



**HONEYBEE SWARM** forms on the branch of a tree. A typical swarm consists of a queen and several thousand other bees, representing about half of the population of a hive they have left abruptly in the

late spring in order to establish a new colony. The conelike shape and close packing of bees in this swarm are characteristic and will be maintained for hours or days until a new nest site has been found.

# The Regulation of Temperature in the Honeybee Swarm

*Honeybees must be warm in order to fly. Therefore the temperature of an immobile swarm must be closely controlled so that when scout bees have found a new nest site the swarm is ready for a fast takeoff*

by Bernd Heinrich

The swarming of honeybees is a late-spring phenomenon in which a queen and several thousand other bees depart abruptly from a hive, leaving another queen and the remainder of the residents to stay on. In a matter of hours or a few days the swarm establishes a domicile of its own in a new place. In the interlude, however, the bees behave strangely. The swarm coalesces into a beardlike mass on a tree branch or some other firm object. It remains there virtually immobile except for a few scouts that go off to search for a suitable living place, such as a hollow tree. If the swarm is shaken, most of the bees drop to the ground. They are too cool to fly: their flight muscles cannot function until they are warmed up. Yet when the time comes to move to the new home, the swarm is airborne in less than a minute. Apparently the swarm regulates its temperature in some way. I have investigated the matter in both free and captive swarms and have found that the bees have a remarkably fine-tuned system of thermoregulation. On reflection one can see that in a Temperate Zone climate such a system is essential to the swarm's ultimate success in establishing a viable hive.

The primary function of swarming in the "European" honeybee *Apis mellifera* (it was imported to North America from Europe) is the reproduction of colonies. Usually the queen and about half of the workers of a colony leave when the hive becomes overcrowded. A daughter queen (perhaps more than one) is left behind.

A related phenomenon is "absconding," in which the entire colony leaves if its domicile becomes unsuitable. Some species of honeybee abscond more readily than others. The difference may lie in the adaptation of the bees to their climate. In the Asian Tropics the giant honeybee (*Apis dorsata*) and the dwarf honeybee (*A. florea*), which normally build their hanging combs in the open, abscond frequently, probably in order

to move to areas where food is more abundant. The third tropical honeybee, the Indian bee (*A. indica* or *A. cerana*), builds its combs in cavities and also absconds readily, as does the African race of *A. mellifera*, which is the "killer bee" that has spread northward at a rate of about 50 kilometers per year since its introduction into South America.

Warm climate explains why the three tropical species and the southern races of *A. mellifera* abscond so readily. The colonies have much to gain by taking advantage of shifting food resources, and they do not need to lay up large stores of food to survive a Temperate Zone winter. To be this mobile means to travel light and not to spend much time choosing a site for a nest.

The honeybee in the north Temperate Zone, however, has to be quite discriminating about the kind of cavity it occupies. The opening must be small, and the size of the cavity must be such that the swarm can control its temperature during the winter. Moreover, once a cavity has been occupied the bees have to lay up much larger stores of food than they can carry with them, since the food is in effect the fuel that heats the hive. The bees must therefore have the social responses necessary for managing their food resources with maximum efficiency. They will not be able to leave the nest or the area when conditions are the worst—in the winter. Such bees are adapted for staying rather than for moving. Their swarming is focused more on reproduction than on finding better housing.

No amount of stored food and no social response in managing the internal environment of the hive can prevail long against the wind and cold of the northern winter if the bees are not in a suitable shelter. Finding, evaluating and competing to occupy suitable domiciles is therefore central to the biology of north Temperate Zone honeybees. It calls on a number of behavioral adapta-

tions, in all of which thermoregulation is of primary importance. It is instructive to consider the adaptations as a backdrop to the thermoregulation.

An important prerequisite to success in swarming is the timing. The reason swarms usually issue from hives in the spring is that the bees then have time to find a suitable place to live, to occupy it, to fill it with honeycomb and to stock the comb with stores of honey for the coming winter.

While the queen and most of the other bees in a newly formed swarm hang almost motionless from some object that is usually near the hive they have left, several scout bees begin the search for new quarters. They make up the small part (less than 5 percent) of the total population that seems to be primarily concerned with exploring rather than with the work of the hive. In an established hive the scouts are usually the bees that look for new food sources, such as flowers coming into bloom and weak hives that can be robbed. In the swarm they are the bees that look for potential hive sites.

The importance of the kind of site they find is suggested by studies that Thomas D. Seeley of Yale University has made of swarms near Ithaca, N.Y. He has found that the highest rate of mortality in the hive is during the winter and that the death rate is inversely correlated with the quality of the nest cavity. He has also found that scout bees give close attention to the size of the opening to a potential nest site, to the internal temperature and to internal convection currents. The scouts pace off the interior dimensions of the cavity. According to Seeley's measurements, the volume of the cavity chosen as a domicile is usually between 20 and 100 liters (roughly between a cubic foot and four cubic feet).

Martin Lindauer of the University of Würzburg studied honeybee swarms in Munich after World War II when he was working at the Munich Zoological Insti-



tute. He found that most of the swarms chose cavities in the ruins that then abounded in the city. Eventually he was able to predict which potential hive a given swarm would occupy.

Lindauer observed that scout bees, some of which he had marked, would sooner or later begin to "dance" on the surface of a clustered swarm, in the

same way that dancers in an established hive indicate the distance and direction to potential sources of food. Sometimes several scouts simultaneously advertised different cavities. Before dancing, a scout visited a cavity several times; it would stop advertising the site if the cavity became too wet or too hot or changed unfavorably in some other

way. The scouts also were attentive to one another's dance, visiting the other potential home sites indicated by the dances. Eventually all the scouts repeatedly visited and advertised the same site.

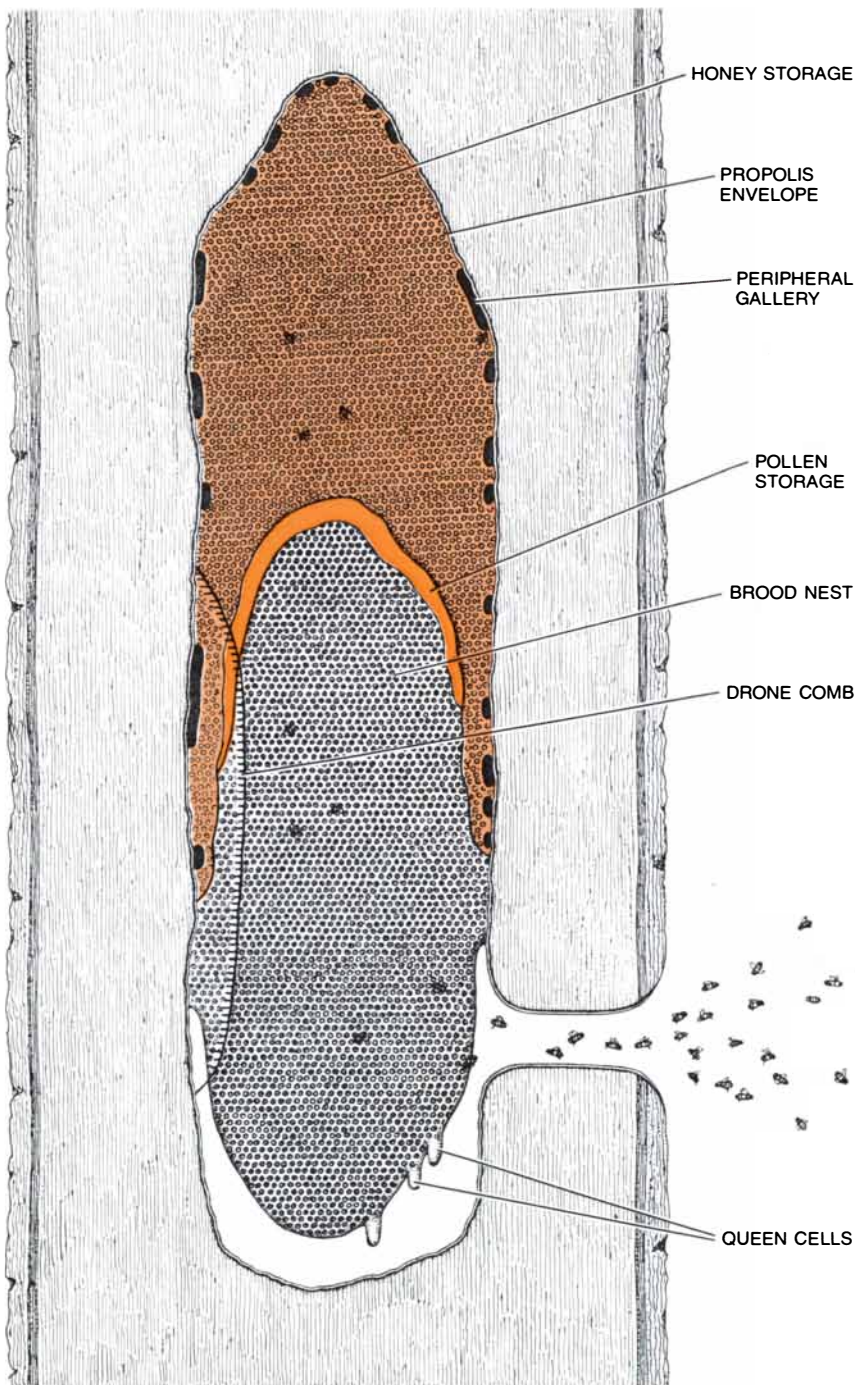
At this stage the question becomes how the swarm is aroused and guided to the site. Seeley and his colleagues observed marked scouts that had been investigating an empty hive and dancing on the swarm. About half an hour before the swarm lifted off the scouts made rapid buzzing runs into the hive. The runs appear to be an alerting signal and are not always followed by a take-off of the swarm, which suggests that the almost instantaneous takeoff may be prompted by another signal.

Once a swarm has taken flight it moves slowly at first in a cylindrical formation some 10 meters in diameter. Presumably the flight is slow because the bees are checking for the odor of the queen substance: 9-oxodec-2-enoic acid. (A swarm may take off without a queen, but it will not travel far.) The swarm soon accelerates to a speed of about 11 kilometers per hour, but some bees, the "streakers," dart much faster through the group in the direction of the new cavity. Lindauer and Seeley think the streaker bees may be the scouts pointing the way.

The scouts also point the way chemically, particularly when the goal is near. They arrive at the entrance of the cavity ahead of the mass of bees and release scent from the Nassanoff glands at the tip of their abdomen. The scent appears to serve as a final marker for the swarm. In a few minutes the thousands of bees stream into the cavity. Within hours they are cleaning out debris, building comb and foraging for nectar and pollen. A new colony has been established.

If the scouts from a swarm are unsuccessful in finding a suitable cavity in a few days or do not reach a consensus on which of several alternatives is the best one, the workers start to build comb on the object from which they are hanging. The more they build, the less likely they are to leave, since the comb represents a substantial investment of effort. Open hives may survive in places where the winter is mild, but in the Temperate Zone the bees in an open hive invariably die during the winter because they are unable to keep warm without a suitably insulated shelter.

The measurement of temperature in beehives dates back at least a century. It has long been known that the hive serves as an incubator of the larvae and pupae. The bees maintain the temperature of the brood at 35 or 36 degrees Celsius (close to 95 degrees Fahrenheit). When the air temperature is low, the bees crowd on the brood and shiver; the rapid contraction of their muscles generates body heat. When the air temperature is high, the bees reduce the internal



**TYPICAL NEST SITE** in a partly hollow tree is depicted on the basis of a number of natural nests inspected by Thomas D. Seeley of Yale University and Roger A. Morse of Cornell University. It is such a site that scout bees from a swarm examine carefully and repeatedly while the swarm waits in its characteristic clustered form. Once the scouts have reached a consensus on a site they alert the swarm, which is able to take off quickly because the bees have maintained its core temperature near 35 degrees Celsius, the optimum level for flight. The swarm flies to the site, moves in rapidly and begins to build the various structures portrayed here.

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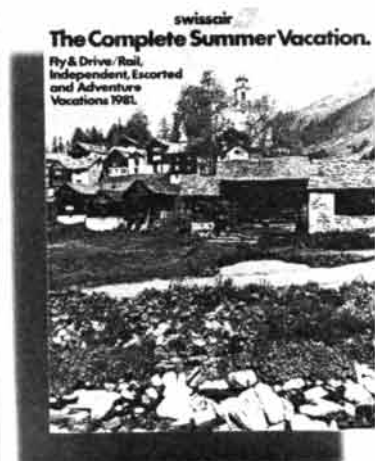


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temperature by fanning and by evaporative cooling. If the brood is allowed to cool below 30 degrees C., the larvae or pupae die or emerge with developmental defects such as deformed wings. The temperature is not rigidly controlled in sections of the hive that do not contain brood, and so thermoregulation has been thought to be needed primarily for the immature bees.

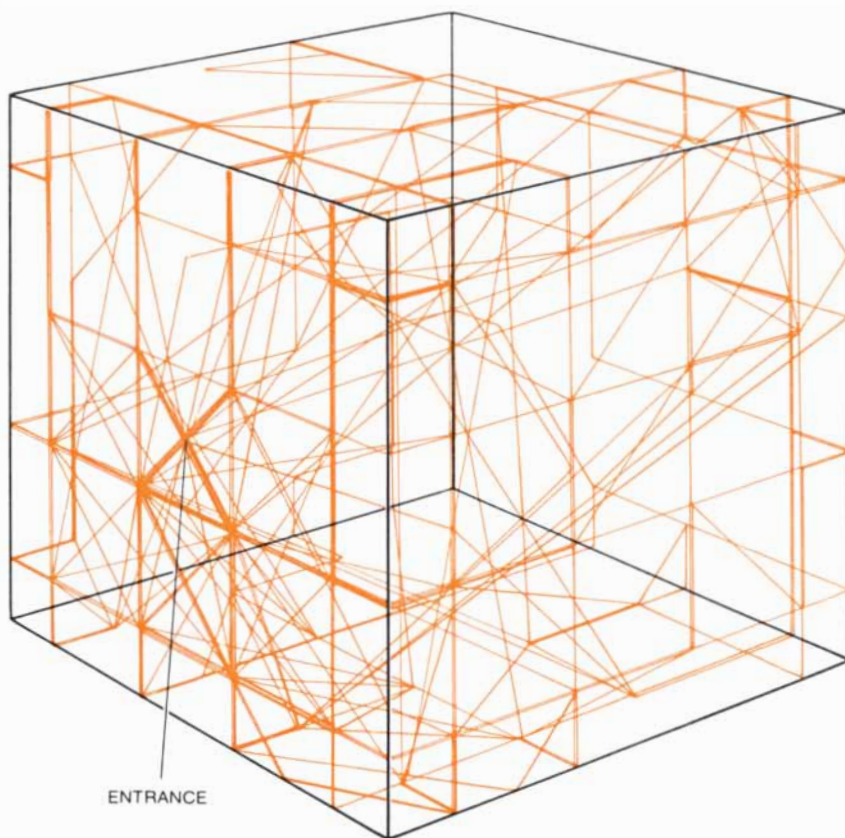
A swarm consists entirely of adult bees without eggs, larvae, pupae or comb, suggesting that thermoregulation would be absent. My preliminary measurements showed, however, that the core of the swarm is generally maintained at almost the same temperature as the temperature of the brood in a hive and either remains constant or increases when the outside temperature decreases. These observations raised two questions I sought to answer. First, how do the bees in the core of the cluster regulate their body temperature with respect to changing external temperature when they are individually experiencing the relatively constant or increasing temperature of the core? Second, what is the functional significance of thermoregulation in the swarm?

I captured many swarms by shaking them from their branches and brought them into the laboratory to assess their

temperature and metabolic rate in large respirometry vessels. The lid of such a vessel has many small holes that serve for ventilation, as a foothold for the bees (enabling them to form their swarm cluster under the lid) and as openings for the insertion of measuring devices. When I measured respiration, I sealed a second lid of solid Plexiglas over the perforated lid; air from the sealed system was circulated through an oxygen analyzer to determine the rate of expenditure of energy, which is to say the production of heat.

I also observed free swarms that were maintained on a window ledge outside my laboratory at the University of California at Berkeley. In some of them I had implanted a dozen or more thermocouples, the leads from which came into the laboratory so that I could record the reading of each thermocouple continuously for hours or days on a strip-chart recorder. The free swarms responded to ambient conditions, but with the captive swarms I could vary the ambient temperature from zero to 30 degrees C.

All the swarms showed steep temperature gradients from the core to the mantle, or perimeter. The highest temperatures were near the core. Both small swarms of 2,000 bees and swarms 15 times larger maintained a core tempera-



**PATTERN OF MOVEMENT** of a single scout bee on several inspections of a cubical box is represented in a somewhat simplified form on the basis of a reconstruction made by Seeley. The colored lines show the paths of the bee; they have been straightened for simplification. Seeley employed a grid system that enabled him to keep track of the position of the exploring bee.

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ture of about 35 degrees C. Although the core temperature varied considerably, it was independent of the ambient temperature. Since the rate of passive cooling in a swarm is a function of the surface area and the ambient temperature, the results showed clearly that the core temperature is actively regulated. This was a surprising result because the core includes only a small part of the total population of the swarm.

The mantle of the swarms was usually maintained at a much lower temperature. If the ambient temperature went down, the temperature of the mantle followed, remaining two or three degrees higher. This pattern appeared, however, only when the ambient temperature was relatively high. If it went below 20 degrees C., the temperature of the mantle stabilized. These results show that the mantle temperature is regulated in such a way that it remains close to the ambient temperature but does not go below about 17 degrees. The temperature of the rest of the swarm usually varied in a fairly smooth gradient between the 36-degree maximum of the core and the 17-degree minimum of the mantle.

Such were the general patterns revealed by many measurements, but I also found instructive variations and exceptions. For example, the captive swarms often had lower temperatures than the free ones, presumably because there is less activity in a captive swarm. When a small swarm was maintained at five degrees C. or less for several days, bees hung in seemingly lifeless chains from the tightly contracted cluster. The body temperature of these bees was close to the ambient temperature and the bees eventually dropped off. Most of them had an empty honey crop, possibly because they had exhausted their food reserves by shivering. The bees that remained on the mantle of the swarm, maintaining a body temperature of about 17 degrees C., were able to crawl but were not able to fly.

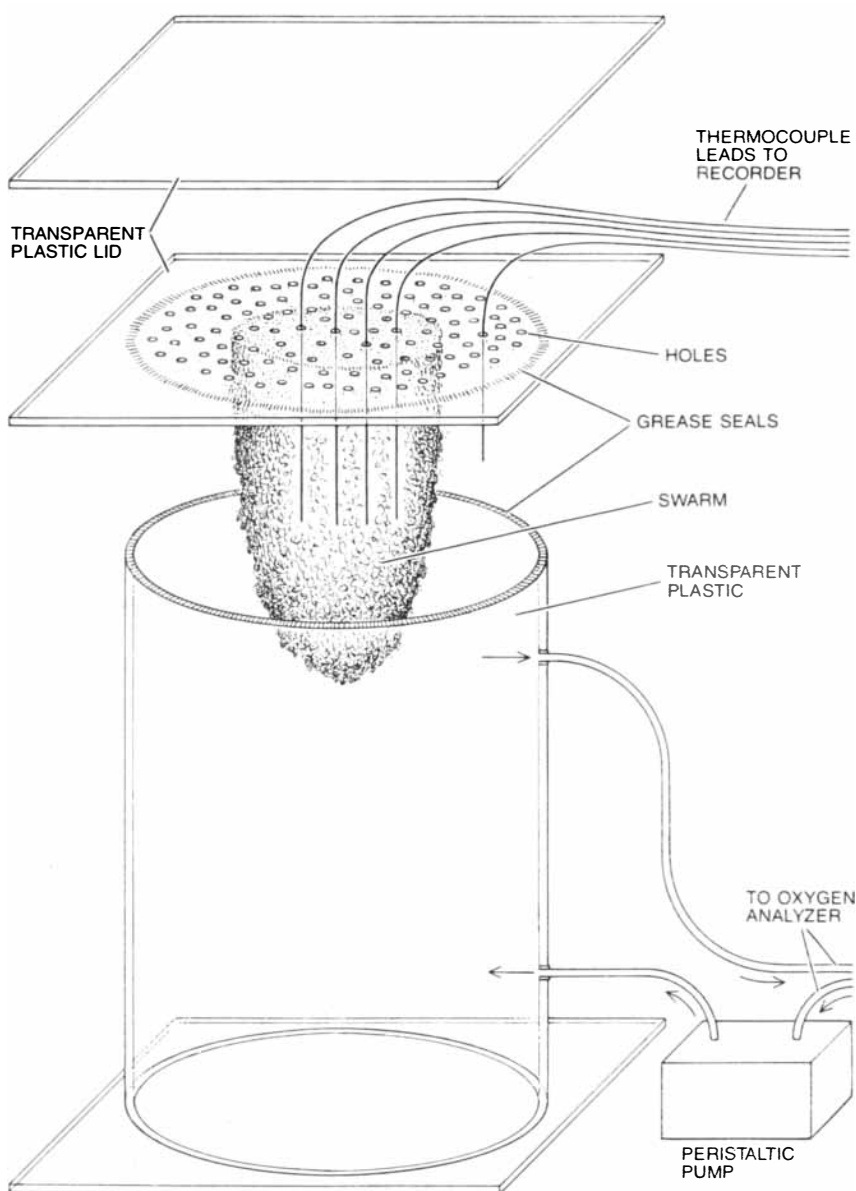
Bees usually came and went from a free swarm, and during the daytime the mantle of such a swarm was significantly warmer than the mantle of a captive one. The mantle temperature of the free swarms fluctuated above the minimum during the day. In a free swarm that was ready to take off, however, the temperature gradient disappeared as the temperature of the mantle reached the core temperature of 36 degrees C.

**H**ow is the temperature of the core regulated? It seemed reasonable to suppose that when the external temperature is dropping or the entire swarm is warming up for flight, the swarm as a whole expends more energy to counteract the increasing loss of heat. If that is the case, a small swarm should have a higher metabolic rate than a large one, and all swarms should show an elevat-

ed metabolism at relatively low external temperatures. Measurements did not support this supposition. The metabolic rate in all swarms was surprisingly low, averaging close to the resting metabolism of individual bees, with only a small increase at lower air temperatures. Moreover, in swarms of from 1,800 to 16,000 bees where the passive cooling rate varied by a factor of eight there was little or no tendency for small groups to have a higher metabolic rate than large ones. In fact, some of the highest metabolic rates were recorded in large swarms. Since for geometric reasons a large swarm has a greater proportion of its bees at the core than a small one has, and since the resting metabolic

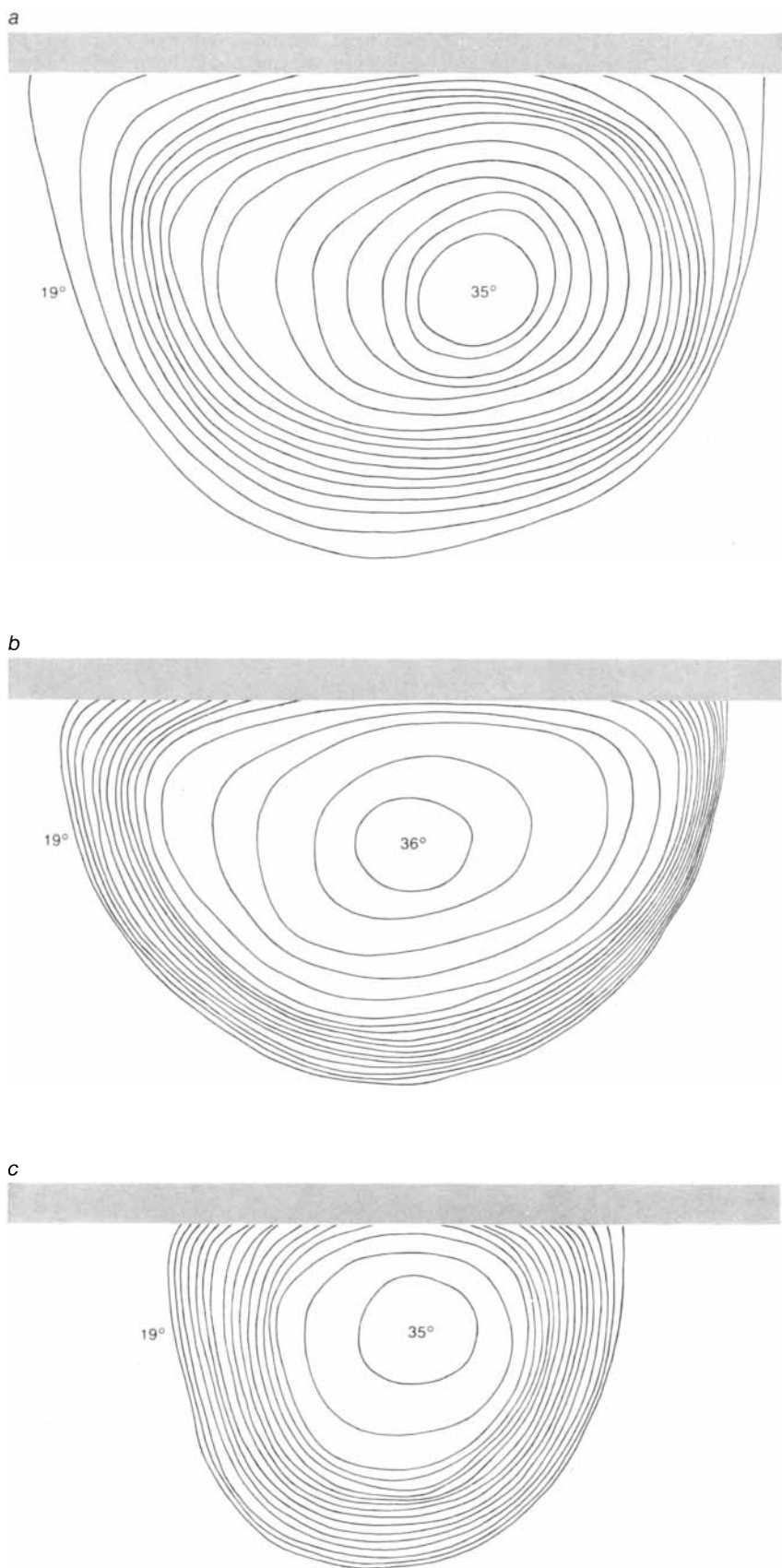
rate is a direct function of body temperature, the observed metabolic rates of large swarms could be mainly understood in terms of the passive production of heat by heated bees rather than in terms of heat production to keep warm.

The gross measurements did not reveal how much effort the bees have to put into generating heat actively, but calculations based on the passive cooling rate of bees made an estimate possible. A bee in the core cooling only passively would need to consume oxygen at a rate of .39 milliliter per gram of body weight per hour in order to maintain its temperature. This calculated rate is some 10 times lower than the consumption that would inevitably be required



**EXPERIMENTAL APPARATUS** was devised by the author to measure the temperature and metabolic rate of captive swarms. It is shown here in an exploded view. The holes in the lower lid serve as a foothold for the bees and as a source of ventilation. During a measuring period the solid lid is sealed over the ventilating lid and air is circulated from the closed system to the oxygen analyzer to determine the rate of expenditure of energy by the bees. At the same time the apparatus provides a means of measuring the temperature in parts of the swarm.





**INTERNAL TEMPERATURES** of a swarm at a low external temperature of 2.5 degrees C. (36.5 degrees Fahrenheit) were recorded in a captive swarm. Each isotherm line shows a temperature difference of one degree C. One reading (a) is for a swarm of some 5,300 bees, including a queen; the swarm was divided into two swarms, one with a queen (b) and one without (c).

by the idling metabolism of a resting bee with a body temperature of 35 degrees C. Hence even when the temperature outside the swarm is a chilly five degrees, bees in the core of a large swarm should have a problem getting rid of excess heat. Similar calculations indicate that in a small swarm (about 1,000 bees) the bees in the core would need approximately equal rates of passive heat production and heat loss to maintain their core temperature near 35 degrees. In a still smaller swarm even the bees in the core would have to shiver to maintain a temperature of 36 degrees.

The data suggested that most swarms, consisting of from 5,000 to 30,000 bees, would have no problem heating up internally. Since in such swarms the core temperature is generally held near 35 degrees C., this temperature must represent an upper set point the bees actively avoid exceeding. A small swarm of fewer than 1,000 bees should therefore be found to have a core temperature somewhat lower, and that is what my measurements showed.

How do the bees in the core avoid overheating? Again the problem can be analyzed by first examining the response of the entire swarm and then observing the behavior of individual bees. As the ambient temperature about a swarm rises, the swarm greatly expands in length and circumference. By thus increasing its surface area it achieves a larger passive loss of heat. In addition the bees on the mantle are more widely spaced and their heads are pointed outward, whereas at a lower air temperature they are bunched tightly together and their heads are pushed like shingles under the abdomens of the bees above them. The high-temperature configuration should facilitate the flow of air and heat through the mantle.

The excess heat, however, is mainly in the interior of the swarm. There must be a mechanism to move the heat from the core to the mantle. Watching swarms maintained in a transparent container, I observed that at low air temperature a swarm is an almost solid mass of bees. As the air temperature rises and the swarm expands one can see hanging curtains of immobile bees. The curtains form passageways along which bees travel rapidly from the core to the mantle and back. The passageways also serve as ventilating ducts.

The overall pattern of temperature regulation in the swarm does not reveal how the responses are coordinated. Is there some kind of central direction? Do the bees in the core communicate a need for heating or cooling by sound or chemical signals to the mantle bees that control the swarm's rate of heat loss? Or does each bee act independently?

Several experiments failed to demonstrate direct communication or cooperation. First, swarms with and swarms without a queen maintained the same

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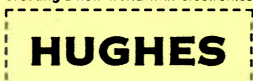
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A structural and thermal test model of NASA's Galileo Probe is undergoing a series of tests simulating every environment that the Hughes-built probe will experience from launch through descent into the Jovian atmosphere in the late 1980s. The model recently passed a descent simulation with temperatures ranging from -260°F through 240°F and pressures ranging from a vacuum through 235 pounds per square inch -- all in a span of 48 minutes. The Probe contains six instruments that will measure atmosphere characteristics to a depth corresponding to at least 10 times the pressure of air at sea level of Earth. This will be the first direct sampling of the Jovian atmosphere in an attempt to learn its composition and what causes the stunningly colorful weather patterns.

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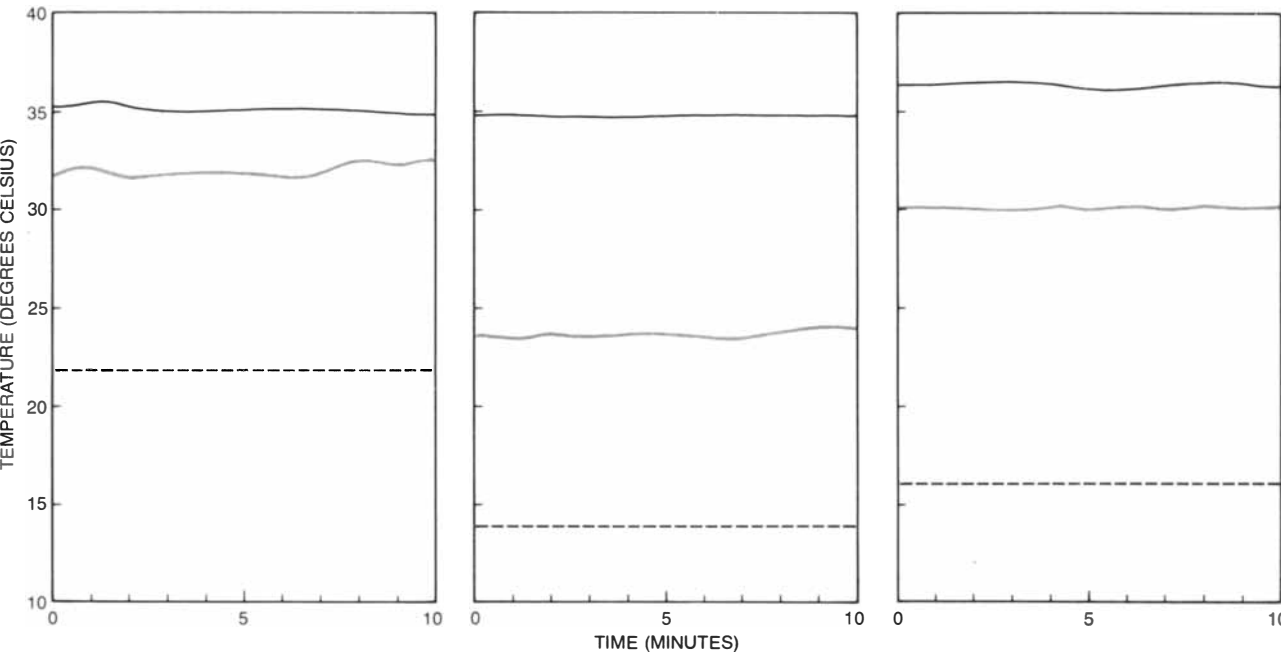
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core temperature. This finding ruled out the possibility that chemical signals from the queen in the interior of the swarm served as a thermoregulatory directive. Next I created a swarm in which the bees of the core were separated from the bees of the mantle by thin gauze. The swarm had the same temperature profile as other swarms. This finding

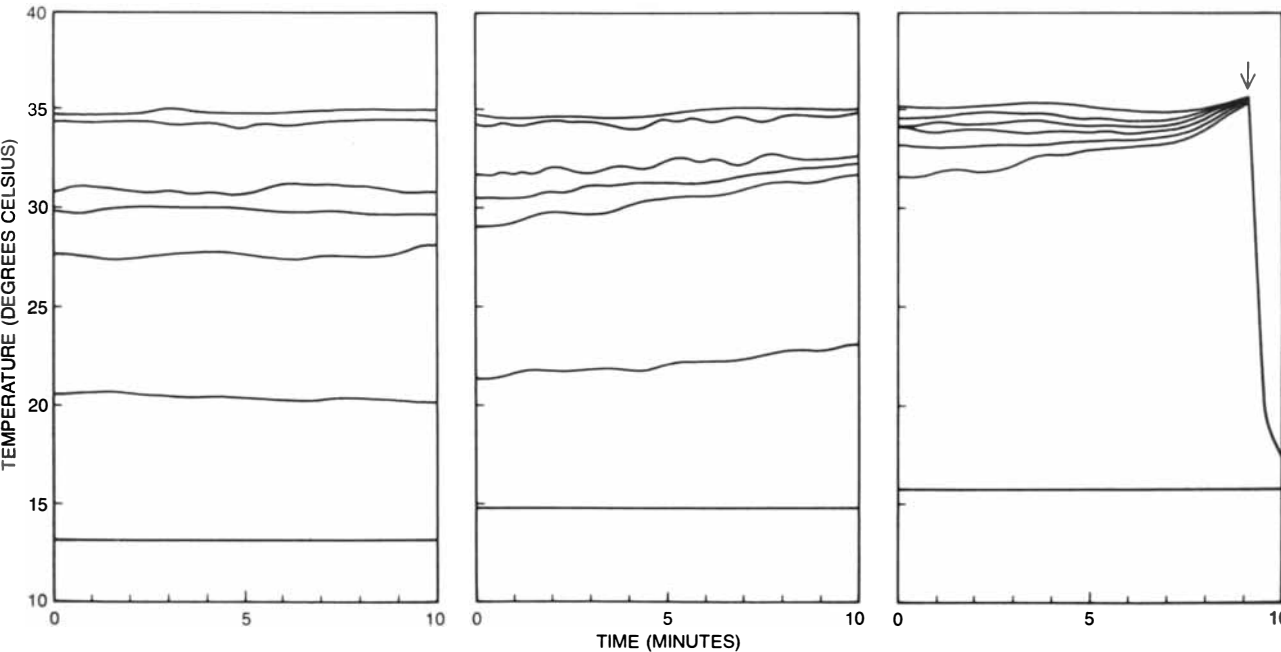
showed that even when the bees of the core could not individually sample the temperature surrounding the swarm, the core could nonetheless be maintained at a constant temperature in spite of fluctuating exterior conditions. Third, when I made tape recordings of the sounds generated by the bees in the core or the mantle at a low exterior temperature

and played the recordings back into the core or the mantle at a high exterior temperature (and vice versa), no changes in the core temperature were evoked. Finally, pumping air from the core of a swarm held at five degrees C. into one at 20 degrees (and vice versa) had no effect on either core temperature. The findings indicate that neither sounds nor chemi-



**TEMPERATURE RECORDINGS** of a free swarm of 5,000 bees were made continuously over a period of several days and are reflected here for three times: 6:30 P.M. on June 7, 3:00 A.M. on June 8 and

10:00 A.M. the same day. The broken black lines show the ambient temperature. The gray line records the temperature of the mantle (perimeter) of the swarm, the solid black line the core temperature.



**TEMPERATURE OF SWARM** before it took off to move to a new nest was recorded at 7:00 A.M., 8:00 A.M. and 10:00 A.M. on June 4. The arrow indicates when the swarm took off. The bottom curve records the ambient temperature, the next curve the mantle tempera-

ture, the next three curves record the temperature at points about halfway into the swarm and the top two curves the core temperature. The temperatures converged toward the core temperature in the two hours preceding takeoff. This swarm contained some 28,000 bees.

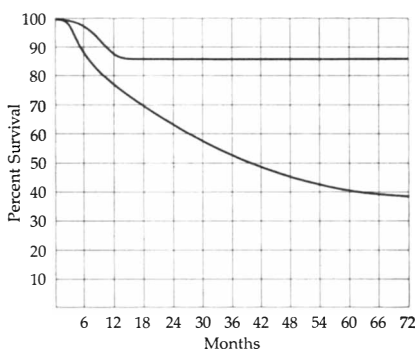
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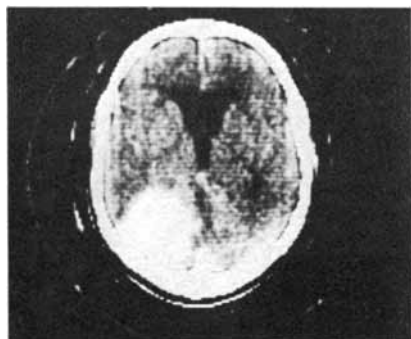
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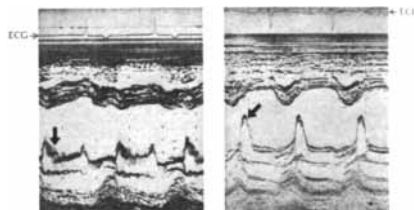
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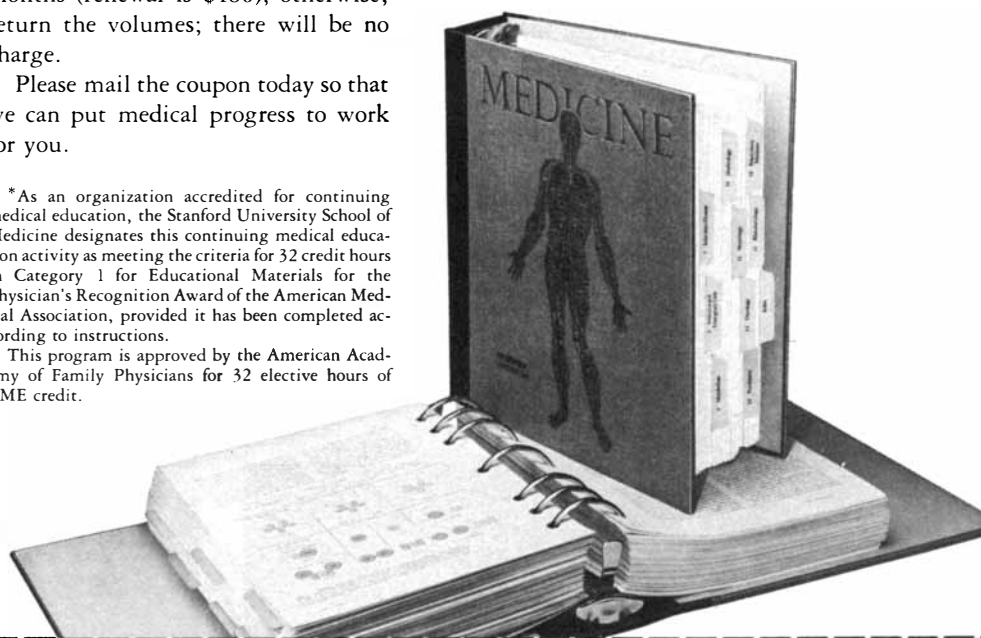
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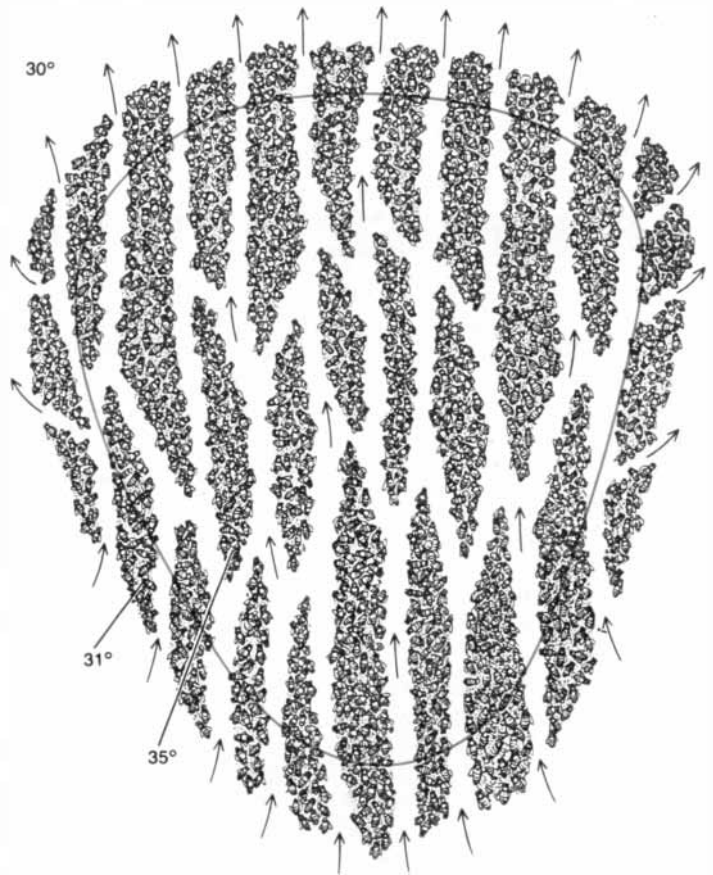
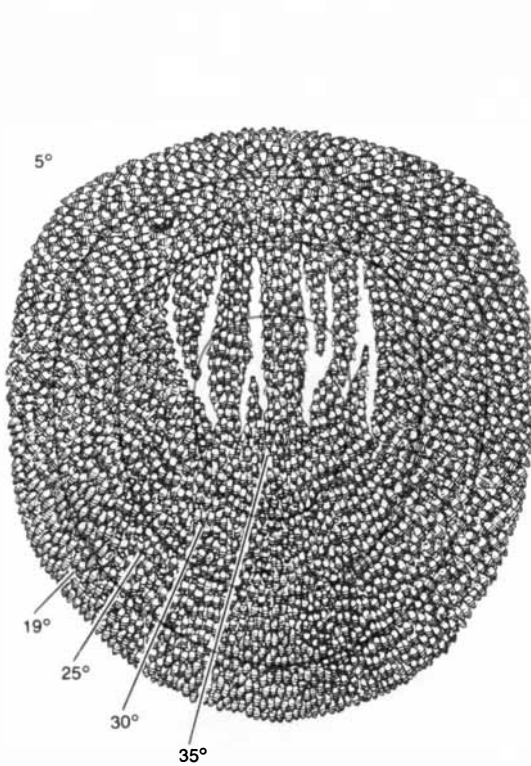
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**SCHEME OF TEMPERATURE REGULATION** by a typical bee swarm is indicated for a low ambient temperature (*left*) and a high one (*right*). In the low-temperature condition the bees cluster close together, with the bees on the perimeter adopting a shinglelike formation, the adjacent layer of bees shivering to generate heat and the bees

near the core giving off heat at their resting-metabolism level and forming corridors to dissipate heat. When the external temperature is high, the bees of the mantle assume a more open stance, most of the bees are at resting metabolism and the swarm forms a number of corridors that contribute toward the dissipation of heat (*arrows*).



**BEES OF THE MANTLE** assume different positions at low and high external temperatures. When the outside temperature is three degrees C. (*left*), the bees are packed close together and nearly every

bee has its head under the abdomen of a bee above it. At an external temperature of 25 degrees C. (*right*) the bees of the mantle are more widely spaced and most of them have their head oriented outward.

cal signals are involved in the thermoregulatory response of the swarm. Apparently the bees in the core and the mantle do not "tell" one another about the local temperature.

It was more informative to examine the behavior of individual bees. The German biologist Anton Büdel had shown that the bees in the mantle tend to be predominantly the older workers, the foragers, and that the young "house" bees tend to be inside the swarm. Moreover, M. Delia Allen of the North of Scotland College of Agriculture had shown that the older bees are better at regulating their body temperature, particularly by shivering. The young bees have little capacity for shivering and generating their own heat. In experiments that give bees a choice of temperature the younger ones seek out higher temperatures than the older ones. If bees in a swarm behave similarly, these facts fit my model of temperature regulation, in which the core bees are heated passively and the mantle bees shiver to generate heat in order to keep from being chilled below 13 degrees C., the minimum body temperature below which they lose motor coordination and fall from the cluster.

I fitted bees with a hairlike thermocouple embedded in the thorax and returned them to the mantle. The temperature measurements showed that they regulated their thoracic temperature, keeping it above 13 degrees. If they were disturbed, they crawled deeper into the cluster, and their thoracic temperature rose within minutes to more than 30 degrees. Thus I learned that the mantle bees function at temperatures well below the core temperature and also derive considerable heat from their fellows in both the mantle and the core.

It is evident that the mantle bees affect and are affected by the thermoregulatory responses of bees in the interior without direct communication. When the core temperature is high, the bees in the mantle receive heat from the core, replacing heat they lose to the environment and thereby retarding their cooling rate and reducing their burden of heat production for thermoregulation. Indeed, since the excess heat that must be dissipated is generated passively in the interior of the swarm, it should help the thermoregulation of the core if the mantle bees do not generate heat, so that the temperature gradient in the swarm is outward and the outward flow of heat is facilitated.

Do the bees in the mantle shiver to maintain an elevated temperature in the interior or do they merely attempt to regulate their own temperature at about 19 degrees C.? The data are consistent with the hypothesis that they regulate only their own temperature but that in doing so they also help the core bees. When mantle bees are cooled by a low



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ambient temperature, they crawl into the swarm, plugging the passageways for convective heat loss from the core and also reducing the mantle's surface area and porosity. I tested the hypothesis by transferring a swarm from an environment of about one degree C. to room temperature (about 20 degrees). As the hypothesis predicted, the immediate response was a drop in the core temperature and a rise in the mantle temperature as the mantle bees loosened their tight formation.

Alternatively, by crowding and shivering the mantle bees retard the loss of heat from the core. If they are too effective in retaining heat within the swarm, the core bees can partly overcome the effect by moving to the exterior, thereby creating convection currents in the swarm. There is no evidence that bees in one part of the swarm know what the temperature is in another part and modify their behavior accordingly. The bees act independently, but the result is a co-ordinated response that is beneficial to the entire swarm.

**I**t is important for all the bees of a swarm to be able to leave together to occupy a suitable nest site soon after it has been found and evaluated. Thermoregulation of the swarm is critical in all aspects of finding a new nest and occupying it. The mantle must be maintained above 15 degrees C. at all times, otherwise the bees in it could not be aroused for the takeoff.

It is not immediately obvious why the core should be held at about 35 degrees C., particularly at night. That temperature is, however, the one required for taking flight quickly. A honeybee needs from four to six minutes to warm up to 35 degrees from about 20 degrees by shivering. Hence there is no great disadvantage in letting the mantle temperature fall below the flight temperature, provided that the core is kept warm and bees can enter it (or shiver) to warm up. By skimping on active metabolism (shivering) for generating heat the bees of the mantle prolong the swarm's limited reserves of food.

Honeybees that are about to swarm gorge themselves on honey before they leave their hive. This honey not only must fuel thermoregulation while the swarm waits to occupy a new hive but also must serve as a fuel for the scouts. It is also the substrate from which the initial combs of the new hive are built. The bees cannot skimp too much on the expenditure of energy for regulating the temperature of the swarm, however, or the swarm's response to the discovery of a new domicile would be too slow. Thermoregulation makes possible a quick response in a range of weather conditions at the most critical stage of the colony cycle: the competition for a suitable nest site that will thereafter serve the new colony indefinitely.

A woman in a white uniform, likely a flight attendant, is leaning over a man who is sleeping in an airplane seat. The man is wearing a light-colored shirt and a dark vest. Another man, wearing glasses and a dark suit, is sitting in the seat next to him, looking towards the camera. The background shows the interior of an airplane cabin with windows and overhead lights.

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