximately three-fold to 1.5% at low T_A (5°C). It was concluded that T_c was regulated exclusively by appropriate adjustments of the rate of heat production. However, reducing the porosity of the swarm mantle should also increase internal CO_2 concentrations, even if metabolic rate does not change.

(B) *Evolutionary significance*

One of the major sources of mortality in honeybees is overwintering. Successful overwintering is achieved in large part by occupying a suitable nest site (Seeley, 1978), and a critical factor in the colony strategy of honeybees is thus to find and occupy a suitable nest site. When bees do not find a suitable nest site and build their combs on open branches (Lindauer, 1954; personal observations) they do not survive through the winter, at least in north-temperate regions.

Hives emit their swarms generally in the spring, while there is still time for the incipient colonies to establish themselves and lay up stores of honey to provide fuel for thermoregulation through the winter. Thus, there can be numerous swarms searching at the same time for a possibly limiting supply of suitable nest sites.

It is important that all of the bees of the swarm are able to depart to occupy a suitable nest site soon after it has been found and evaluated. Swarm thermoregulation is critical in all aspects of the process of finding a new nest and transferring to it.

The outside of the swarm must at all times be maintained above 15 °C, for if the bees cool significantly below this temperature they become immobile and are no longer able to arouse, or be aroused (Free & Spencer-Booth, 1960). Cooled bees either drop from the swarm cluster, or if the rest of the swarm departs, they are left behind.

It is not immediately obvious why the inside of the swarm cluster should be regulated near 35 °C, the same as brood temperature, particularly at night. However, 35 °C is a temperature that has significance to the bees in more than one way; it is the temperature near that required for rapid flight (Heinrich, 1979). It is understandable, therefore, that even the temperature of the outside of the swarm is brought to this temperature before the bees leave. Honeybees require 4–6 min to warm up to 35 °C from 20–23 °C (Figs. 13, 22). Thus, since only several minutes are required for warm-up before take-off is possible, there is no great disadvantage to allow the temperature of the bees in the swarm mantle to decline below the optimum temperature for flight, provided they are warm enough to arouse. By skimping on active metabolism (shivering) for heat production, the mantle bees prolong the swarm's food reserves.

Swarming honeybees gorge themselves before leaving the hive (Combs, 1972). This honey is used for thermoregulation while the swarm waits to occupy a new hive, as fuel by the scouts looking for new nest sites, as well as a substrate out of which the initial combs that provide a receptacle for newly collected honey are built.

Severe skimping of energy expenditure has the consequence of limiting the bees' ability to vigorously search out nest sites, and to respond to scouts that might find suitable nest sites, unless by chance environmental temperatures are high, possibly during a short portion of the day. However, thermoregulation of the swarm cluster allows the bees to respond quickly, in a range of weather conditions, in the most critical stage of the colony cycle: the finding and scramble competition for a suitable nest site that must henceforth serve the perennial colony.

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