Energetics of Honeybee Swarm Thermoregulation

Abstract. *Honeybee swarms regulate their core temperature at a high set point (near 36°C) and the mantle at a low set point (near 15°C). The temperature gradient from core to mantle permits considerable energy economy, and it is abolished only shortly before swarm takeoff.*

Thermoregulation in the honeybee *Apis mellifera mellifera* has been studied in relation to individual bees (*1*) and to hive responses at both high (*2*) and low ambient temperatures (*3, 4*). In contrast, except for two isolated reports (*5, 6*), each restricted to a few hours of observations on a single swarm, almost nothing is known about possible swarm thermoregulation and swarm energetics.

A swarm, the primary reproductive unit of a colony, usually consists of the old queen and approximately half of the parent colony's workers (*1*). The swarming workers engorge themselves from the hive's communal honey stores before departing from the hive (*7*).

A crucial step in the success of this swarm in founding a new colony is the ability to find (*8*), correctly evaluate (*9*), and occupy a potential nest site such as a hollow tree within which the bees can exert sufficient control of temperature to survive the winter. In this nest-finding process, the bees are constrained by limited amounts of food energy and time. I now report on the thermoregulation of swarms and the mechanisms of management of the swarm's energy resources.

Measurements of swarm temperature (*10*) over a range of air temperature (T_a) 2 to 3 cm adjacent to the swarms, indicated steep gradients from the inside to the outside (Fig. 1), but the temperature of both the swarm core (T_c) and swarm mantle (T_m) were regulated. Both small (< 2000) and large (> 30,000 bees) swarms maintained T_c near 35° to 36°C regardless of air temperature (T_a) (Fig. 2), the same temperature as that found in the brood nest of a hive (*11*). However, unlike brood-nest temperatures that are maintained within ± 0.5°C (*1–4*), T_c fluctuated widely.

Mantle temperatures were maintained at 15° to 21°C regardless of T_a when T_a was between 1° and 16°C. When T_a was greater than 16°C, T_m was unregulated, averaging 2° to 3°C above T_a. In three free swarms in which T_c and T_m were continuously monitored (*11*), there were also steep temperature gradients from core to mantle; but several hours before swarm takeoff, T_m increased and all temperature gradients through the swarm were abolished so that at takeoff T_m was identical with T_c.

At air temperatures less than 16°C the mantle bees were unable to take off in flight but were ready to raise their abdomens and expose their stingers to intruders. Their thoracic temperatures (T_{th}) (*12*) were regulated, being maintained near 15°C, independent of T_a (Fig. 2). Disturbances of the swarm mantle caused alert, flight-ready bees to emerge from the swarm core and sometimes to attack. Bees forcibly separated from the swarm at T_a < 5°C became immobile and incapable of stinging and arousal within minutes. Although bees on the swarm mantle could crawl into the swarm core and warm up to above 30°C in several minutes (*13*), they usually remained in place without crawling into the swarm interior. Thus, even though the bees on the swarm mantle are temporarily incapable of flight at low T_a, they have the option to rapidly warm up by taking advantage of the cluster.

In direct contrast to the one previous observation of one swarm (*6*), I found increases in volume in 14 swarms as T_a increased (Fig. 1). As seen through the transparent plexiglass (*10*), at high T_a swarms consisted of curtains of stationary bees with large open passageways between these curtains. The passageways were used by many bees traveling between the core and the mantle (*13*). At low T_a, these passageways were filled with immobile bees, and the bees on the swarm mantle pointed their heads inward and crowded closely side by side. The density of swarms at 1° to 5°C was 0.13 cm^3 per bee (as in clusters of dead bees), decreasing almost fourfold to 0.50 cm^3 per bee at 30°C (*14*). These measurements indicate that the bees occupy all available space inside the swarm at low T_a. By keeping themselves individually warm by crowding close together and moving into the available space, the mantle bees reduce both the channels for active convective heat loss from the swarm interior, as well as the porosity and swarm surface area for passive convective heat loss from the exterior (*13*). The crowding could account for increased retention of CO_2 in the core observed at low T_a (*6*).

Energy expenditure was determined by measuring the rate of oxygen consumption of whole swarms over a wide range of T_a (*15*). The swarm metabolism mimicked the thermoregulatory response found in vertebrate homeotherms (*16*), being elevated to 1.6 to 3.2 ml of O_2 per gram per hour at 0° to 5°C, reduced to 0.2 to 1.0 ml of O_2 per gram per hour at 12° to 18°C and again increasing to approximately 1.5 ml of O_2 per gram per hour at 28°C. Unlike in vertebrate homeotherms, however, swarms ranging in size at least ninefold had similar weight-specific metabolic rates. Thus, the small swarms were apparently not thermoreg-

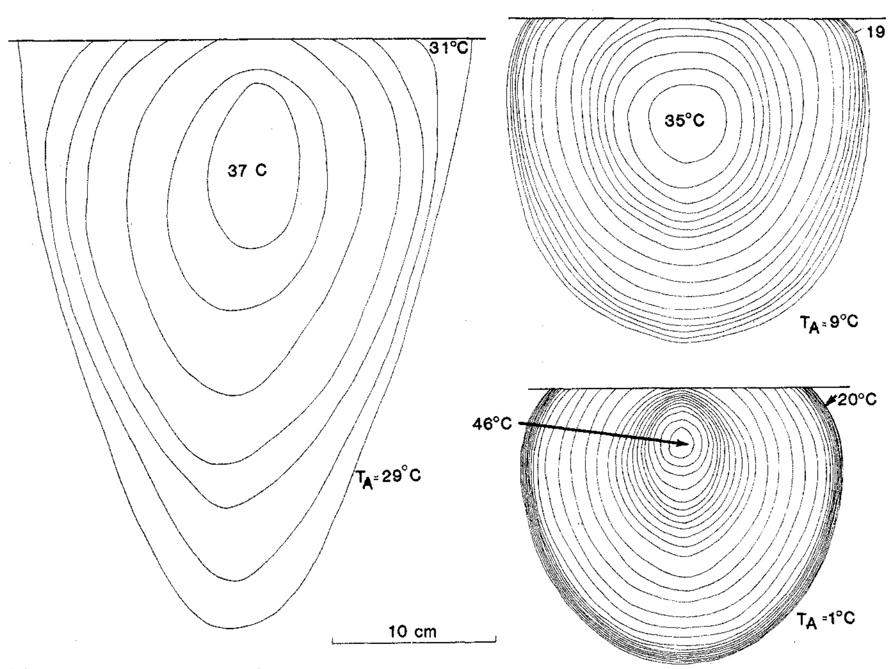

Fig. 1. Temperature profiles and swarm shape and dimensions at three different ambient temperatures. This swarm consisted of 16,600 bees. The 46°C recorded in the swarm core at 1°C was unusual (see Fig. 2).

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ulating at low T_a simply by increasing their rates of heat production, as was predicted by surface-volume considerations.

Resting metabolism (that occurring when the thoracic muscles of the individuals are not being activated by the central nervous system), at least in bumblebees, varies strongly with thoracic temperature (*17*). Calculated values of body temperature–specific resting metabolic rates were compared with measured rates of heat loss from dead swarms that had been heated artificially (*13*). Such comparisons indicated that in moderately sized swarms (> 5000 bees), the heat production from resting metabolism of bees in the swarm core should be more than sufficient to maintain the highest T_c observed down to at least 5°C.

In addition, the potential contributions of resting metabolism of the bees in the different isotherms were summed (*17*) to give a calculation of whole swarm resting metabolism. These calculated values of resting metabolism largely coincided with the measured values of swarm metabolism at ambient temperatures of 2° to 27°C. The high calculated (and measured) metabolism at high T_a was thus due, in part, to the fact that both T_c and T_m were high. As T_a was lowered, T_m declined, allowing for an overall decrease in swarm metabolism since the metabolic contribution of the mantle bees was decreased. When T_a is dropped still lower, the bees on the mantle cluster tightly and the core heats up, resulting again in high net swarm metabolism, this time primarily because of the contribution of the core bees. The bees on the swarm mantle also shiver, resulting in additional elevation of swarm metabolism (*13*). Nevertheless, the overall increase in metabolism is low, due to the low temperature gradient from mantle to air that minimizes the rate of heat loss. The results are consistent with the low rate of food utilization of free swarms (*18*).

The bee swarm must achieve a uniform temperature throughout, like that of a vertebrate homeotherm, before it can fly. A vertebrate homeotherm, however, is unable to maintain a stable core body temperature with steep temperature gradients to the periphery; it must elevate its metabolism to the extent that it is constrained in reducing peripheral temperature to retard heat loss from the core. Thermoregulation of the swarm is a prerequisite for arousal and takeoff of all of the bees during that critical stage of the life cycle when there is often intense scramble competition for a limited number of suitable nest sites. The mechanisms of thermoregulation permit energy economy by conserving the food resources carried by the bees and needed by them in finding and building a new nest.

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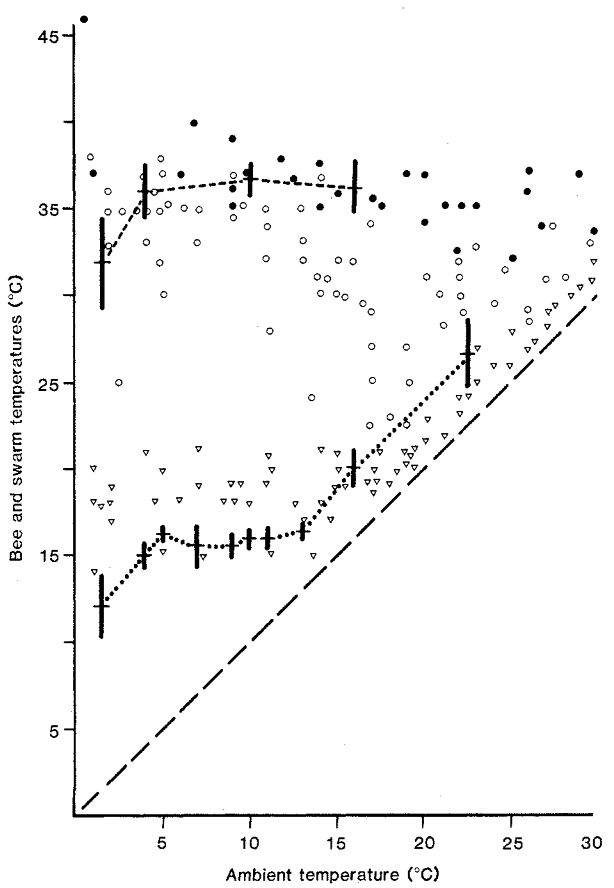

Fig. 2. Swarm and bee thoracic temperatures as a function of ambient temperature. (●) core temperature in swarms of 10,000 to 16,600 bees. (○) core temperatures in swarms of 1800 to 9900 bees. (△) mantle temperatures measured directly under the outermost bees. Dotted line connects the means of thoracic temperatures of bees making up the swarm mantle. Dashed line connects the means of bees that came to the swarm exterior after a disturbance on the swarm periphery. The vertical lines indicate 2 standard errors on each side of the mean.

References and Notes

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10. Swarms were captured in the field and maintained in the laboratory in circular plexiglass respirometry vessels (inside diameter, 29 cm; length, 43 cm), sealed at both ends with a grease seal in removable plexiglass plates. A circular area of the inside lid was honeycombed with 3-mm-diameter holes that served as openings for ventilation, as a foothold for the attachment of swarms, and for the insertion of thermocouple probes on rods marked with a centimeter scale to determine swarm dimensions and location of specific temperatures measured. Temperature measurements were taken to the nearest 0.5°C with an Omega thermocouple thermometer. Air temperature was regulated in a temperature-controlled room.
11. Thermocouples were implanted both in the brood and in the frames between the brood. In free swarms (on a window ledge outside the laboratory), temperatures were monitored by six thermocouples placed throughout the swarm. The temperatures were continuously recorded both day and night with a Honeywell multipoint potentiometric recorder.
12. Thoracic temperatures were measured with a 40-gauge copper-constantan thermocouple and read to 0.5°C on an Omega Engineering thermocouple thermometer.
13. B. Heinrich, *J. Exp. Biol.*, in press.
14. The bees in the swarms were counted. Swarm shapes and sizes were determined by taking external dimensions through the swarm with a probe having centimeter marks. Volumes were determined by projecting the sagittal section of swarms (Fig. 1) onto a grid, and on the assumption that the number of grids counted in from the outside was equal to twice the number of grids through the swarm (uniform dimensions), the volume and bee weight at specific isotherms could be calculated.
15. Oxygen consumption was determined from decreases in its concentration (measured to 0.01 percent) in air from the sealed respirometers pumped through a Beckman E-2 paramagnetic oxygen analyzer. All volumes were corrected to standard temperature and pressure.
16. See G. A. Bartholomew, in *Animal Function: Principles and Adaptations*, M. Gordon, Ed. (Macmillan, New York, 1980), pp. 434–447.
17. The calculations were made from the projected drawings of the isotherms, and the methods described (*14*). The only values of resting metabolism in bees over a range of body temperatures where the possible effect of shivering has been examined, are those by A. Kammer and B. Heinrich [*J. Exp. Biol.* **61**, 219 (1974)]. These values were used because they come close (slightly lower) to the lowest (presumably resting) values observed previously in honeybees [see Kammer and Heinrich above and Cayhill and Lustick (*4*)].
18. O. C. Taylor, personal communication.
19. Supported by NSF grant DEB 77-08430. I thank the Contra Costa and Alameda County police and fire departments, as well as the Ecohouse Swarm Hotline of Walnut Creek, Calif., for their help in referring me to an ample supply of swarms.

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