

## THERMOREGULATION OF AFRICAN AND EUROPEAN HONEYBEES DURING FORAGING, ATTACK, AND HIVE EXITS AND RETURNS

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### SUMMARY

1. While foraging, attacking, or leaving or returning to their hives, both the African and European honeybees maintained their thoracic temperature at 30 °C or above, independent of ambient temperature from 7 to 23 °C (in shade).

2. Thoracic temperatures were not significantly different between African and European bees.

3. Thoracic temperatures were significantly different during different activities. Average thoracic temperatures (at ambient temperatures of 8–23 °C) were lowest (30 °C) in bees turning to the hive. They were 31–32 °C during foraging, and 36–38 °C in bees leaving the hive, and in those attacking. The bees thus warm up above their temperature in the hive (32 °C) before leaving the colony.

4. In the laboratory the bees (European) did not maintain the minimum thoracic temperature for continuous flight (27 °C) at 10 °C. When forced to remain in continuous flight for at least 2 min, thoracic temperature averaged 15 °C above ambient temperature from 15 to 25 °C, and was regulated only at high ambient temperatures (30–40 °C).

5. At ambient temperatures > 25 °C, the bees heated up during return to the hive, attack and foraging above the thoracic temperatures they regulated at low ambient temperatures to near the temperatures they regulated during continuous flight.

6. In both African and European bees, attack behaviour and high thoracic temperature are correlated.

7. The data suggest that the bees regulate thoracic temperature by both behavioural and physiological means. It can be inferred that the African bees have a higher metabolic rate than the European, but their smaller size, which facilitates more rapid heat loss, results in similar thoracic temperatures.

### INTRODUCTION

The African honeybee, *Apis mellifera adansonii*, is well-known for aggressiveness, for rapidity of flight in and out of the hive, for willingness to forage at lower temperatures than the European bee, *Apis mellifera mellifera*, and for great honey

production (see Chandler, 1976; Michener, 1973), as well as for less perfect nest temperature regulation than its European relative (Darchen, 1973).

In other flying insects, maximum activity rates in any one species are a direct function of thoracic temperature (Heinrich, 1974). Furthermore, at least in bumblebees, foraging speed depends on thoracic temperature (Heinrich, 1972). Similarly, during aggressive contests among African dung ball rolling beetles, those with a higher thoracic temperature move the fastest and have a competitive advantage in securing and defending their food in inter- and intra-specific contests (B. Heinrich & G. A. Bartholomew, unpubl.). Might greater activity rates and aggression in the African honeybee also be linked with a higher thoracic temperature?

I here compare the thoracic temperature of free-living individual bees of both sub-species in order to determine if some of the behavioural traits in the two bee varieties may be related to thermoregulatory differences.

#### METHODS

All body temperatures were measured with a 40-gauge copper-constantan thermocouple threaded through a hypodermic needle (O.D. = 0.5 mm) and glued in place so that the couple was in the orifice of the needle. Temperatures were read to the nearest 0.5 °C using a battery-operated Omega Engineering Thermocouple Thermometer.

Foraging and attacking bees were captured either with an insect net or they were grasped with a pair of forceps directly from flowers or from my body. Within about 3 s after being grasped either with forceps or by gloved hand, the thermocouple probe was thrust (through the netting, if present) first into the thorax until the highest temperature was encountered, and then into the abdomen. I examined the accuracy of the measurements by continuously recording the thoracic temperature of heated dead bees in the laboratory with a Honeywell recording potentiometer, grasping these bees with known thoracic temperature, and measuring their thoracic temperature with the portable thermometer. The two readings were within 1 °C in bees heated and maintained at 20 °C above air temperature.

Immediately after body temperatures were recorded the bees were killed by crushing the thorax, placed into small paper triangles, and stored in a sealed container at 100% R.H. They were usually weighed within 1 h to the nearest milligram with a Roller-Smith torsion balance.

Returning bees were grasped immediately (within a second) after they landed on the entrance-board of the hive. Bees leaving the hive were grasped from the entrance-board immediately after they wiped their antennae, the usual indicator that they were about to fly. After a bout of measurements at any one hive where I was capturing, probing and crushing bees, there were generally attacking bees (those that clearly attempted to sting through clothing, or which pursued me), particularly at the African hives.

All of the observations on African bees were made in Kenya during January 1977. Body temperature measurements at ambient temperatures ( $T_A$ ) of 12 °C or less were taken at Molo, at about 2700 m, or at Njoro at about 1800 m. The measurements at  $T_A > 15$  °C and  $< 25$  °C were taken in the vicinity of Nairobi (1500 m), and

those at  $> 25^{\circ}\text{C}$  were taken nearby at Athi River. Thoracic temperatures ( $T_{\text{Th}}$ ) of European bees were also measured after timed durations of continuous flight at different  $T_{\text{A}}$  in a temperature-controlled Modu-lab room regulating to within  $1^{\circ}\text{C}$ . Individual bees were flown after being captured (in an Erlenmeyer flask) as they were leaving an observation hive immediately adjacent to the room. The bees generally flew towards the fluorescent lights against the gauze covering the ceiling. If they landed they were immediately tapped and stimulated to resume flight. Measurements were taken of bees immediately after they landed, or after they were captured between gloved thumb and forefinger.

Body temperatures of free-flying European bees were recorded in Berkeley, California during January–March 1978. Those in the Modu-lab room were measured in August and September, 1978.

Thoracic volumes were determined by the water displaced by over 60 thoroughly hydrated thoraces that had been wetted in detergent solution and rolled across filter paper to take up excess external moisture.

## RESULTS

### *Apis mellifera adansonii*

*Leaving the hive.* African honeybees begin to forage early in the morning at low temperatures. I observed 'near maximal' traffic in and out of African hives at ambient temperatures ( $T_{\text{A}}$ ) of  $8\text{--}10^{\circ}\text{C}$ , when sunshine was available at 08.00 h. However, in the absence of sunshine, few bees were leaving the hive at temperatures  $< 9^{\circ}\text{C}$ .

I compared the body temperatures of bees inside the brood nest with those at the hive entrance while leaving. The thoracic temperatures ( $T_{\text{Th}}$ ) of 15 bees perched upon the brood combs varied from  $31.0$  to  $34.5^{\circ}\text{C}$ , with a mean of  $32.4^{\circ}\text{C}$ . Abdominal temperatures of these bees ranged from  $28$  to  $34^{\circ}\text{C}$ , with a mean of  $31.0^{\circ}\text{C}$ .

The  $T_{\text{Th}}$  of bees leaving the hive was on the average  $5^{\circ}\text{C}$  higher than that of the bees in the brood nest, and it was up to  $14^{\circ}\text{C}$  above  $27^{\circ}\text{C}$ , the minimum for level flight. Thus, as bees leave the hive from the warm interior they nevertheless increase the temperature of their thoracic musculature before initiating flight. Thoracic temperature of bees leaving was also independent of external  $T_{\text{A}}$  from at least  $7.5$  to  $17^{\circ}\text{C}$  (Fig. 1). Bees leave the hive in rapid flight that may be a consequence of their high  $T_{\text{Th}}$ .

Abdominal temperature ( $T_{\text{Ab}}$ ) was variable, but on the average it was approximately  $12^{\circ}\text{C}$  above  $T_{\text{A}}$ . The wide range in abdominal temperature, and its dependence on  $T_{\text{A}}$ , suggest that the abdomen cools passively after the bees leave the warm brood nest.

*Returning to the hive.* At  $T_{\text{A}} < 25^{\circ}\text{C}$  in shade the  $T_{\text{Th}}$  of bees returning to the hive was, at near  $30^{\circ}\text{C}$ , on the average  $7^{\circ}\text{C}$  lower than that of bees leaving (Tables 1 and 2). At least between  $10$  and  $16^{\circ}\text{C}$  the  $T_{\text{Th}}$  of returning bees was independent of  $T_{\text{A}}$  (Fig. 2). The lowest  $T_{\text{Th}}$  of returning bees was  $27^{\circ}\text{C}$ , the minimum to sustain level or descending decelerating flight.

At  $T_{\text{A}}$  near  $24^{\circ}\text{C}$  worker bees returning in sunshine were on the average  $3^{\circ}\text{C}$  warmer than those returning during overcast. However, drones returning during overcast had an average  $T_{\text{Th}}$  of  $41^{\circ}\text{C}$ , being about  $7^{\circ}\text{C}$  warmer than workers under

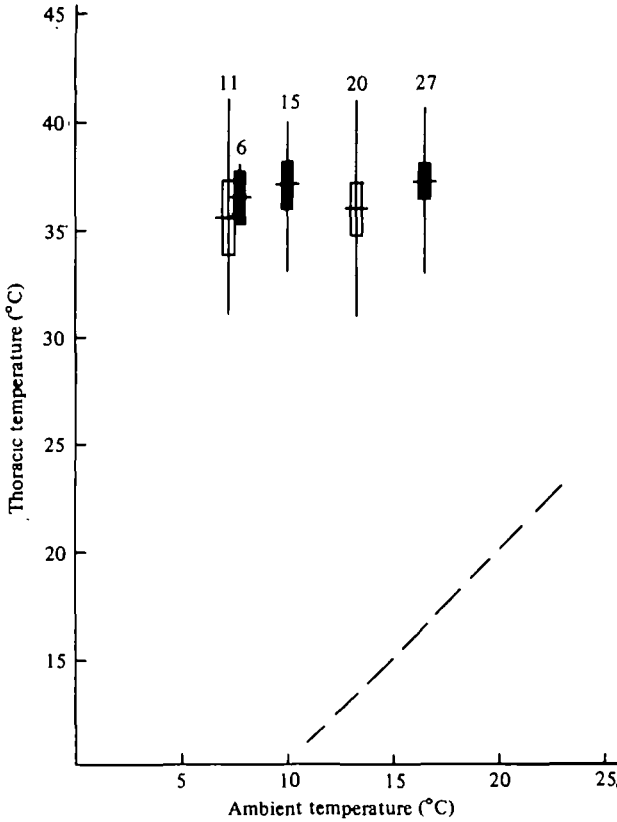


Fig. 1. Thoracic temperatures of bees leaving the hive. Open boxes = *A. m. mellifera*, filled boxes = *A. m. adansonii*. Vertical lines indicate range. Boxes enclose 2 s.e. on each side of the mean. Numerals indicate sample size.

Table 1. Comparisons of thoracic temperatures between *adansonii* and *mellifera*

(Indicated are means (s.e.) and  $N$ , and ambient temperature ( $T_A$ ). None of the four means where data for both are available are significantly different at  $P < 0.05$  level.)

	<i>adansonii</i>				<i>mellifera</i>			
	$\bar{x}$	s.e.	$N$	$T_A$	$\bar{x}$	s.e.	$N$	$T_A$
Leaving hive	37.2	(1.77)	48	8-17	35.9	(0.53)	31	8-14
Foraging	31.9	(0.25)	60	11-22	31.3	(0.16)	97	12-23
Returning to hive	30.3	(0.18)	103	10-17	30.1	(0.21)	46	7-14
Attacking	37.5	(0.22)	123	8-20	37.7	(0.26)	66	7-19
Feeding on honey	34.1	(0.66)	9	7.5	—	—	—	—
On brood	32.4	(0.36)	13	—	—	—	—	—

the same conditions. The workers apparently allow their  $T_{Th}$  to rise passively during flight under moderate  $T_A$ . The results do not differentiate whether the drones were warmer than the workers due to the regulation of a higher set-point, or due to passive temperature increase related to lower rates of passive cooling because of their greater mass.

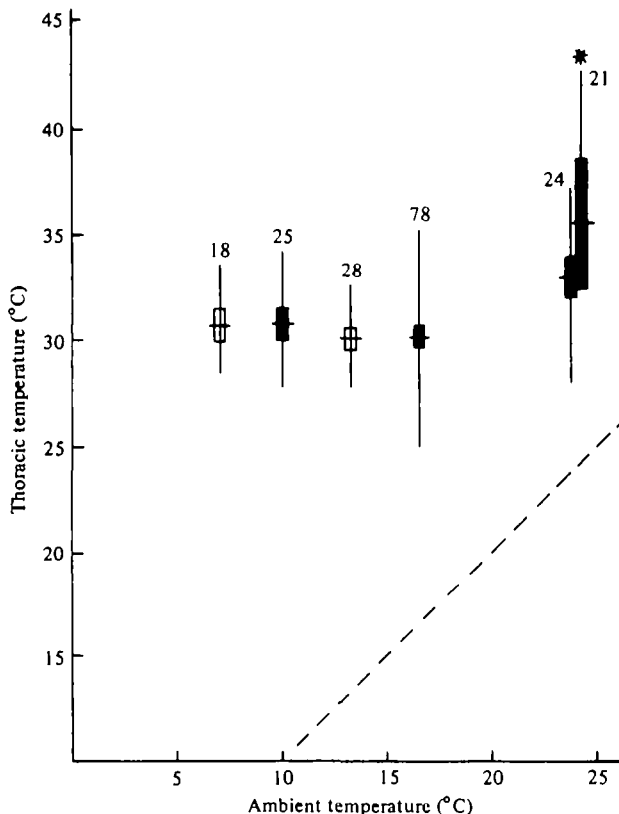


Fig. 2. Thoracic temperatures of bees returning to the hive. Symbols as in Fig. 1. \* = in sunshine. Others were in shade, during overcast, or before sun-up.

Table 2. Comparisons of thoracic temperatures at  $T_A = 7-25^\circ\text{C}$  in shade or overcast at different flight activities

(The numbers indicate the difference between means (*t*-value, *N*), and level of significance of the difference.)

	<i>adansonii</i>	<i>mellifera</i>
Leaving vs. returning	6.94 (20.1, 152) $P < 0.001$	5.75 (9.29, 77) $P < 0.001$
Leaving vs. attacking	0.32 (0.78, 154) $P < 0.05$	1.85 (2.77, 97) $P < 0.01$
Leaving vs. foraging	5.31 (12.3, 108) $P < 0.001$	4.59 (7.81, 128) $P < 0.001$
Returning vs. attacking	7.26 (23.1, 209) $P < 0.001$	7.60 (18.4, 112) $P < 0.001$
Returning vs. foraging	1.63 (4.31, 163) $P < 0.001$	1.16 (3.98, 143) $P < 0.001$
Attacking vs. foraging	5.63 (13.9, 166) $P < 0.001$	6.44 (19.1, 163) $P < 0.001$

At a given  $T_A$  abdominal temperatures of bees that had been in flight outside the hive were uniformly low in comparison with that of bees leaving the hive. The average difference in temperature between  $T_A$  and  $T_{Ab}$  was  $5^\circ\text{C}$  in shade and this difference was independent of  $T_A < 24^\circ\text{C}$ .

The loaded returning foragers had lower  $T_{Th}$  than the unloaded bees leaving to initiate foraging, and their  $T_{Th}$  was independent of their weight (Fig. 3). However, since average nectar and pollen loads were relatively small (Table 3), about 6 mg

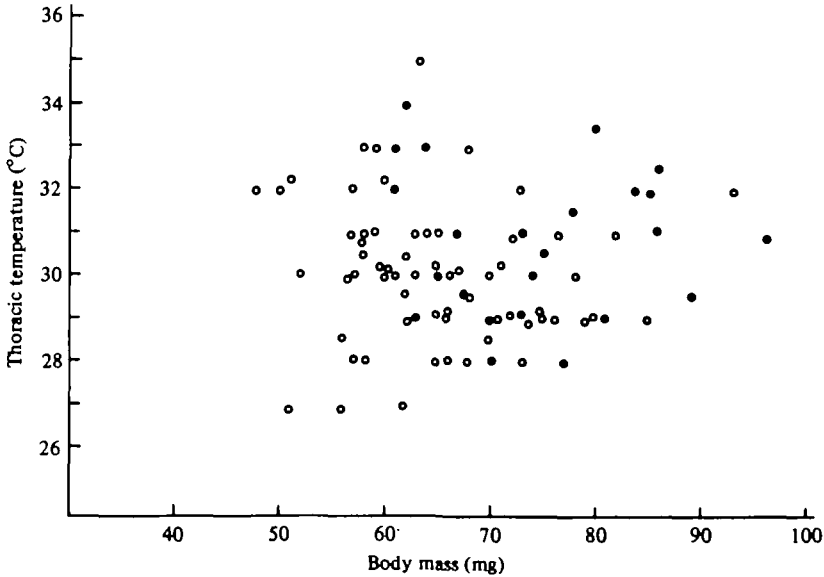


Fig. 3. Thoracic temperature of *A. m. adansonii* returning to the hive in relation to body weight at 10 °C (●) and 15.5–17.0 °C (○).

Table 3. *Body weights (mg), foraging loads (mg) of adansonii and mellifera*

(Numbers indicate means (s.e.) and sample size. Thoracic volumes ( $\mu\text{g}$ ) refer to means and sample size only.)

	<i>adansonii</i>	<i>mellifera</i>
Weight leaving hive	60.8 (0.72) 67	92.7 (1.44) 31
Weight returning	66.5 (0.84) 168	115.7 (1.77) 34
Thoracic volume	31.03, 87	36.15, 65

(vs. about 23 mg in the European bee), a possible effect of wing-loading on  $T_{\text{Th}}$  cannot be discounted.

**Hive defence.** Attacking bees flew rapidly back and forth as well as around and at persons near the hive. The  $T_{\text{Th}}$  of these 'attacking' bees were as high or higher than those of bees leaving the hive (Fig. 4, Table 1), even though the bees often spent a minute or more in rapid and continuous flight before they were captured and their body temperatures measured. Abdominal temperatures had decreased, being markedly lower than those of bees inside the hive, and in contrast to  $T_{\text{Th}}$ ,  $T_{\text{Ab}}$  were closely correlated with  $T_{\text{A}}$ .

The difference between  $T_{\text{Th}}$  and  $T_{\text{A}}$  was inversely correlated. For example, although the average  $T_{\text{Th}}$  at  $T_{\text{A}}$  of 24 °C was 39 °C, while that at 8 °C was 35.5 °C, the difference between  $T_{\text{Th}}$  and  $T_{\text{A}}$  was nearly two times greater (27.5 vs. 15 °C) at 8 °C than at 24 °C (Fig. 4).

There was a tendency for the bees attacking in the immediate vicinity (1–3 m) of the hive to be warmer than those attacking at greater distances. For example, at Molo, at  $T_{\text{A}}$  of 9 °C, the average  $T_{\text{Th}}$  of attacking bees was 35.4 °C 1–5 m from the hive and 33.1 °C at 5–10 m, even though  $T_{\text{A}}$  was 3 °C higher when the measurements

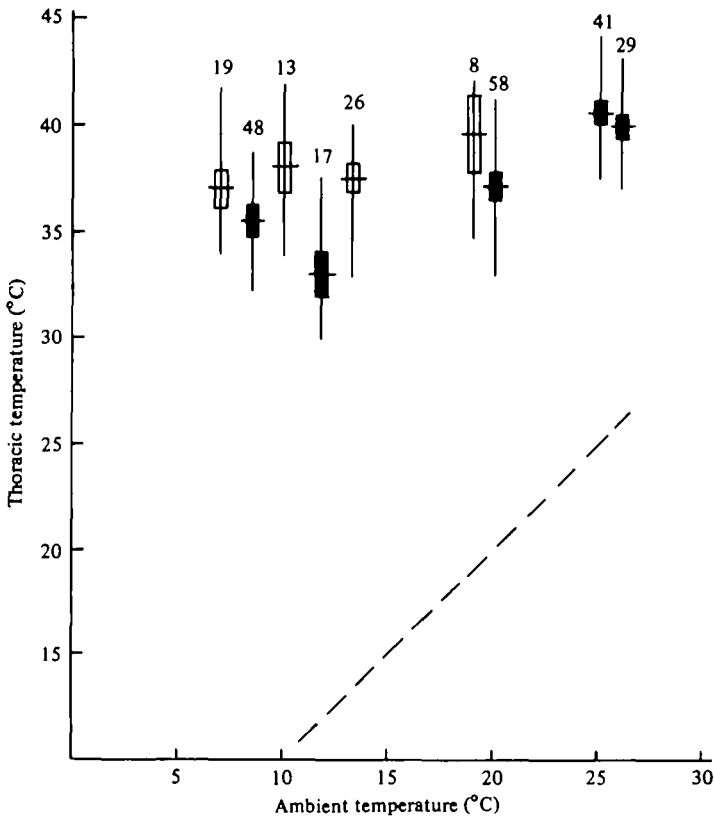


Fig. 4. Thoracic temperatures of attacking *A. m. mellifera* captured within 1-3 m of the hive, and *A. m. adansonii* 1-5 m from the hive (at 8-9 and 20 °C), 5-10 m from the hive (at 12 °C) and at approximately 60 m from the hive (at 26 °C). Symbols as in Fig. 1.

at the greater distance were made. The difference is significant ( $P < 0.01$ ). However, at higher  $T_A$  (26 °C), average  $T_{Th}$  were higher (40-41 °C), but insignificantly different at 2 and 50 m from the hive. Apparently bees returning to the hive sometimes attack as well as those leaving; some of the attacking bees still carried pollen loads.

**Foraging.** Independence of  $T_{Th}$  from  $T_A$  was observed during foraging (Fig. 5), as it was during the other three activities examined. Thoracic temperatures were regulated (31-32 °C) at lower levels than during exit from the hive and during attacking, but they were 1-2 °C higher than during return to the hive at given  $T_A$  (Tables 1 and 2). Abdominal temperatures were low and unregulated, as during other activities. At high  $T_A$ , sunshine caused increases of both  $T_{Th}$  and  $T_{Ab}$ . However, neither flight activity nor sunshine were necessary to create a high  $T_{Th}$ ; relatively stationary bees feeding on honey in combs outside of the hive at 7.5 °C before sun-up maintained an average  $T_{Th}$  of 34.1 °C, which was 2 °C higher than that of bees foraging from flowers at 21 °C in sunshine at noon.

Abdominal temperatures varied more widely than  $T_{Th}$ . They averaged about 5 °C above  $T_A$  during both foraging and return to the hive in both bee varieties. Bees leaving the hive, however, had relatively high  $T_{Ab}$ . At low  $T_A$  (7-10 °C), the temperature excess ( $T_{Ab} - T_A$ ) of the *adansonii* abdomen averaged 13 °C. (That of

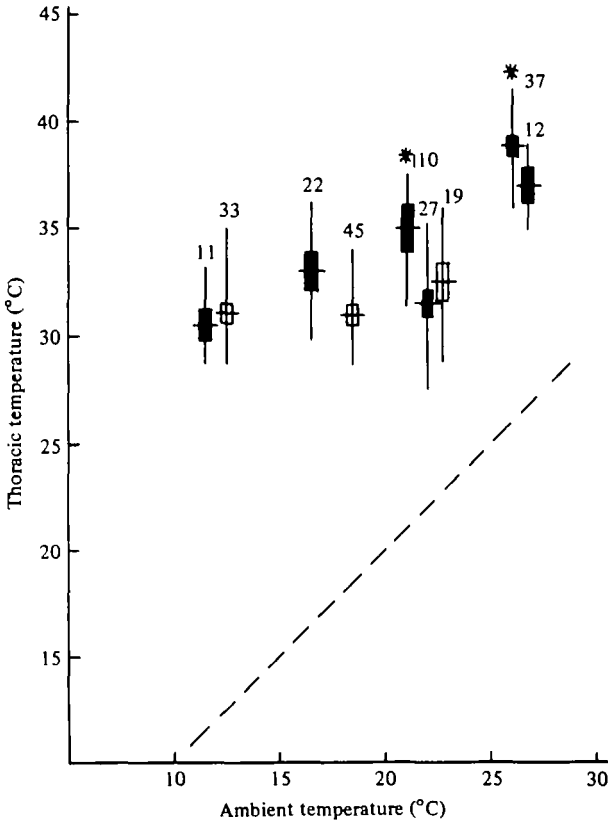


Fig. 5. Thoracic temperature of foraging honeybees; *A. m. mellifera* on *Eucalyptus* sp. and *A. m. adansonii* on *Bidens pilosa* and *Petraea volubilis*. Symbols as in Figs. 1 and 2.

*mellifera* was 5 °C higher.) Bees attacking in the hive vicinity had intermediate temperature excess of the abdomen between leaving and returning bees, but those attacking > 50 m from the hive had low  $T_{Ab}$ , like foraging bees.

#### *Apis mellifera mellifera*

In contrast to African honeybees, there were few bees entering and leaving the colonies at 9 °C during a *Eucalyptus* honeyflow. Nevertheless, thoracic temperatures of the European honeybee were insignificantly different ( $P < 0.001$ ) from the African variety during hive exits and returns, during foraging, and while attacking (Table 1). As in *adansonii*, there were highly significant differences ( $P < 0.001$ ) in  $T_{Th}$  between bees leaving, returning or foraging. Thoracic temperatures of bees attacking were significantly ( $P < 0.01$ ) different from bees exiting from the hive but this difference was less pronounced in comparison with the other activities (Table 2).

The  $T_{Th}$  of *A. m. mellifera* were also measured in a temperature controlled room, both as a function of duration of continuous flight, and as a function of  $T_A$ . Thoracic temperatures were independent of flight duration from 15 s to 4 min at  $T_A$  of 20 and 30 °C (Fig. 6). However, at a  $T_A$  of 10 °C some of the bees had a  $T_{Th}$  near 27–28 °C, the lower limit for level flight, after half a minute of flight. None of the



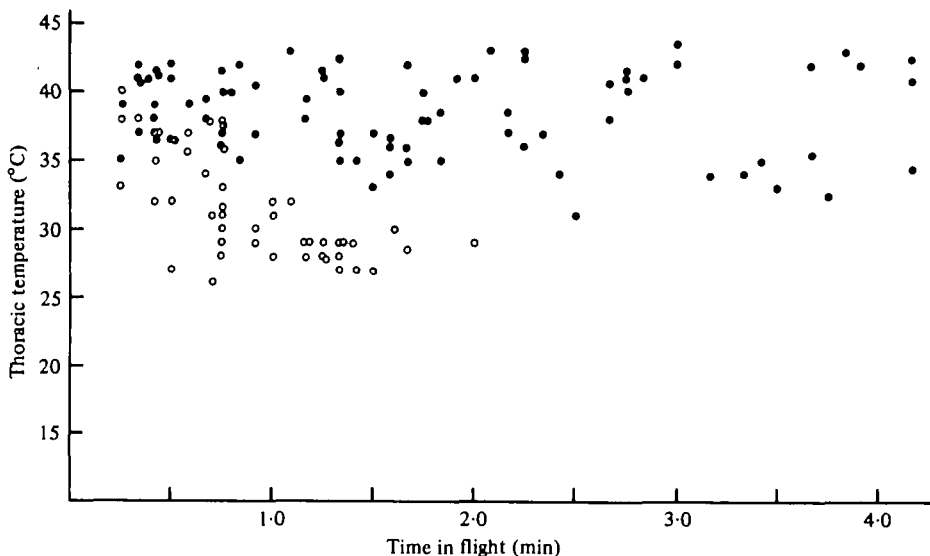


Fig. 6. Thoracic temperature of *A. m. mellifera* as a function of duration of continuous flight at ambient temperatures of 10 (○), 20 (◐) and 30 °C (●).

bees remained in continuous flight at 10 °C for longer than 2 min, even when they were repeatedly prodded to attempt to stimulate them to continue flying.

Bees that were allowed to land at 10 °C sometimes increased their  $T_{Th}$  up to 39 °C by warm-up. The average  $T_{Th}$  of 16 bees that had *not* been prodded to induce them to fly (the bees engaged in intermittent rather than continuous flight) was 34.5 °C after 2 min at 10 °C. The passive cooling rate (determined in dead bees) is described by the equation  $\log (T_{Th} - T_A) = 1.56 - 0.29 \text{ min}$ , which predicts that a bee with a  $T_{Th}$  of 40 °C at  $T_A$  of 10 °C should cool to 17.6 °C within 2 min if it did not actively resist its passive rate of cooling.

Bees which were in continuous flight did not regulate their  $T_{Th}$  at  $T_A$  from 10 to 25 °C; as already mentioned, they did not fly for more than 2 min at 10 °C, and from 15 to 25 °C their  $T_{Th}$  paralleled 15 °C above  $T_A$  (Fig. 7). However, at  $T_A > 25$  °C the bees depressed the temperature excess they generated during flight from 15 °C to an average of 5 °C at 40 °C. Bees flew uninterruptedly at 40 °C for as long as they were allowed (5 min), without stopping to cool, even though  $T_{Th}$  reached 46 °C.

Some of the bees flown in the temperature-controlled room attacked me, concentrating their attention on the stinger-studded black gloves used to catch them. The tendency to attack was strongly correlated with  $T_A$  (and hence  $T_{Th}$ ). At 15 °C none of the bees attacked. But the attack frequency increased to 27, 46 and 73% at  $T_A$  of 25, 30, and 40 °C, respectively.

#### DISCUSSION

Thermoregulation in honeybees has been examined as a function of the hive response both to low temperatures (Southwick & Mugaas, 1971) and high temperatures (Lindauer, 1954; Lensky, 1964). Metabolic responses of groups of bees have

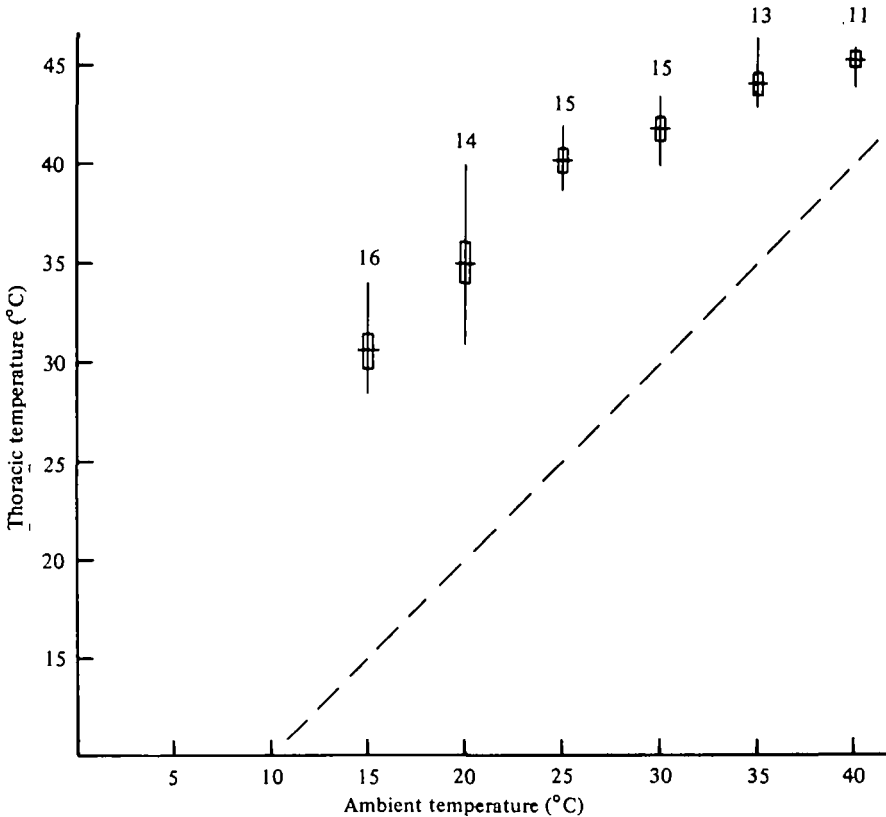


Fig. 7. Thoracic temperature of *A. m. mellifera* as a function of ambient temperature after two or more minutes of continuous flight in a temperature-controlled room. Symbols as in Fig. 1.

been examined (Cahill & Lustick, 1976; Brückner, 1975). Esch (1960) measured the body temperature of individual bees during different activities in and out of the hive, and extended the work with Bastian (Bastian & Esch, 1970) to examine the physiological bases of heat production in the thorax. However, despite the great wealth of information on honeybee thermoregulation, it has not been conclusively demonstrated whether or not honeybees maintain their thoracic temperatures ( $T_{Th}$ ) independent from ambient temperatures ( $T_A$ ).

The data from the present study show that the European honeybees do not fly continuously at 10 °C or less, apparently because they cannot maintain the minimum  $T_{Th}$  for flight. Furthermore, during continuous flight,  $T_{Th}$  is not regulated at  $T_A$  from 15 to 25 °C; it increases directly with increasing  $T_A$ . Thoracic temperature during continuous flight is regulated only at  $T_A > 25$  °C. However, the bees had thoracic temperatures *independent* from  $T_A$ , indicating thermoregulation, during hive exits, foraging, attack and return to the hive at  $T_A$  as low as 7 °C and up to 25 °C.

At the present time it is not known how the bees maintain their  $T_{Th}$  independent from  $T_A$  at  $T_A < 25$  °C when they are not necessarily in continuous flight for long durations. However, bees warmed up after cooling when not forced to remain in

continuous flight; they maintained  $T_{Th}$  up to 39 °C at  $T_A$  of 10 °C by intermittent warm-up following intermittent flight. Intermittent flight occurs naturally during foraging, affording the opportunity for warm-up while perched on flowers at low  $T_A$ . Possibly the  $T_{Th}$  of bees returning to the hive at low  $T_A$  were sufficiently high for flight because the return flights had been short and the bees had not had time to cool. Alternatively, if the bees had been foraging far from the hive they could have stopped to warm up *en route* after cooling to  $T_{Th}$  near 27 °C.

Foraging at low  $T_A$  may be costly both in terms of time and energy for warm-up. But it is not known if the reluctance of most bees to forage at low  $T_A$  is due to few flowers offering nectar at these temperatures, to energetic costs that would minimize profits, or to individual differences among the bees of any one hive. In the present study both the African and the European bees were observed foraging from *Eucalyptus* flowers at the relatively low  $T_A$  near 10 °C.

Thoracic temperatures were stabilized during continuous flight of 20 s or less at  $T_A$  of 30 °C (Fig. 6), and after 2 min of continuous flight at  $T_A$  of 25–15 °C (Fig. 7). The bees could fly without stopping to warm up, or to cool down, at  $T_A$  from 15 to 40 °C. Under laboratory conditions the bees could maintain a high  $T_{Th}$  at  $T_A < 15$  °C by stopping flight and engaging in warm-up, and they maintained continuous flight at  $T_A$  from 30 to 40 °C by physiologically preventing their flight muscles from exceeding 46 °C. During continuous flight at intermediate  $T_A$  (15–25 °C) they allowed  $T_{Th}$  to drift passively;  $T_{Th}$  followed approximately 15 °C above  $T_A$ .

The greater the flight metabolism, the greater the work load, and the heat production rate, and sometimes the  $T_{Th}$  (Heinrich, 1975). However, in the present study, loaded bees returning to the hive had a *lower* rather than a higher  $T_{Th}$  than 'empty' bees leaving. The reason for this apparent discrepancy could be that the bees leaving the colony had not yet been in flight, while those returning had engaged in continuous flight before their temperatures were measured. However, whether by behavioural or by physiological mechanisms, the different  $T_{Th}$  represent *regulated* states, rather than passive functions of different rates of heat production simply as a by-product of their respective flight metabolisms, since  $T_{Th}$  were independent of  $T_A$ , and hence they were maintained despite *different* passive cooling rates. Additionally, since the bees leaving the hive were hotter than those within it, it is clear that the bees which already have a  $T_{Th}$  sufficient for flight while they are within the colony engage in additional warm-up before leaving. Possibly at  $T_A \leq 10$  °C, this pre-flight warm-up behaviour allows them to fly farther before they have to stop and warm up again in order to continue flight to their destination.

Bees defending the nest (attacking) typically pursue, circle and rapidly manoeuvre in flight. Obviously such flight behaviour is not possible with a low  $T_{Th}$  just sufficient to maintain level flight. Are the attacking bees hotter than other bees because they have a higher flight metabolism, or is attack behaviour directly correlated with a high  $T_{Th}$ ?

At least in the African bees, aggressiveness was in part correlated with  $T_A$  (and hence  $T_{Th}$ ). At  $T_A$  of 26–29 °C, bees pursued for at least 50 m from the hive, while at 18 °C, the bees pursued only up to about 5 m. At the higher  $T_A$ , unlike at low, many returning foragers had high  $T_{Th}$  (> 40 °C), and at least some of these foragers

(those carrying pollen loads) may have attacked because they were already hot. At 7 °C the bees were capable of maintaining a minimum  $T_{Th}$  for flight and foraging, but at increasing distance from the hive convective cooling caused  $T_{Th}$  to decline below the temperature normally maintained while initiating attack. It is thus possible that the drop in  $T_{Th}$  stopped the attack behaviour, even though it did not preclude flight. Since the attacking bees were hotter the closer they were to the hive (and the less distance they had flown) it is probable that their high  $T_{Th}$  is not a consequence of the attack behaviour, but on the contrary, at least in part a cause of it. Similarly, in the flight room, only those European bees attacked which had a high  $T_{Th}$  because they were in flight at a high  $T_A$ . However, attack behaviour is obviously not only a function of  $T_{Th}$ ; the very aggressive African bees were, on the average, no hotter than the European bees.

Unlike some other insects (Heinrich, 1974), particularly moths and beetles Bartholomew & Heinrich, 1973, 1978) in whom  $T_{Th}$  during flight is a function of size, the African honeybees, which are about 66% the mass of European bees when empty though only 17% lower in thoracic mass (Table 3), did not show a correspondingly lower  $T_{Th}$ . Since they are smaller they must necessarily have a greater passive cooling rate, which would result in lower body temperatures in flight, if their metabolic rates were equal. These data indicate that, on the average, they have a greater energy expenditure during foraging, aggression, as well as flight to and from the hive, than do the European bees.

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