coarse-particle contribution from sea spray and a higher fine-mode S concentration; these results suggest that sea spray may contribute to the background tropospheric submicrometer mode as well.

During the winter of 1976 in the Punta Arenas, Chile, region, fine-mode S concentrations were much lower than in the summer of 1977 (*13*). In a 1-week sampling period, the winds were southwesterly and the ground was covered by ~ 30 cm of snow, so that local terrestrial biological and soil contributions were minimal. (During the 2-week sampling period in the summer of 1977, the winds were generally westerly, although for $3^1/_2$ days some calm periods, northerly winds, and easterly winds were recorded.) The winter size distribution shows higher coarse-particle S concentrations than the summer values, perhaps due to a greater sea spray contribution in the higher-velocity southwesterly winds during that season, and fine-particle S concentration of ~ 10 ng/m^3, the lowest value measured in this investigation.

Figure 1b shows the time-sequence streaker data for S at Chacaltaya Mountain and Patacamaya, Bolivia. The two locations, separated by a distance of 100 km and an elevation of 1400 m, display similar time variation patterns in S concentration. Prior to noon on 14 January 1977, S concentrations averaged ~ 100 ng/m^3 or higher. From 14 January until noon on 16 January S concentrations remained below the detection limit of ~ 20 ng/m^3 at Chacaltaya and at nearly the same value at Patacamaya. After this episode, the S concentrations returned to their initial values at both locations; these results suggest large-scale meteorological effects on the observed S concentrations. During the episode of low S concentrations at Chacaltaya, the concentrations of the crustally derived elements such as Fe were also very low, although at Patacamaya larger amounts of Fe were found. Some soil dust may contribute to the aerosol at Patacamaya (*13*).

Local meteorological conditions such as rain or snow at these high elevations do not suggest an explanation for the low concentrations of S observed at both locations from 14 to 16 January. Nor do wind and atmospheric pressure readings from nearby La Paz, Bolivia, exhibit anomalies during this episode. Nevertheless, the chemical data suggest that there occurred during this period a large-scale incursion of air containing atypically low aerosol S concentrations, such as a subsidence of upper tropospheric or stratospheric air. The winter 1976 samples from Punta Arenas may also have been obtained during an atypical episode.

These data from remote locations on the South American continent indicate that fine-particle S concentrations are lower by at least a factor of 4 than corresponding values measured in nonurban western U.S. sites, by similar sampling and analysis techniques, and lower by a factor of 100 than sometimes found in the eastern United States (*1*). A fine-particle mode of S, averaging ~ 50 ng/m^3 (~ 150 ng/m^3 SO_4^{2-} equivalent), is observed with the cascade impactors at continental South American sites. The streaker data give somewhat higher values than the impactors, but the South American streaker values are still approximately one-fourth as large as the corresponding western U.S. samples (*14*). Occasionally higher values may occur, such as in Brazil, possibly due to forest burning (*5*), and lower values may also be observed, for example, the fine-particle mode of S during the winter near Punta Arenas and the January episode at two locations in Bolivia. On the average, aerosol S concentrations are much lower in nonurban South America than values used in previous calculations of the global S cycle (*15*).

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Keeping a Cool Head: Honeybee Thermoregulation

Abstract. *At high ambient temperatures, honeybees regulate head temperature by evaporative cooling of regurgitated honeycrop contents. Thoracic temperature is secondarily stabilized as heat flows from thorax to head by means of passive conduction and physiological facilitation resulting from accelerated blood flow. The mechanism permits flight at the extraordinarily high ambient temperature of 46°C without overheating the head and thorax despite prodigious amounts of heat produced as a by-product of flight metabolism. In contrast, at low ambient temperatures, thoracic rather than head temperature is regulated; no liquid is regurgitated, and the head is heated passively by conduction both in flight and while stationary.*

The common honeybee, *Apis mellifera*, has colonized near-arctic and temperate regions as well as humid tropical and hot desert environments. Honeybees can fly at air temperatures (T_A) as low as 10°C, some 18°C lower than their minimum muscle temperature for flight (*1*) and 8°C below the minimum temperature required for the generation of action potentials (*2*). On the other hand, they also regularly fly in the deserts of southwestern United States at T_A near

46°C (*3*), where even the desert cicada, *Diceroprocta apache*, active in the hottest part of the year, loses motor control because of overheating in 1 to 3 seconds of flight (*4*).

The thoracic temperature (T_{Th}) of honeybees increases an average of 15°C above T_{A} during free flight at T_{A} from 15° to 25°C (*1*) as a by-product of the intense flight metabolism. Furthermore, the rate of energy expenditure (and heat production) is always high in flight; it does not diminish during flight at high T_{A} when overheating from the flight metabolism is imminent (*5*).

Although the regulation of heat production for thoracic temperature stabilization is well known for honeybees while they are grounded and have their flight muscles available for shivering (*2, 6*), it had not been elucidated how these insects prevent overheating (and how they are able to fly) at high T_{A}.

In some large flying insects, including sphinx moths (*7*), bumblebees (*8*), and some dragonflies (*9*), overheating of the thorax during flight is prevented by shunting heat to the abdomen with the blood circulation. In honeybees, however, the aorta in the narrow petiole between thorax and abdomen is greatly enlarged by being convoluted into loops (*10, 11*). This results in a great increase in surface area of the vessel that could function as a countercurrent heat exchanger to retain heat in the thorax. The anatomy thus appears to be adapted to maximize heat retention in the thorax, thereby facilitating flight at low T_{A} at the expense of flight at high T_{A}, unless an alternate mechanism for heat dissipation is used. This hypothesis (*8*) has not been previously examined, and at least three other hypotheses for the functional significance of the aortic loops have been published in the last 80 years (*10–12*).

One potential alternate mechanism of heat loss, besides possible heat transfer to the abdomen by the blood, is that the head acts as a dissipator of heat from the thorax by evaporative cooling. The regurgitated fluid sometimes observed in honeybees (*13*), bumblebees (*8*), as well as in a sphinx moth (*14*) has been speculated to have possible significance in evaporative cooling, but adequate data have been lacking. In addition, the regulation of head temperature and the regulation of body temperature by evaporative cooling have not previously been demonstrated for any flying insect. I now report on the physiology of the regulation of head temperature in the honeybee, and I examine the significance of the capacity for T_{Th} and for flight at high T_{A}.

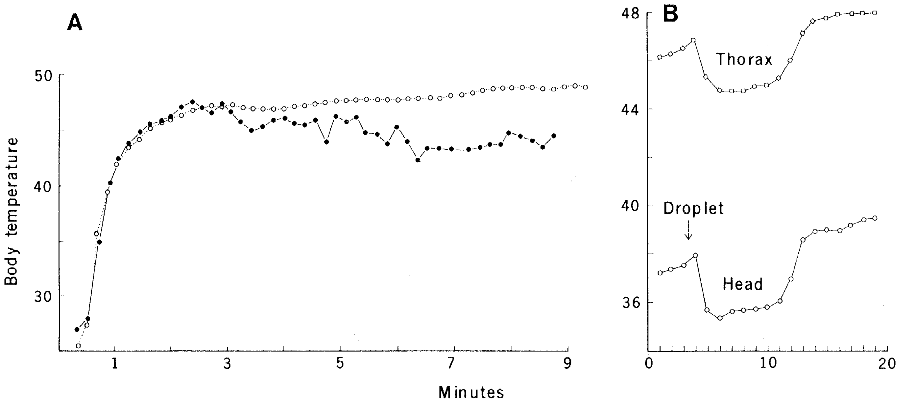

Fig. 1. Reduction of head and thoracic temperature resulting from evaporating honeycrop contents on the "tongue." (A) Continuously recorded head temperature of a live bee (●) heated on the head with a beam of light from a heat lamp. After about 2 minutes of heating, the bee regurgitated fluid, and head temperature dropped. After the same bee was killed, it was heated as before to determine the effect without regurgitation (○). (B) Changes in T_{H} and T_{Th} in a dead bee heated on the thorax and suspended in an air stream (32 m/sec) at 28°C after 4 μl of honeycrop contents were placed on the tongue.

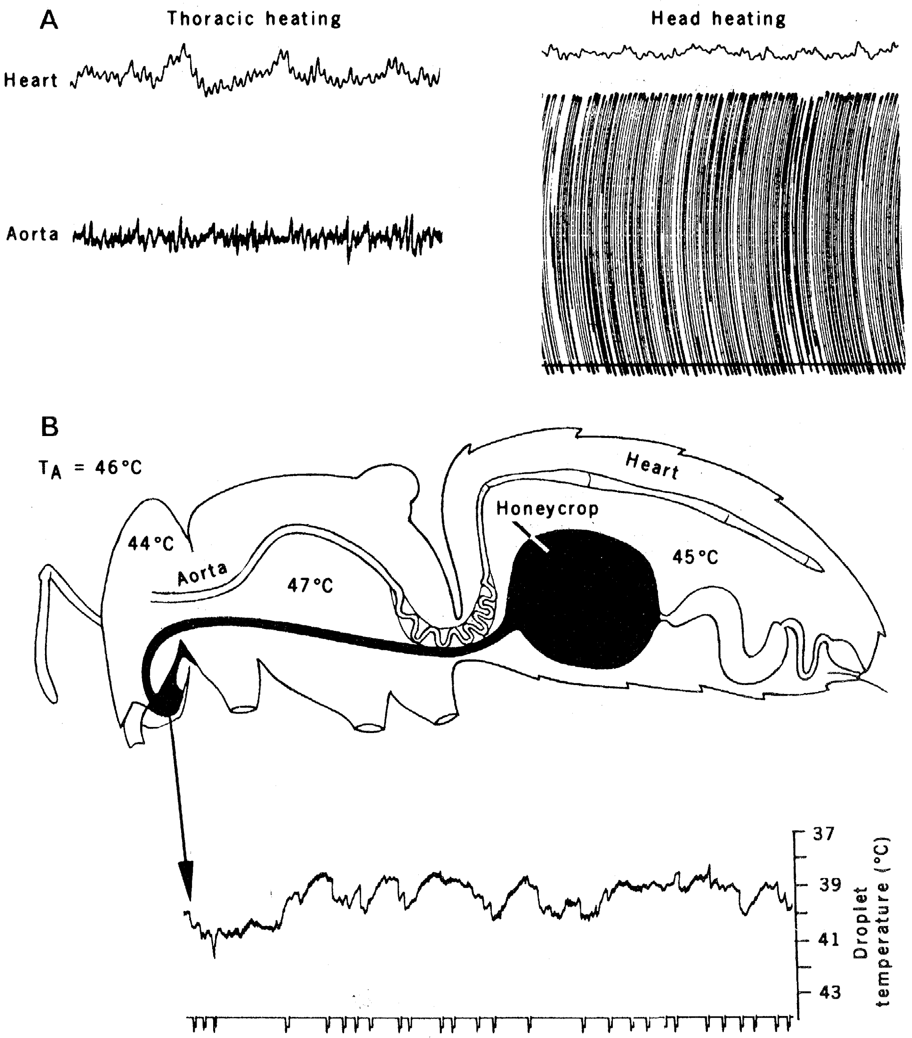

Fig. 2. (A) Concurrently recorded mechanical activity of the heart and the aorta while the thorax and then the head of the same bee were heated to near 45°C. The records each span 13.5 seconds. (B) Diagrammatic section of a honeybee showing the main features related to thermoregulation, and typical body temperatures maintained during continuous free flight at 46°C. Lower graph shows continuously recorded droplet temperature of a bee heated on the head (T_{H} = 47° to 48°C, T_{A} = 24°C, relative humidity = 30 percent). Tongue-wagging events were observed visually and recorded manually.

Thoracic, head (T_H), and abdominal temperatures (T_{Ab}) were measured in bees in free flight (*15*), while they were tethered and spontaneously endothermic, and while they were heated with a narrow beam of light from an incandescent lamp focused onto the head or thorax (*16*). The activities of the heart and the aorta were concurrently recorded in the tethered bees (*17*).

At $T_A < 30°C$, T_H was not regulated, but it was always elevated when T_{Th} was elevated. In 44 endothermically heated bees, head temperature excess ($T_H - T_A$) was always a relatively constant fraction [$\bar{X} = 0.61$, range = 0.28 to 0.84, standard error (S.E.) = 0.017] of thoracic temperature excess ($T_{Th} - T_A$) regardless of T_A. The mean ratio of T_H excess to T_{Th} excess in 28 dead bees was 0.53 (0.34 to 0.74, S.E. = 0.018), which was significantly [two-tailed t test, $P < .01$] lower than the 0.61 observed in the live, endothermic bees. Thus, 0.53/0.61 or 87 percent of the heat flow to the head could be accounted by passive conduction whereas 13 percent was due to active heat transfer. Similarly, bees in free flight at 16°C (near the lowest possible temperature for continuous free flight), had a T_H averaging 24°C; T_H rose 9°C (to 33°C) at the 10°C higher T_A of 26°C. Since T_{Th} over this range of T_A under the conditions of measurement is not regulated in free flight—averaging 31° and 40°C at 16° and 26°C, respectively (*1*)—the T_H excess of the bees was approximately half the T_{Th} excess; thus, the flying bees also failed to use either variable heat flow from the thorax or another mechanism to regulate T_H.

In contrast to the observations at low (< 30°C) T_A, during free flight at high T_A the bees dramatically regulated both T_{Th} and T_H. Because of this ability, they were able to remain in continuous free flight up to T_A of 46°C, a feat to my knowledge undemonstrated for any other insect of their size and metabolic rate. At T_A of 46°C, T_H of 40 bees averaged 2°C below T_A (range = 41° to 46°C), rather than 7°C above as at T_A from 16° to 26°C. The excess of T_{Th} was reduced from the 15°C observed at low T_A (16°C to 26°C) to less than 0.5°C above T_A at 46°C.

The reduction in the thoracic temperature excess was not due to heat dissipation by the abdomen. In sphinx moths (*7*) and bumblebees (*8*), which use the abdomen as a thermal window to vary rates of heat loss, the temperature excess of the abdomen is greater at higher than at lower T_A. In contrast, in the honeybees ($N = 150$), the abdominal temperature excess was approximately 2°C at low T_A; rather than being higher at high T_A, it was usually diminished to zero or negative. Also in contrast to sphinx moths (*7*), bumblebees (*8*), and dragonflies (*9*), the honeybees increased T_{Ab} little or none when they were exogenously heated on the thorax to lethal temperatures.

The ability to actively dissipate heat to reduce T_H and T_{Th} by at least 10°C was due primarily to evaporative cooling from the head. All bees examined under the microscope immediately after they had been flying at 46°C had a droplet of fluid in the fold of the tongue. The droplet sometimes extended over the front of the thorax between the first two pairs of legs. Similarly, 31 of 33 tethered bees extruded a nectar droplet when heated on the head with the heat lamp. (The two that failed to extrude a droplet had empty honeycrops.) Both head and thorax cooled substantially as a result of evaporation from regurgitated honeycrop droplet (Fig. 1). The temperature of the droplet, which was always below T_H, T_{Th}, and T_{Ab}, fluctuated as the bees moved the droplet in and out (Fig. 2). Appearance of a droplet on the tongue in tethered bees always resulted in a decline in T_H of 2° to 8°C, followed within seconds by a similar decline in T_{Th} (Fig. 1). The cooling effect of the droplet would be potentially much greater at 46°C in flying bees subjected to greater convection and lower relative humidity (25 percent) than that observed in the experimentally pinned-down bees in still air at room T_A (26°C; relative humidity = 30 to 35 percent).

How does evaporative cooling from the head reduce T_{Th}? As already indicated, heat is transferred passively between thorax and head; cooling the head automatically results in cooling the thorax as heat flows passively along the temperature gradient. In addition, heat is apparently also actively transferred by blood circulation. Heating the heads of 27 bees invariably resulted in large-amplitude aortic pulsations in the head (Fig. 2), and pulses of low temperature (as much as 0.1°C below T_H) entered the head in synchrony with heart pulsations. Unlike other insects that use the abdomen as a heat radiator (*7*–*9*), honeybees respond to thoracic heating neither by violently pumping the abdominal heart nor (in 29 bees) by increasing T_{Ab} significantly ($P < .05$). However, in 9 of 21 bees, thoracic heating resulted in aortic pulsating in the head.

I conclude that the coiled aorta in the petiole of the honeybee indeed acts as an efficient countercurrent heat exchanger that is not physiologically bypassed or eliminated. With the abdomen thus unavailable as a major heat sink for metabolically produced heat in the thorax, the honeybee can fly at high T_A primarily because it can evaporatively cool the head, using regurgitated honeycrop contents. The mechanism is analogous to that observed in birds, which use the mouth to evaporate fluid to regulate head and core body temperature (*18*). The bee's mechanism is economical in that it preserves the meager blood supplies (a maximum of 5 μl) (*19*) while eliminating water from nectar that must in any case be concentrated to make honey in the hive.

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16. Body temperatures of tethered bees were measured with 46-gauge copper-constantan thermocouples implanted ~ 1 mm into the body and glued in place with a mixture of resin and beeswax. Body and ambient temperature (within 1 cm of the bee) were continuously recorded with a multichannel potentiometric recorder (Honeywell).
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