

## MECHANISMS OF BODY-TEMPERATURE REGULATION IN HONEYBEES, *APIS MELLIFERA*

### II. REGULATION OF THORACIC TEMPERATURE AT HIGH AIR TEMPERATURES

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#### SUMMARY

1. Honeybees could remain in continuous free flight at extremely high air temperatures (up to at least 46 °C).

2. The metabolic rate in free flight, 80–85 ml O<sub>2</sub> g body weight<sup>-1</sup> h<sup>-1</sup>, was independent of air temperature ( $T_A$ ) over a span of at least 22 °C.

3. The bees' ability to fly at high  $T_A$  was due to their ability to maintain thoracic temperature ( $T_{Th}$ ) near  $T_A$  despite prodigious rates of heat production. Mechanisms of preventing  $T_{Th}$  from overheating at high  $T_A$  were investigated.

4. Bees in flight at high  $T_A$  regurgitated fluid from their honeycrop and large droplets sometimes spread over the anterior portion of the thorax.

5. Bees without the first two sets of legs, or without a 'tongue', maintained as low  $T_H$  and  $T_{Th}$  as intact bees.

6. The abdomen serves only a minor function as a heat exchanger. In tethered bees, heating of the thorax to 45–50 °C resulted in significant, yet relatively little, temperature increase of the abdomen above that of dead or non heat-stressed animals. Similarly, in free flight abdominal temperatures ( $T_{Ab}$ ) were close to  $T_A$  at all  $T_A$ .

7. Thoracic heating to near lethal temperatures did not result in droplet extrusion from the mouth nor in significant physiologically facilitated heat transfer to the head. Furthermore, it resulted in no, or in relatively small, changes in pulsation of the aorta and the heart.

8. However, the bees prevented the head from overheating, and the head served as a heat sink for excess heat from the thorax. Keeping  $T_H < T_A$  resulted in keeping  $T_{Th}$  near  $T_A$ .

9. It is concluded that during flight at high  $T_A$  regulation of  $T_H$  by evaporative cooling is the primary mechanism of reducing  $T_{Th}$ .

#### INTRODUCTION

The ability of honeybees to produce prodigious amounts of heat by the flight muscles and to maintain an elevated thoracic temperature during most activities in and out of the hive (Esch, 1960; Heinrich, 1979*a*; Kronenberg, 1979) is now well

documented. Honeybees maintain their  $T_{Th}$  on the average 15 °C above  $T_A$  during continuous flight at  $T_A$  from 15 °C to 25 °C (Heinrich, 1979*a*). The heat that elevates body temperature is an obligatory product of their flight metabolism. Since in honeybees, as in moths other endothermic insects,  $T_{Th}$  of 46–48 °C are near lethal body temperatures, how is it possible that bees in some areas, such as the deserts of southern Arizona, regularly fly at  $T_A$  in excess of 40 °C and up to 47 °C (E. G. Linsley; G. D. Waller, personal communication)? Continuous flight at the high  $T_A$  would probably not be possible without efficient heat-dissipation capacity.

It appears on anatomical evidence that honeybees, unlike bumblebees (Heinrich, 1976), could make only limited use of the abdomen as a heat exchanger, nevertheless they fly at much higher  $T_A$  than bumblebees. Do they rely on an alternate cooling mechanism? Esch (1976) has speculated that they may employ evaporative cooling from fluid on their tongue, a mechanism which reduces head temperature (Heinrich, 1979*b*). I here examine the interrelationship between head and thoracic temperatures, and the physiological capacities that allow these bees to dissipate excess heat from the thorax and to fly at high  $T_A$ .

#### MATERIALS AND METHODS

Procedures for most of the experiments were largely as described by Heinrich (1979*b*).

Rates of oxygen consumption were measured using a Beckman E-2 paramagnetic oxygen analyser sensitive to 0.001% oxygen. The bees were flown in a glass respirometer (volume = 3.88 l) only after  $T_A$  inside it had equilibrated to the  $T_A$  of the temperature-controlled room. The bees had warmed up and were ready for flight before being placed into the respirometer jar. They began to fly (and the measurement began) immediately after they were dropped into the respirometer. The oxygen content of the air in the respirometer was measured immediately before a flight and after it. The latter air sample was withdrawn with a syringe within 10 s after the bee stopped flying. The data of oxygen consumption were corrected to standard temperature and pressure. For the most part the bees repeatedly bumped into the sides of the jar. When a bee settled on to the floor of the jar after a short flight it was shaken lightly and flight resumed. The bees were tarsectomized to ensure continuous flight. (Bees without tarsi could not get a grip on the side of the vessel.) Flight durations were at least 4.5 min.

In the experiments comparing body temperatures of intact bees with those without either the first two sets of legs or without the 'tongue' (galea, maxillae and tongue), all animals were briefly (< 20 s) anaesthetized with CO<sub>2</sub> 10 min prior to the measurements. The effects of potential changes in relative humidity (which increased sometimes from 20% to 40% after a period of working in the temperature-controlled room) were controlled by flying experimental and control bees alternatively in the room. In order to induce the bees to fly continuously without pause they were (when indicated) tarsectomized. Tarsectomized bees were unable to cling to the ceiling or walls, and they flew without interruption. As indicated elsewhere (Heinrich, 1979*a*) 3 min of flight was a sufficient duration to achieve a stable body temperature.

Mechanical in-out displacement of the abdomen to stimulate abdominal pumping in dead bees (unless indicated otherwise) was accomplished by gluing the tip of a rod to the tip of the abdomen in a bee fastened by the thorax. The rod was made to move in and out at any of a range of frequencies from  $< 80$  to  $> 600$  times per minute, using an electro-mechanical solenoid driven by electrical pulses.

## RESULTS

(A) *Metabolic rate*

There was considerable variability in the metabolic rate among individual bees, but there were no adjustments in metabolism as a function of air temperature over a 22 °C range of  $T_A$ . Metabolic rates from 20 measurements of flights (4.5–10 min each) ranged from 69 to 103 ml  $O_2$  g body weight<sup>-1</sup> h<sup>-1</sup>, averaging 85 at 20 °C and 80 at 42 °C (Table 1). Mean duration of continuous flight for the ten measurements each at 20 °C and 42 °C was 8.3 min and 9.1 min respectively. Measurements were terminated after 10 min of flight even though the bees were willing to fly longer.

(B) *Thoracic temperatures*

Honeybees in continuous free flight generate an average temperature excess of 15 °C at  $T_A$  from 17 °C to 25 °C (Heinrich, 1979a). At  $T_A > 25$  °C the temperature excess diminishes. In the present study I measured thoracic temperatures of bees in continuous free flight at  $T_A \geq 40$  °C.

Some bees remained in continuous ( $> 3$  min) free flight at  $T_A$  up to 46 °C. The thoracic temperatures of free-flying bees tended to be close to  $T_A$  at  $T_A$  of 46 °C (Fig. 1). Some individuals flew with a  $T_{Th}$  as much as 1 °C below  $T_A$ , although in one instance a  $T_{Th}$  of 50 °C was measured (Fig. 1).

Most bees that were not tarsectomized tended to land frequently, and an attempt was made to keep them in flight by tapping them (with a pencil) as soon as they landed. It is possible that the short flight interruptions which I was not always able to prevent had an effect on  $T_{Th}$ , but it is probably that it was slight. One intact bee flew without a single pause at 46 °C for 5 min 15 s before I was able to capture it and measure its temperature. Thoracic temperature of this bee was 48 °C, which is within the range observed in other bees that had been in flight for only three minutes. In addition, tarsectomized bees, that flew without pause, had similar  $T_{Th}$  to those of intact bees (Fig. 1). Some individuals were apparently unable to fly continuously at  $T_A = 46$  °C since they stopped flying up against the light and crawled into dark crevices, including the folds of my clothing.

Bees flying at high  $T_A$  often brushed their heads and bodies with their first two sets

Table 1. *Metabolic rates (ml  $O_2$  g body weight<sup>-1</sup> h<sup>-1</sup>) of honeybees in continuous free flight at 20 °C and 42 °C*

$T_A$	$\bar{X}$	Range	S.E.	N
20 °C	84.6	69.0–103.0	3.65	10
42 °C	79.7	69.1–99.5	3.13	10

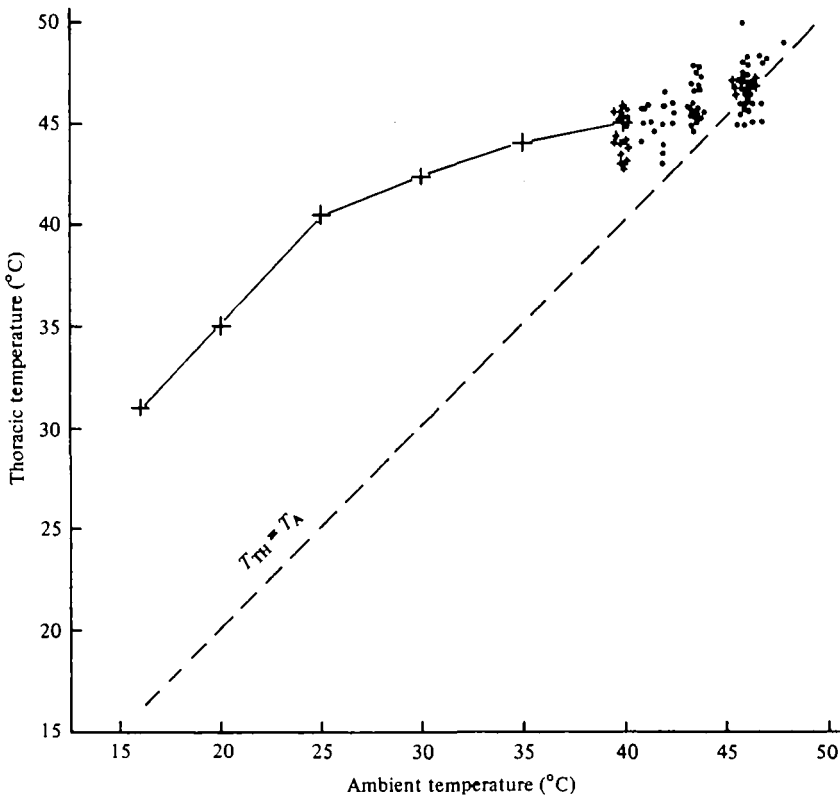


Fig. 1. Thoracic temperatures in free flight as a function of ambient temperature at  $T_A > 40^\circ\text{C}$ . The mean values at  $T_A < 40^\circ\text{C}$  (from Heinrich, 1979) are indicated for comparison. Small crosses indicate  $T_{\text{Th}}$  of tarsectomized bees.

of legs. Esch (1976) also observed this behaviour and presumed that the bees were rubbing regurgitated fluid over their bodies. However, I did not see bees actually spreading regurgitated syrup over their bodies, and I tested the possible thermoregulatory significance of the behaviour. If the brushing behaviour has a thermoregulatory role then body temperature should increase at high  $T_A$  if the legs are removed. However, bees without the first two sets of legs flew with the same, or slightly lower body temperatures, as those which were intact (Table 2).

### (C) Abdominal temperature

Do the bees transfer excess heat from thorax to abdomen? Bees with thermocouples implanted in both thorax and abdomen generally showed a small increase in  $T_{\text{Ab}}$  concomitant with increases of  $T_{\text{Th}}$ . The temperature excess of the abdomen was usually directly proportional to the temperature excess of the thorax, as would be predicted on the basis of passive conduction. However, when the bees were pinned down and allowed to be spontaneously endothermic, the ratio of temperature excess in the abdomen relative to that in the thorax (Table 3) was 0.233, which was slightly more than the 0.197 observed in dead heated bees and slightly less than the 0.284 in bees heated on the thorax to 45–50°C. The difference in the ratios between bees that

Table 2. Body temperatures ( $^{\circ}\text{C}$ ) of intact honeybees, and those with the first two sets of legs removed, during free flight at  $46^{\circ}\text{C}$

( $N = 34-43$  for each of the six categories.)

	Head temperature			Thoracic temperature			Abdominal temperature		
	$\bar{X}$	Range	s.e.	$\bar{X}$	Range	s.e.	$\bar{X}$	Range	s.e.
Intact	44.1	41.0-46.0	0.13	46.3	43.0-50.0	0.17	45.0	44.0-46.0	0.11
Legs removed	43.7	42.0-45.5	0.13	45.5	43.0-45.5	0.16	45.0	44.0-46.0	0.11

Table 3. Ratios of abdominal temperature excess ( $T_{Ab} - T_A$ ) ( $^{\circ}\text{C}$ ) relative to thoracic temperature excess ( $T_{Th} - T_A$ ), during endothermy and thoracic heating of live and dead bees

	$\bar{X}$	Range	N	s.e.
Live (endothermic)	0.233	0.107-0.398	26	0.018
Live (heated)	0.284	0.103-0.556	29	0.023
Dead (heated)	0.197	0.061-0.375	29	0.017

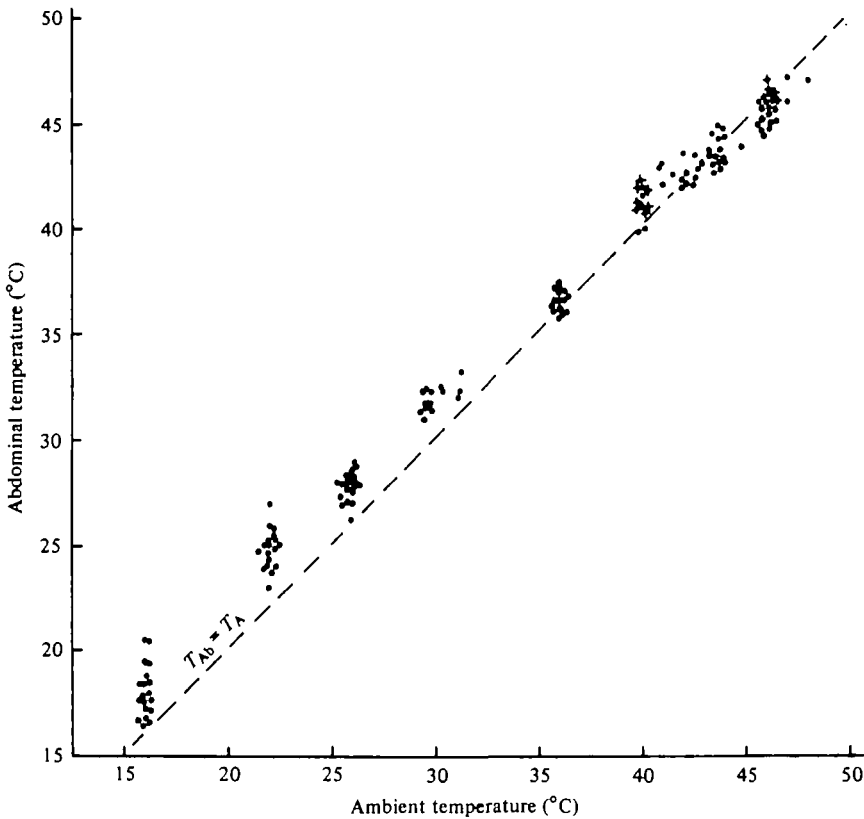


Fig. 2. Abdominal temperatures during free flight as a function of ambient temperature.

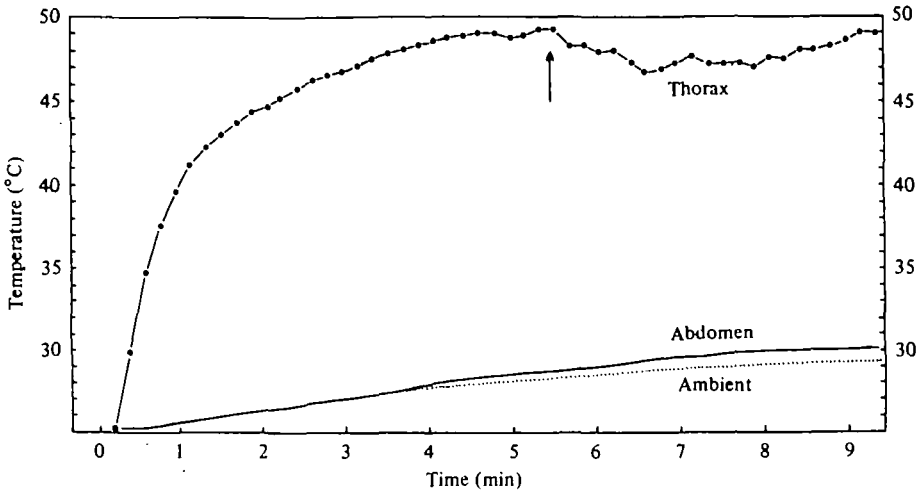


Fig. 3. Body temperatures of a honeybee during 9 min of thoracic heating, showing the reduction in  $T_{Th}$  following a droplet extrusion from the mouth (at arrow), as well as the relatively little heat transfer to the abdomen. Abdominal temperature shown is the difference in the temperature excess between that observed in bees heated when alive and when heated after being killed (see Methods).

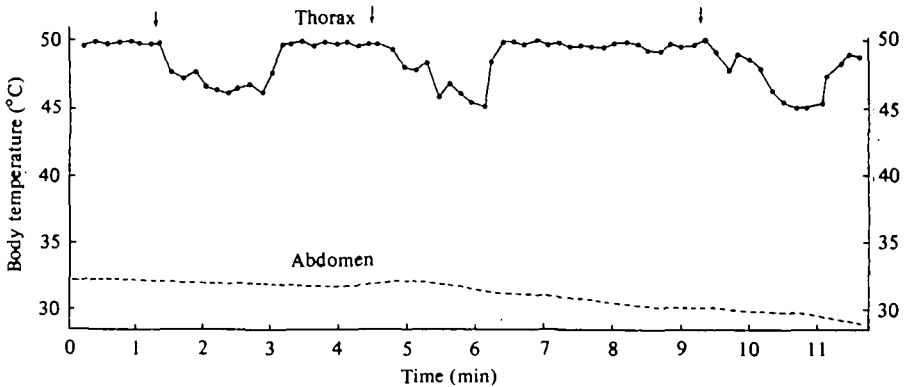


Fig. 4. Thoracic temperature of a bee which initiated three bouts of droplet extrusion (at arrows) during overheating of the thorax.  $T_A = 28.5^\circ\text{C}$ . The broken line indicates the difference from  $T_A$  in  $T_{Ab}$  live -  $T_{Ab}$  dead.

were dead (heated) and live (endothermic) ( $t = 1.43$ ) and between live (endothermic) and live (heated) ( $t = 1.69$ ) are not significantly different ( $P > 0.05$ ). However, the difference in the ratios between dead (heated) and live (heated) is significant ( $P < 0.01$ ;  $t = 3.04$ ). These data thus suggest that the bees transport heat into the abdomen in response to thoracic overheating. It should be noted, however, that unlike in bumblebees (Heinrich, 1976), the amount of active heat transfer to the abdomen is so small that it is not obvious. It is only statistically demonstrable.

Increases in abdominal temperature concomitant with thoracic cooling, which is routinely apparent in bumblebees (Heinrich, 1976), was not observed in the honeybees at any time. Apparently the abdomen is, on the whole, thermally insulated from the thorax, despite the blood flow that must occur between these two body parts.

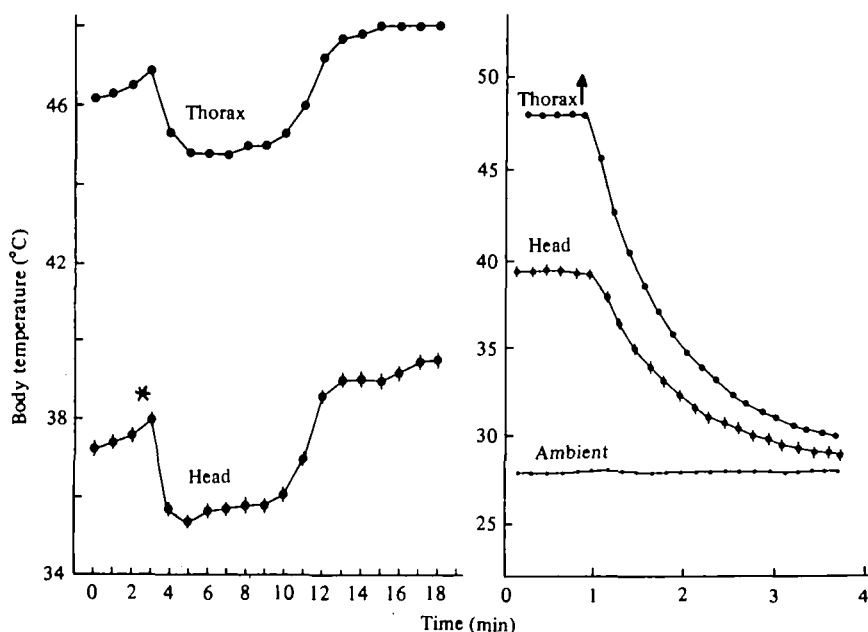


Fig. 5. Effect of a  $4 \mu\text{l}$  droplet of honeycrop contents on  $T_H$  and  $T_{Th}$ . The droplet was placed on to the tongue of a dead bee suspended in the air stream ( $32 \text{ m/s}$ ) of a wind tunnel at  $28^\circ\text{C}$ . The bee was heated with a narrow beam of light focused on to the thorax throughout the experiment (left), and until upward pointing arrow (right). Star indicates where the fluid droplet was applied.

Abdominal temperatures of bees which had been in free flight were close to  $T_A$  at all  $T_A$  (Fig. 2). At  $T_A$  of  $16\text{--}30^\circ\text{C}$ ,  $T_{Ab}$  averaged  $2^\circ\text{C}$  above  $T_A$ , while at  $T_A$  of  $46^\circ\text{C}$ ,  $T_{Ab}$  was usually at  $T_A$  or  $1^\circ\text{C}$  below  $T_A$ .

Bees which were pinned down and heated on the thorax did not extrude fluid from the mouth, unless  $T_H$  exceeded  $47^\circ\text{C}$ . When the thorax was heated to near  $50^\circ\text{C}$  with the heat lamp, head temperature generally exceeded  $45^\circ\text{C}$  and the bees sometimes extruded a nectar droplet. The appearance of the fluid was followed almost immediately by a drop in  $T_{Th}$  of an average of  $3\text{--}4^\circ\text{C}$  (Figs. 3 and 4), ranging up to  $6^\circ\text{C}$ . Even though the thorax of these bees was obviously heat-stressed, and they were losing heat from the thorax by way of the head, little or no heat transfer to the abdomen was observed. Where both  $T_{Th}$  and  $T_H$  were measured simultaneously, all decreases of  $T_{Th}$  were preceded or concurrent with decreases of  $T_H$  (Fig. 5).

#### (D) Cooling rates

The average mass of the head of a honeybee was  $10.25 \text{ mg}$ , and that of the thorax was  $32.50 \text{ mg}$ . Assuming a specific heat for the two body parts of  $0.8 \text{ cal g}^{-1} \text{ }^\circ\text{C}^{-1}$  (Krogh & Zeuthen, 1941), it becomes feasible, knowing the cooling rates, to determine the rates of heat loss from both head and thorax at any specific temperature difference they maintain. Heat is withdrawn into the head from the thorax, and differences in cooling rates of the two body parts between intact animals and those with the head

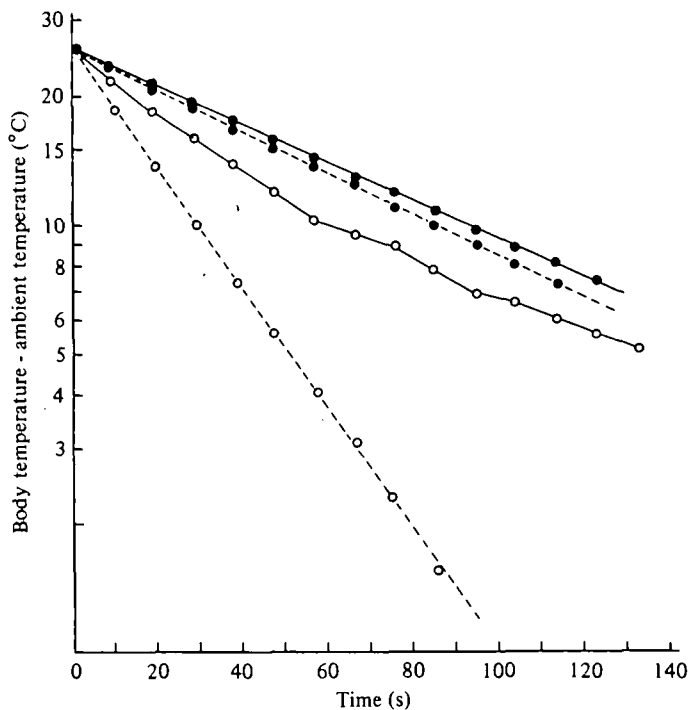


Fig. 6. Cooling curves of thorax (●) and head (○) of intact dead bee (—), and in the same bee (with same thermocouple implantation) with the head removed from the thorax (---).

severed might be used to estimate to what extent the head serves as a heat sink for excess heat from the thorax.

It could not be determined from superficial observations whether or not cooling in live animals is passive or physiologically retarded or facilitated. Bees may activate the flight muscles and produce heat (Bastian & Esch, 1970). Whether or not specific cooling curves in live bees are passive can only be determined by monitoring muscle activity during cooling, and by comparing them with those of dead bees. In those cooling curves of live bees where the temperature decrease was exponential, as in dead bees, the head temperature declined in parallel with  $T_{Th}$  (Fig. 5). In view of the large difference in mass between head and thorax this result could not occur unless there was extensive heat flow between the two body parts.

The log-transformed cooling curves of dead bees were linear, except for the initial decline in the temperature of heads still attached to the thorax (Fig. 6). In dead bees,  $T_H$  declined rapidly until it achieved a difference of several degrees Centigrade from  $T_{Th}$ , and then it declined at the same rate as  $T_{Th}$ . Heat was thus initially lost faster from the head than it was from the thorax. However, after a temperature difference was achieved between thorax and head, heat must have flowed passively from thorax to head at the same rate that it was lost from the head. The greater the temperature difference between thorax and head, the greater the expected passive conductive heat flow. The decline in head temperature was rapid and linear only when the head was separated from the thorax and could no longer receive replacement heat from the thorax (Fig. 6).



Table 4. Slopes of cooling curves in log (body-ambient temperature) per minute of head and thorax in intact bees, and after the heads were detached from the thorax

(Multiply by 2.303, the natural logarithm of 10, to get  $^{\circ}\text{C min}^{-1} ^{\circ}\text{C}^{-1}$  temperature difference.)

	Intact			Head off		
	$\bar{X}$	S.E.	N	$\bar{X}$	S.E.	N
Head	-0.3492	0.02064	10	-1.0074	0.05886	10
Thorax	-0.2844	0.00966	10	-0.3216	0.01008	10

Severed heads cooled on the average 2.9 times faster than when they were attached to the thorax. On the other hand, heads on the thorax had nearly the same cooling rates ( $0.80^{\circ}\text{C min}^{-1} ^{\circ}\text{C}^{-1}$ ) as the thorax without the head ( $0.74^{\circ}\text{C min}^{-1} ^{\circ}\text{C}^{-1}$ ) (Table 4). It can be concluded that any change in  $T_H$  must immediately affect  $T_{Th}$ , and vice versa, due in great part to the physical proximity that permits the passive transfer of heat from the portion of higher temperature to that of lower temperature.

#### (E) Activity of the heart and aorta

The heart and aorta could pump blood between head, thorax and abdomen, and the pulsations in these organs could reflect mechanisms of temperature control.

Heating of the thorax produced an ambiguous response from the abdominal heart. During some thoracic heating experiments the aorta increased the frequency and amplitude of its pulsations (Fig. 7), while during others it declined its activity (Fig. 8, see also Table 2, Heinrich, 1979*b*). Part of the ambiguity may be due to the fact that head temperature increased at the same time (but to a lesser degree) as the thorax was being warmed.

The activity of the abdominal heart showed little change with thoracic heating. Heating of the abdomen resulted in increased frequency of the abdominal heart (Fig. 8) but no change in the aorta (Fig. 7). On the other hand, heating of the head always resulted in aortal pulsations in the head (Fig. 7).

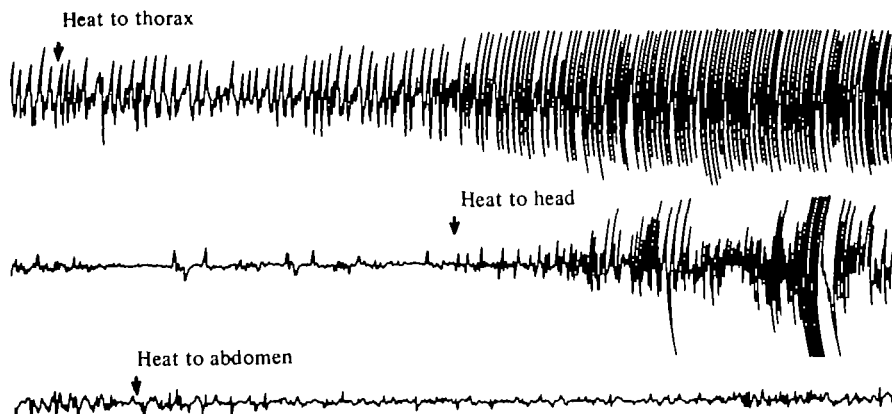


Fig. 7. Response of the aorta in the head during heating of the thorax (first trace), heating of the head (second trace), and abdominal heating (third trace) of the same bee. Thoracic temperature was  $35\text{--}50^{\circ}\text{C}$ ,  $35\text{--}37^{\circ}\text{C}$  and  $38^{\circ}\text{C}$  in the three traces, respectively. The records are each 1 min in length.

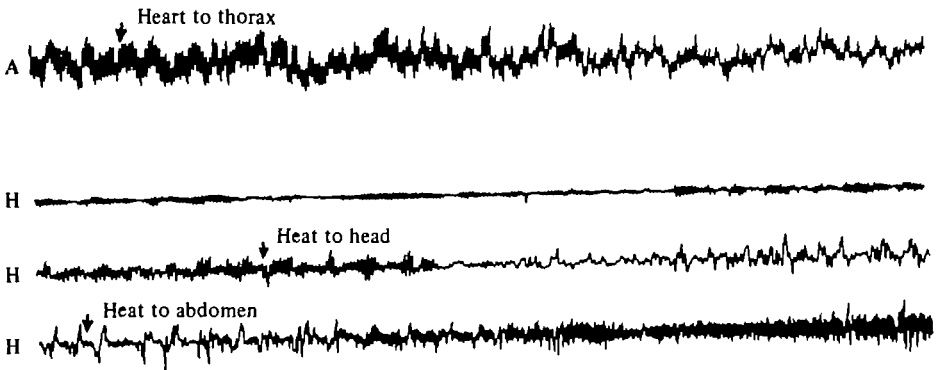


Fig. 8. The first two traces show synchrony between pulsations of the aorta (A) and the heart (H). These traces also show the response of the aorta and the heart to thoracic heating. Third and fourth traces show the response of the abdominal heart to heating of the head and abdomen, respectively, in the same bee. Thoracic temperature in the first two traces increased from 33 to 44 °C. In the third and fourth traces  $T_{Th}$  was 38–39 °C, and 34 °C, respectively. Each of the records span 1 min.

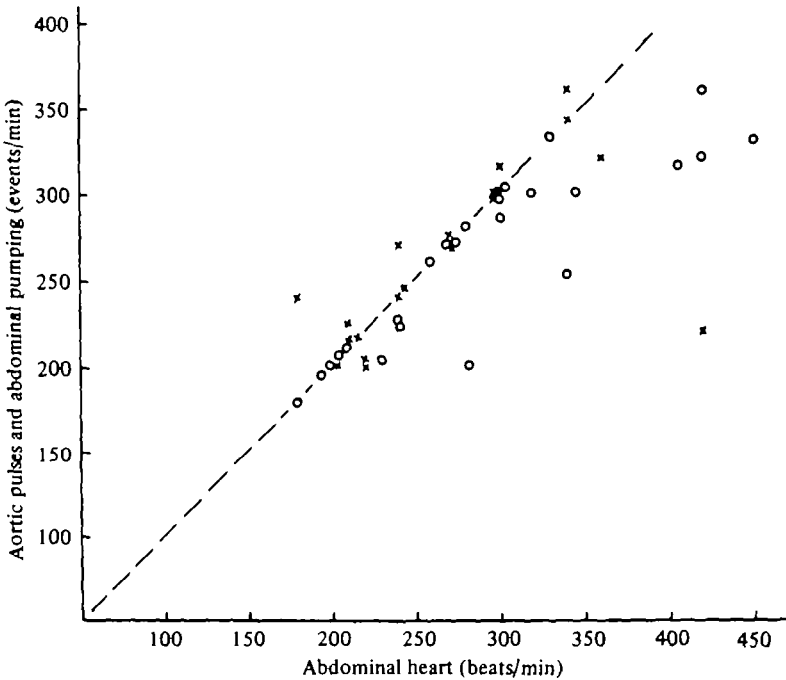


Fig. 9. Aortic pulses (x) and abdominal pumping (O) in relation to the frequency of the heartbeat in the abdomen.

Although the aortal and heart pulsations were often both at the same or similar frequency as that of the abdominal pumping movements (Figs. 8 and 9), they were at other times also at entirely different frequencies and amplitudes, both with respect to each other and with respect to the abdominal pumping movements (Heinrich,

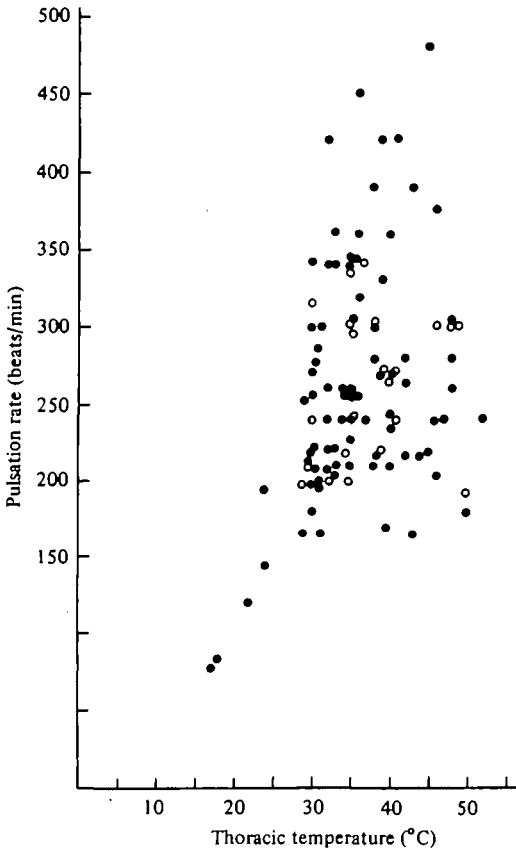


Fig. 10. Pulsation rate of the heart in the abdomen (●) and the aorta in the head (○) as a function of  $T_m$ . The data are from 33 bees.

1979*b*). Neither heart nor aortal beats thus had pulsation rates set at specific head or thoracic temperatures (Fig. 10).

These results suggest that, unlike in sphinx moths (Heinrich, 1971) and bumblebees (Heinrich, 1976), in honeybees the abdominal heart is not recruited for facilitated heat transfer to the abdomen.

#### (F) *Forced ventilation*

The abdominal ventilatory movements, while functioning in gas exchange for the thoracic muscles, must necessarily withdraw moisture and produce evaporative cooling. Is the magnitude of the evaporation sufficient to cause significant changes in body temperature?

A major problem in experimentally analysing the possible role in evaporative cooling is that only live bees ventilate, and ventilation is almost always associated with heat production and heat transfer, so that evaporative cooling effects are obliterated.

Table 5. *Body temperatures (°C) of bees during continuous free flight in the temperature controlled room at 40 °C*

(All of the bees were tarsectomized.)

	Head temperature				Thoracic temperature				Abdominal temperature			
	$\bar{X}$	Range	s.e.	N	$\bar{X}$	Range	s.e.	N	$\bar{X}$	Range	s.e.	N
No tongue (14% R.H.)	40.5	39-42	0.18	20	44.2	43-46	0.16	20	40.6	40-42	0.17	13
Tongue present (14% R.H.)	41.0	40-42	0.17	20	44.1	42-46	0.23	20	41.1	40-42	0.20	12
Tongue present (67% R.H.)	41.7	40-43	0.17	20	44.6	43-46	0.18	20	41.3	40-42	—	8

I made an attempt to determine empirically the effect of evaporative cooling by abdominal ventilatory movements using recently killed bees with their abdomen pumped in and out by a mechanical device (see Methods) to simulate abdominal pumping movements. The bees were examined at 40-44 °C (R.H. = 25%). They were allowed to equilibrate to  $T_A$ , while  $T_{Ab}$  and  $T_{Th}$  were continuously monitored. In live bees abdominal pumping movements were generally of 0.5 mm amplitude, with a frequency of 150-400 per minute. In the experiment the abdomens were mechanically pumped at amplitudes from 0.5 to 3 mm, and at frequencies from 80 to 600 per minute. Before pumping began,  $T_{Th}$  and  $T_{Ab}$  averaged 0.6 °C and 0.4 °C below  $T_A$ , respectively. Mechanical pumping, even at the maximum amplitude and frequency, did not result in additional body temperature depression beyond 1 °C. However, in one of the eight bees examined the abdominal body wall ruptured, and  $T_{Ab}$  then declined by 9 °C.

The possibility remained that the dead bees had closed spiracles. However, similar results were obtained in two live bees that were not endothermic after they were anaesthetized with CO<sub>2</sub> (which results in spiracle opening). These results diminish, but do not totally rule out, the possibility that the bees use evaporative cooling from the tracheal system for body temperature regulation.

#### (G) *The 'tongue'*

As already indicated, the only clearly demonstrable effect on reducing the thoracic temperature excess could be observed in bees that regurgitated fluid from the honeycrop and held it on their tongue. However, bees which had their tongue experimentally removed also regurgitated honeycrop contents, and a droplet could be seen extending from the mouth. The presence of the tongue is apparently not necessary for thermoregulation. Bees with their tongue removed were able to maintain as low or lower body temperature as unoperated bees. At  $T_A = 40$  °C bees without their tongue had a mean  $T_H$  and  $T_{Th}$  of 40.5 °C and 44.2 °C, respectively. Unoperated controls flying at the same temperature (also at 14% R.H.) had mean  $T_H$  and  $T_{Th}$  of 41.0 °C and 44.1 °C (Table 5). However, when unoperated bees were flown at high R.H. (67%) at 40 °C, their  $T_H$  was significantly ( $P < 0.01$ ) higher, averaging 0.7 °C above that observed in unoperated bees flying at 14% R.H. at the same  $T_A$ . Thoracic temperatures averaged 0.5° higher at the higher R.H. (Table 5).

## DISCUSSION

Honeybees when not in flight are well-known to elevate and regulate their thoracic temperature using their flight muscles to generate heat. The lower the air temperature, the more the flight muscles are activated (Bastian & Esch, 1970), and the more heat is produced to counteract cooling (Free & Spencer-Booth, 1958; Allen, 1959; Cahill & Lustick, 1976). During flight, however, the muscles are unavailable for shivering. Heat is necessarily produced as a by-product of the flight metabolism, and the temperature excess generated during flight is, in part, a function of  $T_A$  (Heinrich, 1979*a*), but whether or not the metabolism is varied to counteract cooling and maintain a stable body temperature was not known.

The rate of oxygen consumption is a measure of the metabolic rate and the rate of heat production in animals such as bees which do not accumulate an oxygen debt. The metabolic rate of honeybees in fixed flight or on a flight mill at room temperature averages 60–70 ml O<sub>2</sub> g body weight<sup>-1</sup> h<sup>-1</sup> (Hocking, 1953; Bastian & Esch, 1970; Sotavalta, 1954). The present data indicate that bees in free flight average a slightly higher metabolic rate (80–85 ml O<sub>2</sub> g body weight<sup>-1</sup> h<sup>-1</sup>), and the metabolism is not significantly different during flight at 20 °C and at 42 °C. The bees thus make no adjustments of heat production to stabilize  $T_{Th}$  during flight. They produce as much heat during flight at 42 °C, when they could potentially overheat, as they do at 20 °C when they are near the lower temperature limit of continuous free flight. These results on metabolism and heat production are similar to those observed in bumblebees (Heinrich, 1975*a*); during flight the flight muscles must necessarily produce prodigious amounts of heat and the bees do not have the option of reducing metabolic rate to prevent overheating.

Honeybees during uninterrupted free flight generate an average thoracic temperature excess of 15 °C between  $T_A$  of 15 °C and 25 °C (Heinrich, 1979*a*). As shown in the present study, however, they are able to reduce the temperature excess until they are, at  $T_A = 46$  °C, able to fly with a  $T_{Th}$  identical with  $T_A$ , despite the same amount of heat production as at  $T_A \leq 25$  °C. These results indicate the operation of an efficient cooling mechanism(s).

As shown previously (Heinrich, 1979*b*), the bees lower  $T_H$  by several degrees Centigrade below  $T_A$  at high  $T_A$  by regurgitating and evaporating fluid from the ventral portion of the head. The isolated head cools approximately three times faster than the thorax, which has three times greater mass. In the intact animals, however, head and thorax have nearly identical cooling rates, although the absolute temperature of the head is always less than that of the thorax after both have been heated to similar temperature. These observations indicate that heat must flow from thorax to head, and that the head acts as a heat sink for the thorax. At low  $T_A$  when no fluid is regurgitated from the head, this results in an elevated  $T_H$ . But at high  $T_A$  when the head is cooled by evaporation of water to temperatures below  $T_A$ , the heat flow from the thorax to the head appears to be sufficient to bring  $T_{Th}$  to  $T_A$  despite prodigious amounts of heat production.

The evaporative cooling from the regurgitated honeycrop contents is perhaps the primary mechanism of reducing body temperature at high  $T_A$ . However, it need not

be the only mechanism. In addition, there is evaporative cooling from the tracheal system. Is this cooling sufficient to affect body temperature?

During flight the honeybee inspires air by the first thoracic spiracle as well as the abdominal spiracles, and expels the air through the second thoracic spiracle (Bailey, 1954). Both the thorax and the abdomen could thus yield water to inspired, sub-saturated, air and thus cause cooling by evaporation. However, evaporation from the tracheal system has been found to account for a temperature depression of not more than 1 °C, in the migratory locust, *Schistocerca gregaria* (Church, 1960) and not more than 1.6 °C in the Tsetse fly, *Glossina morsitans* (Edney & Barrass, 1962). Calculations of potential body temperature changes in honeybees (Heinrich, 1975*b*) also suggest that the role of evaporation is not a major factor in thermoregulation. In the present study the data on forced ventilation in bees corroborate previous observations. Evaporation from the tracheal system cannot account for the major portion of the body temperature reduction observed.

Honeybees have minute quantities of blood. Beutler (1936) found a maximum volume of 5  $\mu$ l per bee. Evaporative cooling using these precious body fluids is probably not a feasible strategy unless it is combined with means of very rapid regeneration of these fluids. On the other hand, the bees carry relatively enormous amounts of nectar in their honeycrop, and this nectar must be evaporated to honey in any case.

In contrast to sphinx moths (Heinrich, 1971; Casey, 1976), dragonflies (Heinrich & Casey, 1978), and bumblebees (Heinrich, 1976), honeybees do not use the abdomen as a significant heat exchanger for thoracic temperature stabilization. In part this may be due to the convolutions of the aorta in the petiole (Snodgrass, 1925; Wille, 1958) which would act to prolong the time that cool blood from the abdomen could traverse the petiole area. The longer the time required for the cool blood to traverse the petiole area the more there is opportunity for heat in the blood returning to the abdomen to be recovered by counter-current exchange and returned to the thorax. Retention of heat in the thorax would reduce the energetic cost of warm-up and permit the maintenance of a high  $T_{Th}$  at low  $T_A$ . Bumblebees, which individually incubate their blood clusters with their abdomen, do not have the aortic convolutions and are able to temporally by-pass the potential counter-current heat exchanger in the abdomen by shunting blood into and out of the thorax alternately (Heinrich, 1976). The same mechanism used to heat the brood is apparently also used to prevent overheating during flight. The honeybees do not have this option of heat dissipation due to their morphological design for heat conservation that allows them to fly at relatively low  $T_A$  ( $\approx 15$  °C) despite their small size and lack of insulation.

The temperature regulation system of the honeybee, which involves the depression of core (thoracic) temperature under high internally produced heat loads at high  $T_A$ , has some analogues with that of birds. Birds also do not sweat, but they evaporate water from the mouth, transferring heat out of the body core by way of the blood circulatory system as well as by conduction (see Bartholomew, 1977). The mechanism allows birds to conserve electrolytes (that would be lost in animals that sweat). In bees, on the other hand, the analogous cooling mechanism conserves the meagre body fluids, as well as the sugars in the crop.

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