

THE HONEY BEE CLUSTER AS A HOMEOTHERMIC SUPERORGANISM

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Abstract—1. In winter, oxygen consumption of honey bee (*Apis mellifera* L.) clusters resembles that of birds and mammals.

2. Intact clusters of 10–20,000 bees increase metabolism when exposed to cold environmental temperatures. Below 10°C, metabolic rate ($W\text{ kg}^{-1}$) increases as a function of decreasing ambient temperature following the relation $MR = 7.96 - 0.24 T$ (Fig. 1).

3. Insulative properties of the cluster are estimated and discussed.

4. At moderate ambient temperatures (10–14°C), the cluster “breaks” resulting in a massive increase in total surface area for heat exchange and concomitant large increase in metabolism.

INTRODUCTION

Honey bees of the genus *Apis* (family Apidae) probably originated in the Asian or African tropics (Ruttner, 1978). As such, there was little selective pressure for thermoregulatory adaptation to cold environmental temperatures. The species of *Apis* still found inhabiting tropical regions, including the African race (*A. mellifera adansonii*), the Indian bee (*A. indica*) and the giant and dwarf honey bees of Asian tropics (*A. dorsata* and *A. florea*), do not thermoregulate well and die when exposed to cold temperatures. They do not form tight winter clusters or store the large amounts of surplus food characteristic of the western honey bee (*A. mellifera*) which has been introduced worldwide (Martin, 1974; Morse, 1975; Michener, 1979). The latter bees, *A. mellifera*, inhabiting north temperate regions, encounter winter temperatures well below freezing for extended periods and have developed a precise thermoregulatory system (see Seeley & Heinrich, 1981, for review).

Most northern species of insects diapause through the winter, but honey bees pack together in a dense cluster usually containing between 5000 and 40,000 individuals in a natural cavity or man made hive. The volume and physical dimensions (height, width, depth) of the nesting cavity are crucial to winter survival (Seeley, 1977; Seeley & Morse, 1978).

It is well known that when examined singly, bees are not substantially different from tropical or summer insects in their responses at air temperatures below 13°C, and continued cold exposure to temperatures lower than 6–8°C results in death (Free & Spencer-Booth, 1958, 1960; for review see May, 1979). Individual or small groups of honey bees have a limited ability to thermoregulate (Cayhill & Lustick, 1976; Chauvin, 1968; Heinrich, 1980; Prisch, 1923; Roth, 1965). Esch (1960) and Heusner & Stussi (1964) found that isolated bees outside the nest regulated their heat production around a thoracic temperature of 35–36°C in moderately warm weather. At night or in cold temperatures, the individual bee is ectothermic and does not regulate well (Allen, 1968; Esch, 1968; Heusner & Roth, 1963; Heusner & Stussi, 1964).

A migratory swarm of bees, or a cluster in a nest, however, is a highly organized physical and social structure and effectively thermoregulates as a superorganism over a wide range of temperatures (Free, 1977; Gary, 1975; Heinrich, 1981a,b; Southwick & Mugaas, 1971). The nesting cluster can survive the continued cold exposure of a north temperate winter (although the swarm is unable to do this, probably because of lack of food stores rather than a thermoregulatory limitation) (Free, 1977; Nagy & Stallone, 1976; Owens, 1971). The term, superorganism, specifically applying to collective characteristics of colonies of social insects, is widely found in the early entomological literature of this century (Thomas, 1975).

I previously reported that above 10°C, intact bee clusters show complex thermoregulatory patterns with large amplitude circadian rhythms of metabolism (Southwick, 1982). I report here on the metabolic cost and modes of thermoregulation in intact clusters of bees exposed for extended periods to cold ambient temperatures of +10 to –20°C.

MATERIALS AND METHODS

Colonies of honey bees, *Apis mellifera* L., were maintained at an apiary located in an abandoned apple orchard on the campus of the State University of New York College at Brockport, Monroe County (43°12'N 77°58'W). Following standard fall management practices (Farrar, 1968), colonies housed in Langstroth hives were reduced to two deep supers (50 × 48 × 41 cm) in September 1980. Wooden blocks were placed in each hive reducing entrances to about 1 × 4 cm.

Test hives containing intact colonies were placed in a controlled temperature cabinet, and oxygen consumption, \dot{V}_{O_2} , was measured in an open circuit system following the methods described in Southwick (1982). Photoperiod was controlled using a timer and 15 W incandescent lamp inside the temperature cabinet. Bee colonies were usually allowed to accommodate to their new environment overnight. Each test temperature was set and maintained for at least 24 hr. Following metabolic measurements, the bees were weighed (live and dry) and total number of bees estimated from live weight samples.

RESULTS AND DISCUSSION

Metabolism

Minimal values of oxygen consumption were consistently achieved at night as much as 24 hr after a test temperature was set. The range of minimum metabolic rates calculated from consumed oxygen varied with temperature of the air entering the hive.

When cabinet air temperature was decreased below 10°C, cluster metabolism increased. Minimum metabolic rates maintained for at least 15 min during the 24 hr exposures to each test temperature are plotted in Fig. 1. A least squares fit of 19 data points yields:

$$MR = 7.96 - 0.24 T \quad (r = 0.65, P < 0.01)$$

where MR is metabolic rate in $W\ kg^{-1}$ and T is environmental temperature in °C. The correlation coefficient test of significance was taken from Table Y in Rohlf & Sokal (1969). The regression is statistically significant with about 42% of the variation in metabolism explained by variation in ambient temperature. The equation, then, has only marginal value in predicting metabolic rate of a cluster when air temperature is known. Some of the variability in metabolism at any one temperature can be attributed to the different masses of the clusters. However, no consistent trend was noted in mass specific MR .

Heinrich (1981a) also found no trend in mass specific metabolism in migratory swarms ranging over 9× in size. It can still be concluded from this data that the lower the ambient temperature, the more work the cluster does to maintain its core and shell temperatures. Similar temperature- MR patterns (although with wider variation) have been reported for food consumption and carbon dioxide output of honey bee colonies kept at cold air temperatures (Free & Simpson, 1963; Free, 1977; Furgala, 1975).

There is a striking similarity between this pattern and that exhibited by most homeotherms which show nearly linear increases in MR with decreasing environmental temperature below the lower critical temperature (for review see Bartholomew, 1982).

Figure 2 shows the bee cluster metabolism regression along with that of selected mammals and birds. The response of the bee cluster resembles that of the ptarmigan (*Lagopus leucurus*), a very well insulated bird (with down feathers even on its feet) inhabiting arctic and alpine regions of western North America.

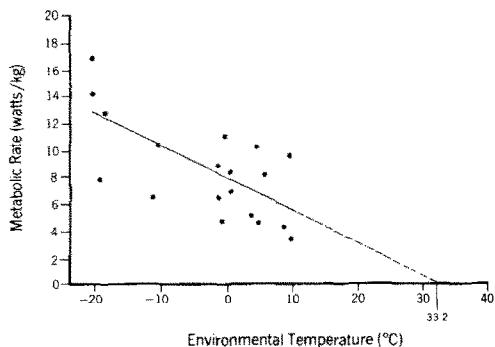


Fig. 1. Metabolism of intact clusters at air temperatures of +10 to -20°C.

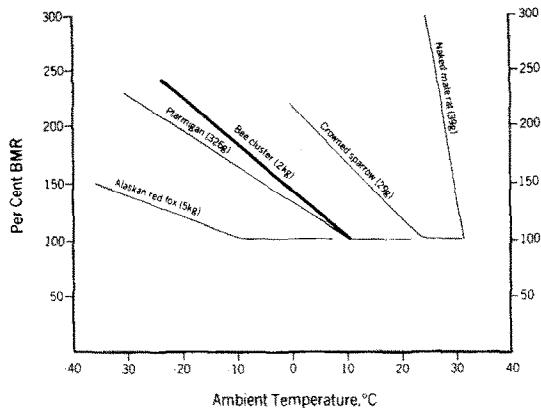


Fig. 2. Response of metabolic rate to environmental temperature in bees, birds and mammals. BMR refers to the basal metabolic rate (at rest and at thermally neutral temperature). (Adapted from Bartholomew, 1982.)

Even at -20°C, these birds need only double their basal metabolic expenditures to remain homeothermic. The migratory white-crowned sparrow (*Zonotrichia leucophrys*) must increase metabolism by 3½ times for thermal balance at -20°C (Southwick, 1980). At the same temperature the honey bee cluster need only increase its metabolic rate by 2¼ times its mean rate at 10°C.

If the rate of metabolic heat production equals the rate of heat loss to the environment, Newtonian cooling would apply to this superorganism, and plotted data for MR and T should fit a straight line that extrapolates to a temperature close to "body" temperature at zero heat production. Such is the norm for homeotherms. Extrapolation of the best fit linear regression intersects the abscissa at about 33°C (Fig. 1), a temperature well within the narrow range of 32-35°C commonly reported to be maintained at the cluster core over a wide range of ambient temperatures (Free, 1977; Heinrich, 1981b; Owens, 1971; Southwick & Mugaas, 1971). Thus, the cluster organism behaves similar to a homeotherm.

Insulation

Utilizing Newtonian cooling, thermal conductance, C , can be estimated. Thermal conductance specifies the net rate of heat transfer per degree difference between the body temperature (T_b) and environmental temperature (T_e).

$$C = \frac{MR}{T_b - T_e}$$

where C is a mass specific conductance in $W\ kg^{-1}\ ^\circ C^{-1}$. The small heat loss by evaporation of water at these cool temperatures is ignored (McNab, 1980). In calculating conductance, I assumed the core temperatures were uniform (I do not have accurate measurements of core temperatures at the times of minimal \dot{V}_{O_2} measurements) at roughly the X-intercept of 33°C (which corresponds to literature values and our own measurements). Then, the slope of MR vs T_a equals C and in this case yields a C value of 0.24 $W\ kg^{-1}\ ^\circ C^{-1}$ that is strikingly within the homeo-

therm range. This indicates an insulative capability equal to that achieved in mammals during the active (α) part of their daily cycle ($0.18\text{--}0.23\text{ W kg}^{-1}\text{ }^{\circ}\text{C}^{-1}$) and nearly as good as their resting values (ρ) ($0.09\text{--}0.16\text{ W kg}^{-1}\text{ }^{\circ}\text{C}^{-1}$), and active values (α) in birds ($0.11\text{--}0.30\text{ W kg}^{-1}\text{ }^{\circ}\text{C}^{-1}$; a ρ value is $0.08\text{ W kg}^{-1}\text{ }^{\circ}\text{C}^{-1}$) of similar mass (Aschoff, 1981; Herreid & Kessel, 1967).

This is particularly remarkable since the bee cluster cannot follow precisely most of the physiological schemes of adaptation which characterize homeotherms (e.g., altering body surface temperatures by blood circulatory shifts resulting from vasomotor activity; central and peripheral nervous control of shivering; non-shivering thermogenesis; and changes in quality, thickness or arrangement of pelage or plumage). However, the bee cluster does mimic birds and mammals by altering exposed surface through "postural" changes, and movements of bees within a clus-

ter are analogous to the adjustments by a homeothermic organism as I describe below.

The rate of heat exchange (gain or loss) between the cluster interior and external environment is a function of the porosity of the cluster and convection currents within it, as well as its relative surface area, and set point temperatures. Heinrich found numerous open passageways in migratory swarms which function in convective heat loss and were much reduced at cool ambient temperatures. Allen (1955) and Meyer (1956) found the bees on the periphery of a cluster are older individuals with a lower temperature preference and greater thermoregulatory ability than the younger bees comprising the core. By crowding and pushing together at low air temperature these outer bees affect cluster size, porosity and openness of the cluster, and thereby lower cooling rates (Free, 1977; Mobus, 1978).

Individual bees have also been shown to shunt

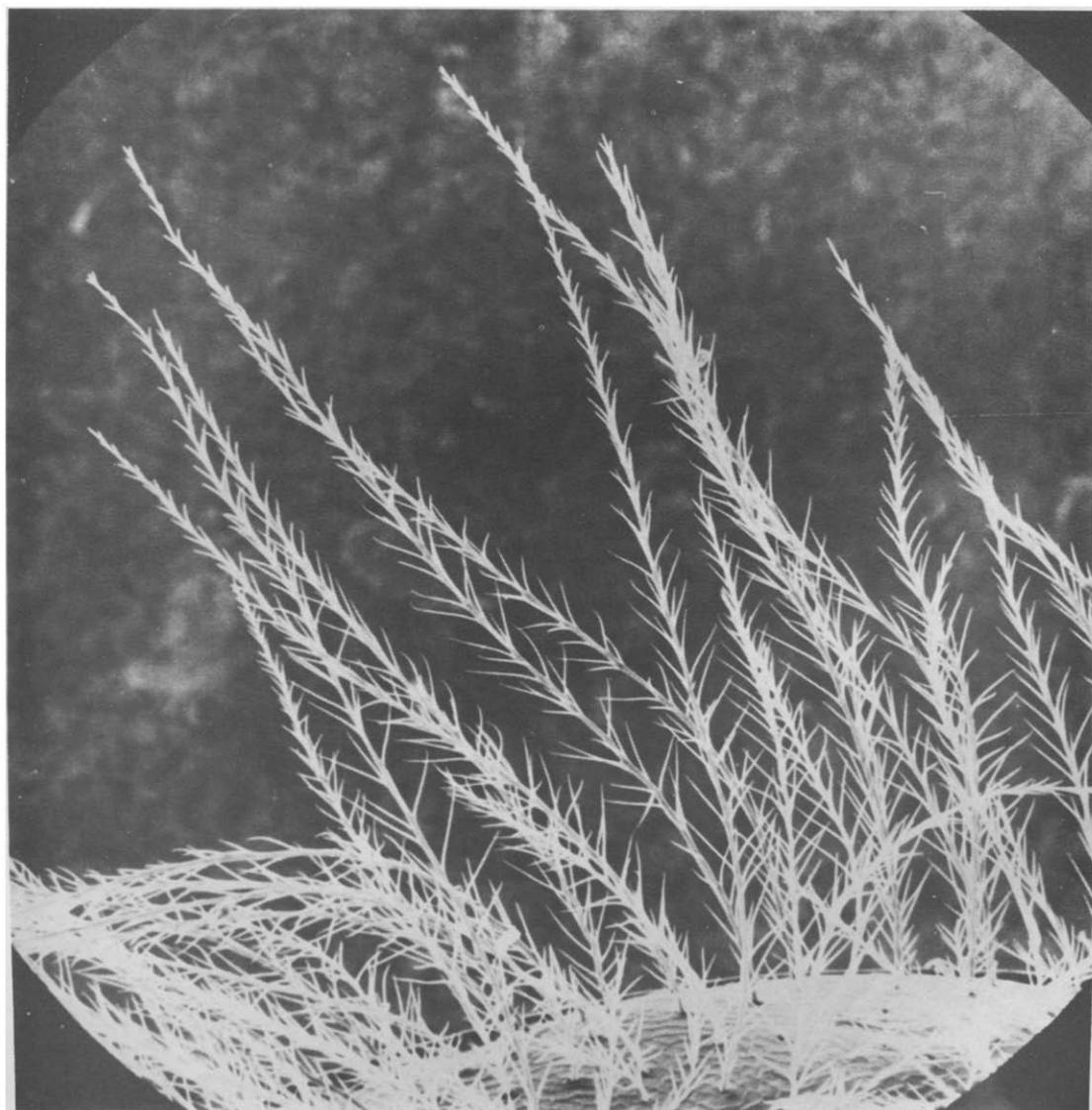


Fig. 3. Scanning electron micrograph of plumose body hairs of *Apis mellifera* (by R. Faure, Institut National Polytechnique de Grenoble, Saint Martin D'Herès, France, used by permission).

blood between the head and thorax and abdomen, thereby adjusting heat retention in the thorax and regulating high head and thorax temperature (Heinrich, 1980). This heat partitioning aids in cluster heat retention as individuals comprising the outer layers orientate with warm heads inward and cool abdomens outward. Additionally, individual bees gain heat through rapid small-amplitude contraction-relaxation cycles of their thoracic wing muscles. During these periods, action potentials from thoracic muscle tissue show trains of impulses of higher frequency than flight frequencies. Heat production results from the low mechanical efficiency of this musculature which makes up the bulk of the thorax, and is among the most metabolically active tissues known (Esch, 1960; Cloudsley-Thompson, 1970). This is the source of heat utilized in pre-flight warm-up in large moths and bumblebees (Bartholomew *et al.*, 1981). Individual bees in the cluster produce heat via the same mechanism.

Clustering

The clustering phenomenon itself precipitously reduces surface area for heat exchange from the sum of the surface areas of individual bees, down to the outermost surface area of the cluster. Simplifying the shape of a single bee to a cylinder, about 1.4 cm in length by 0.4 cm diameter, would yield a surface area of about 1.76 cm². A colony of 20,000 individuals not tightly packed would have a total summed surface area for heat exchange of about 35,186 cm². Individuals in the central area of even the loose colony would not be exposed to air temperatures as cool as those at the extremity. However, tight clustering could reduce the effective area of heat exchange to a minimum of 4189 cm² (for a spherical cluster with a diameter of 20 cm), a reduction of 88%. Heat loss is minimized at colder ambient temperatures by reductions in cluster size. This may explain in part why I found large excursions in metabolic rate as the cluster broke and reformed at air temperatures between 10 and 14°C (Southwick, 1982).

At this moderate air temperature, the bees exhibited marked 24 hr-periodicity in their combined metabolism. Low rates of metabolism averaging 10.1 W kg⁻¹ occurred in the dark when the cluster was tightly packed. At midday, the cluster broke resulting in a 2½ times increase in metabolism averaging 25.7 W kg⁻¹ for 22 intact colonies containing 9480–23,394 bees (Southwick, 1982). The concomitant increase in surface area for heat exchange (as high as 8-fold) could easily account for this change in metabolism.

The comparatively few bees clinging to the outer portion of the tightly packed cluster form several layers (of bees) with most individuals inside the cluster contributing no heat loss surfaces. Of course, with greater numbers of bees in the cluster, relatively fewer will be exposed at the surface. As Heinrich (1981b) recently suggested for bee swarms, bees near the periphery of the cluster but inside the shell may be primary heat producers passively warming the core. The outermost bees provide an insulating layer 25–75 mm in thickness, being packed thorax-to-thorax with a multitude of interlacing thoracic hairs, and with heads pointed inward (Mobus, 1978, per-

sonal observation). The hairs are plumose, closely resembling the structure of bird down feathers (Fig. 3) and probably have similar insulative properties. The plumose hairs trap air resulting in a poorly conducting boundary layer next to each bee's body. Individual bees cannot trap the same proportion of air as birds which are 300–10,000 times larger. However, the several packed layers of bees succeed in trapping similarly high relative volumes of air in an effective insulating coat for the cluster.

Successful overwintering also involves the selection of a nest site in an ameliorated microclimate (Seeley & Morse, 1978). When clusters swarm in late summer and construct combs in exposed habitats (such as on branches of a tree or shrub), they are unlikely to survive the winter in north temperate regions even employing all their thermoregulatory capacity.

It is clear from these results that the patterns of metabolic adaptation to low environmental temperatures by the honey bee cluster, viewed as a superorganism, are qualitatively and quantitatively similar to those demonstrated in active homeothermic birds and mammals. More data are needed on bees exposed to much lower air temperatures and on other north temperate social insects that pass the winter as colonies (e.g. Formicidae).

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