

TEMPERATURE REGULATION OF HONEY BEES (*APIS MELLIFERA*) FORAGING IN THE SONORAN DESERT

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SUMMARY

A heat budget for foraging honey bees (*Apis mellifera* L.) indicated that at 30–35°C all bees are in positive heat balance during flight. Observations of honey bees returning to their hives at high ambient temperatures support the conjecture that honey bees regulate head and thorax temperatures at high T_a by regurgitating droplets of honey stomach contents which are then evaporated. The proportion of returning bees with a droplet on the tongue increased with increasing shade temperature (T_s), from essentially no bees at 20°C to 40% of returning bees at 40°C. Pollen foragers carry relatively little fluid during the hottest periods, and pollen foraging decreased at high ambient temperatures. Thoracic temperatures of pollen collectors are significantly higher than thoracic temperatures of water and nectar gatherers at 40°C (46.13 vs 44°C). Additionally, water and nectar foragers with extruded droplets have slightly cooler heads and thoraces (38.94 and 43.22°C) than bees not extruding droplets (40.28 and 44.18°C). Wing-loading and thoracic temperatures of bees are inversely correlated at high ambient temperatures (35°C) and this is probably caused by a higher propensity of heavier bees to extrude fluid, thus reducing thoracic temperature.

INTRODUCTION

Honey bees have been observed to forage at high ambient temperatures and under intense solar radiation characteristic of summer in the Sonoran desert of southwest North America (Heinrich, 1975). Heinrich (1979*a*, 1980*a,b*) reported that honey bees regulated thoracic temperature above 25°C ambient and that evaporation of water from the mouth is used at high ambient temperatures ($T_a = 46^\circ\text{C}$) to prevent overheating. However in a previous study of foraging patterns of bees on *Agave schottii* in the Sonoran desert, bees were observed to stop foraging at

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ambient temperatures of 35°C. Although Heinrich demonstrated that honey bees could evaporate water for cooling and did so in laboratory conditions, his field studies of honey bee body temperatures were performed at ambient temperatures well below temperatures when evaporative cooling might be necessary (Heinrich, 1979b). Convective cooling also may account for a relatively large proportion of heat loss as demonstrated for other flying insects (Church, 1960; Casey, 1980; Chappell, 1982), obviating high rates of water loss associated with evaporative cooling.

We undertook this study to determine what effect desert ambient temperatures had on bee body temperatures and whether the relationship between climate and body temperature might limit the ability of individual bees to forage. We proceeded by constructing a heat budget for foraging honey bees, then testing our budget in the field by measuring body temperatures of returning and departing foraging honey bees over a wide range of ambient temperatures. In addition, we examined the effect of evaporative cooling and wing-loading on body temperatures of returning foragers, as well as measuring temperatures of pollen foragers. Finally, we attempt to integrate our field and laboratory data to determine the environmental limits to foraging by individual honey bees.

METHODS AND MATERIALS

Laboratory studies

Honey bees (*Apis mellifera caucasica*) were captured in the field, anaesthetized and frozen with dry ice and returned to the laboratory. After defrosting, bees were weighed on a Sartorius balance to the nearest 10^{-4} g, then the head, thorax and abdomen were separated and each part weighed individually. Linear dimensions were measured to the nearest 0.2 mm using calipers, while wing areas were determined from tracing wings on graph paper and either weighing the paper or counting the number of square millimeters contained. Surface areas for body parts were calculated using appropriate geometrical equations.

Oxygen consumption (V_{O_2}) was measured by flying bees in an airtight 4-l glass jar for at least 5 min continuously. A 50 cm³ air sample was removed after the flight period with a syringe and injected into an oxygen analyser (Applied Electrochemistry S-3A) at a constant rate of 25 cm³ min⁻¹ using a perfusion pump. An initial reference gas sample was handled similarly. Both gas samples were injected through a combination of Drierite® and Ascarite® before analysis to remove water vapour and CO₂. Oxygen consumption rate during hovering flight was then calculated for STP conditions using standard equations for closed respirometry systems. Cooling curves for honey bees were determined on freshly killed bees; bees were killed by injecting 1–5 µl ethyl acetate into the thorax at the junction of the thorax and pedicel. Rate of cooling for bees in the absence of forced convection was measured by heating the bees up to 50°C in an oven, then rapidly placing them into a 1000 cm³ Erlenmeyer flask immersed in a constant temperature (25°C) water bath. The temperatures of the bee thoraces were monitored constantly using a 44-ga thermocouple connected to a Bailey Bat-12 thermocouple thermometer which was connected to a channelyser and chart recorder (Bailey Instruments, Inc.). The jar

temperature was recorded simultaneously by scanning with the channelyser every 2 s.

Thoracic conductance (C_{th}) of individual bees was determined at various wind speeds by implanting 44-ga thermocouples in the thorax. The bees were suspended in the centre of a laminar flow wind tunnel by glueing the wings to toothpicks which were anchored in clay. The clay was secured to the sides of the tunnel. A microscope light was used to heat the bee until thoracic temperature (T_{th}) was at least 50°C. The heat source was then switched off and the wind tunnel fan engaged, while continuously recording thoracic and air temperatures (cooling rates were not measured until wind speed stabilized). A similar method was employed for measuring head conductance (C_h), although some error may result in the cooling coefficient since heat is lost at a rate proportional to the difference between the equilibrium head temperature and the temperature of the head at any time (Hegel & Casey, 1982). Abdominal conductance (C_{ab}) at different wind speeds was calculated from the following equation:

$$C_{ab}(v) = C_{ab}(0) \times C_{th}(v)/C_{th}(0),$$

where $C(0)$ is the conductance of the respective body part in the absence of forced convection and $C(v)$ the conductance at different wind speeds.

Field work

Honey bees were captured in the field, held between thumb and finger using a latex glove, and a 40-ga thermocouple implanted in the tip of a 30-ga needle was quickly inserted into either the head, thorax or abdomen. The thermocouple was connected to a Bailey Bat-12 thermocouple thermometer and the temperature of the various body parts was recorded within 3 s. Only one temperature measurement was made per bee to avoid problems with cooling during the measurement period. Shade temperature was recorded at various intervals, usually every 10 min, by using the same probe and holding it in the shade approximately 1 m above soil surface.

Cosine-corrected short-wave radiation was measured with a Li-Cor 200S pyranometer. Ground-reflected radiation was measured occasionally by inverting the radiation sensor over open ground. Wind speed was measured using a hot ball anemometer (Chappell, 1982), which was previously calibrated in a wind tunnel. Both wind speed and radiation were monitored continuously with the sensors located 2 m above ground and recorded on a Hewlett-Packard 7100B dual channel recorder.

Heat budget calculations

Heat budgets of honey bees at various temperatures were calculated using equation 1 (Bartholomew, 1977):

$$Q = S + R + \lambda E + C + M, \quad (1)$$

where Q is total heat flux, S is solar radiation, R is thermal radiation into and away

from the bee, λ is the latent heat of evaporation, E is the rate of evaporation, C is convective exchange with the air and M is the metabolic rate of the honey bee. Net changes in heat ($Q = 0$) were assumed to result in either changes in bee body temperature or variations in the rate of evaporation.

Solar radiation ($S \downarrow$) was determined from the pyranometer measurements, with reflected ground radiation ($S \uparrow$) estimated using an albedo of 25 % (based upon the several measurements with the pyranometer inverted). Incoming long wave radiation ($L \downarrow$) was estimated using the formula of Swinbank (1963) where $L \downarrow = \delta T_a^6$ with $\delta = 5.31 \times 10^{-13} \text{ W m}^{-2} \text{ K}^{-6}$ and T_a is air temperature. Outgoing long wave radiation ($L \uparrow$) was estimated using the Stefan-Boltzman relation, $L \uparrow = \sigma T_s^4$, with T_s the ground surface temperature and $\sigma = 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$. The air and the corresponding surface temperatures used in calculations were 20, 27, 30, 42, and 40, 55°C.

Absorptivity of honey bees was assumed to be 0.91 (Willmer & Unwin, 1981) while surface areas exposed to radiation varied with radiation source. With solar radiation ($S \downarrow$) only 25 % of the surface area was assumed to be irradiated (as in a sphere, Monteith, 1973), while the other forms of radiation ($S \uparrow$, $L \downarrow$ and $L \uparrow$) were assumed to involve 50 % of the surface area (Kenagy & Stevenson, 1982). Bee radiative heat loss was calculated using the Stefan-Boltzman relation, assuming an emissivity of 0.97 with T_s equal to bee surface temperature, which was assumed to be air temperature for flying bees (Mahoney & King, 1977).

Metabolic heat gain was estimated from oxygen consumption measurements, assuming that 80 % of energy produced was in the form of heat (Hegel & Casey, 1982). Normal flight evaporative water loss (cuticular plus spiracular loss) was assumed to be approximately 10 % of the metabolic rate (Heinrich, 1975; Nicolson & Louw, 1982). Convective heat exchange was estimated by multiplying the various body part conductances by the gradients for heat loss ($T_b - T_a$). T_b was the average temperature measured for arriving bees – either head, thorax or abdomen. T_a was assumed to be the mid-point of the T_a range in which the measurements were made. As a result, convective heat loss may be overestimated as conductance is not equal to the convective coefficient, but may be somewhat greater (Kingsolver & Moffatt, 1982).

Budget error analysis

Our heat budget can be criticized because of the inherent error in convective heat loss associated with our use of the conductance, rather than the true convective coefficient. The error associated with our method may result in an overestimate of convective cooling but presumably this is a small error. However our assumption that bee surface temperature equals ambient temperature may be invalid, as Cena & Clark (1972) found that thoracic surface temperatures of bees returning to the hive could be as high as 20°C above ambient at low ambient temperatures. Our estimate of radiational heat loss could be underestimated by 25 % at 20°C.

Our calculation for heat production was determined from the energy cost associated with hovering flight. However, the power needed for flight decreases as forward flight speed increases (Pennycuik, 1972). If bees fly at the minimum power for transport, metabolic heat production during flight is probably lower than

the values in our budget. Since we do not know the change in metabolism with increasing flight speed though, we cannot calculate the error associated with this part of our budget. Changes in radiant heat gain will vary with time of day. If we assume that T_a and T_s are constant (which is unlikely), we can calculate the variation in heat gain dependent only on the change in short-wave radiation. Thus at $T_a = 30^\circ\text{C}$ and $T_s = 42^\circ\text{C}$, bees will gain 0.111 W and 0.146 W when short-wave radiation (S) is 600 and 1200 W m^{-2} , respectively. Short-wave radiant energy was approximately 850 W m^{-2} for our calculated value of 0.121 W under the same T_a and T_s conditions, and our maximum error is 20% .

At low temperatures, then, we may be underestimating heat loss, but at high temperatures when $T_{th} \approx T_a$, our heat budget error is approximately 10% .

RESULTS

Morphometric measurements of returning foragers are given in Table 1. Mean body mass of foragers was 100.8 mg with the thorax accounting for about 40% of the total mass (range $33.6\text{--}48.5\text{ mg}$). Abdominal mass tended to be larger but was also more variable (ranging between 17.9 and 76.5 mg) as a result of differences in the nectar or water load. The abdomen has the largest surface area, corresponding to its large mass; the thorax and head being smaller progressively. Wing area was relatively constant, but wing loading varied as a result of differences in abdominal mass.

Mean oxygen consumption rate of flying bees carrying pollen was $84.65 \pm 12.60\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ ($N=8$) compared to $73.03 \pm 8.85\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ ($N=8$) for nectar carriers. However these values were not significantly different from each other so for purposes of determining heat production during flight the two groups were combined to yield $78.84 \pm 7.59\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$. These values are similar to previously reported metabolic rates (Heinrich, 1980b; Withers, 1981).

Thoracic conductance of honeybees varied between $6.3 \times 10^{-4}\text{ W}^\circ\text{C}^{-1}$ in still air and $5 \times 10^{-3}\text{ W}^\circ\text{C}^{-1}$ at a wind speed of 5.1 m s^{-1} . The increase in conductance was roughly linear with the square root of wind speed (Fig. 1). Head conductance also increased with wind speed, although the rate of increase was less than that of the thorax (Fig. 1).

Table 1. *Honey bee morphometrics*

Body section	Units	\bar{X}	S.D.	N
Body mass	(mg)	100.80	20.20	96
Head mass	(mg)	9.97	1.36	96
Head surface area	(m^2)	2.46×10^{-5}	0.43×10^{-5}	13
Thoracic mass	(mg)	40.70	2.90	96
Thoracic surface area	(m^2)	4.15×10^{-5}	0.29×10^{-5}	15
Abdominal mass	(mg)	46.68	17.44	96
Abdominal surface area	(m^2)	9.00×10^{-5}	1.60×10^{-5}	14
Wing area	(cm^2)	0.36	0.04	76
Wing load	(N m^{-2})	28.27	6.10	76

Bees used in measurements were all returning foragers.

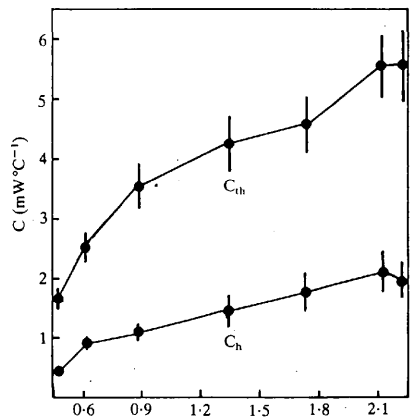


Fig. 1. Thoracic and head conductance of honey bees in relation to the square root of wind velocity. Means \pm 2 standard errors. Points are fitted by straight line least squares regression. $C_{th} = 1.93V^{1/2} + 1.40$ ($r^2 = 0.97$), $C_h = 0.81V^{1/2} + 0.34$ ($r^2 = 0.95$).

Table 2. Heat budget for *Apis mellifera* flying at 3 m s^{-1} under clear sky conditions

Temperature (°C)	Gain		Loss	
20	Metabolism	0.037	Radiant	0.063
	Radiation	0.099	Convection	0.125
			Evaporation	0.004
	Total	0.136		0.192
30	Metabolism	0.037	Radiant	0.072
	Radiation	0.121	Convection	0.064
			Evaporation	0.004
	Total	0.158		0.140
40	Metabolism	0.037	Radiant	0.085
	Radiation	0.143	Convection	0.009
			Evaporation	0.086*
	Total	0.180		0.180

*Water loss rate equal to $0.035\text{ mg H}_2\text{O s}^{-1}$ or $127.4\text{ \% body mass h}^{-1}$.
All values are for 100-mg bee and are expressed in W.
Heat loss by evaporation at 40 °C is determined by subtraction.

Heat budgets of flying honey bees were constructed using body temperatures of bees measured in the field and the appropriate ambient temperatures, thoracic and head conductance measured at different wind speeds, the amount of radiation present under clear sky conditions and the heat production associated with metabolism of flying bees determined in the laboratory (Table 2). With increasing temperature, radiative heat gain and loss increase, and convective heat loss decreases. At the lower temperatures there is a net heat efflux, while evaporative

cooling must occur at the highest temperatures if T_b is kept within normal limits. By iterating this approach at different flight speeds, a family of curves can be constructed relating net heat exchange to ambient temperature (Fig. 2). At slow flight speeds, bees will gain heat at all temperatures, but as flight speed increases, bees begin to gain heat only at progressively higher temperatures.

Field studies

Temperatures of head, thorax and abdomen of both departing and arriving bees are shown in relation to local shade temperature in Fig. 3. Temperatures of departing bees are relatively independent of shade temperatures, but arriving bee temperatures have a sigmoidal relation with increasing shade temperature. Below 40°C , temperatures of both heads and thoraces of arriving and departing bees are maintained above T_a , while abdominal temperatures of arriving bees are nearly always close to ambient temperatures.

To determine the effect of various types of foraging on bee body temperatures, we divided arriving bees into three groups according to their activity immediately before capture for temperature measurement: (1) bees not carrying pollen and with no fluid observed on the proboscis (NPNF), (2) bees not carrying pollen and with fluid observed on the proboscis (NPF), and (3) bees carrying pollen but no fluid regurgitation observed (PNF). Results of these experiments are given in Table 3. Two trends are apparent, (1) bees with fluid extruded are cooler than bees without fluid, and (2) pollen carriers tend to be the hottest bees by $2\text{--}3^\circ\text{C}$ at the highest temperatures. Additionally, as shade temperature increased, an increasing pro-

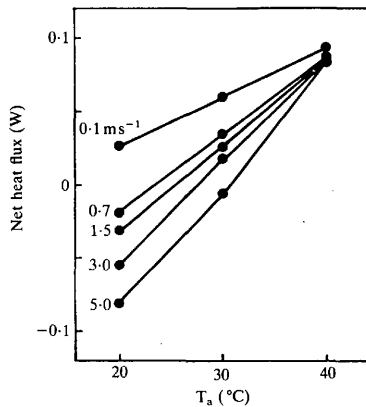


Fig. 2. Calculated net heat exchange (not including evaporative water loss) of honey bees in flight at various velocities plotted against ambient temperature under clear sky conditions. Heat gain would occur at $T_a = 30^\circ\text{C}$ for bees flying at 3 ms^{-1} and at 33°C for bees flying at 5.1 ms^{-1} .

portion of nectar foragers were observed to have fluid on the proboscis, while few pollen carriers ever had fluid droplets (Fig. 4). Stomach content analysis of 19 pollen foragers performed at the time of temperature measurements yielded an average crop content of $1.3 \mu\text{l}$, with 15 of the 19 bees having completely empty crops, compared with a mean content of $7.9 \mu\text{l}$ in fluid-carrying bees. The proportion of foragers with pollen also decreased at the higher temperatures (Fig. 4).

Higher thoracic temperatures with higher wing loads would be expected if metabolic rate was elevated to offset the higher lift requirement. However, as wing load increased, thoracic temperature decreased (Fig. 5) at ambient temperatures above 35°C . This may be explained by assuming that the heaviest bees (those with the higher wing loads) are more likely to use evaporative cooling. The mean weight of droplet-carrying bees is $107.9 \pm 3.0 \text{ mg}$ ($N=23$) compared to $98.7 \pm 2.5 \text{ mg}$ ($N=74$) ($P<0.10$) for foraging bees not carrying droplets.

Foraging bees have an alternative method for controlling body temperature within normal ranges. They can cease flying and allow themselves to lose heat passively. This method typically results in thoracic temperature decreases of about 2°C (42.7 ± 0.2 vs $40.8 \pm 0.4^\circ\text{C}$) within 15 s at ambient temperatures of $36\text{--}37^\circ\text{C}$.

DISCUSSION

Thermoregulation in flying insects has been investigated with respect to effects of metabolic rate, body size, behaviour and orientation and the possible advantages of high body temperatures during foraging (May, 1979; Kammer, 1981; Casey, 1981; Willmer, 1982a). Heinrich (1979c) integrated many of these aspects of thermoregulation in presenting his overview of bumble-bee ecology. Recently, several studies have included the effect of microclimate on body temperature in flying insects in the field (Chappell, 1982; Kingsolver & Moffat, 1982; Willmer, 1982b,c). The studies on *Xylocopa californica* (Chappell, 1982) and *Colias eurytheme* (Kingsolver & Moffat, 1982) indicated that heat budgets calculated from laboratory models can be used to predict temperatures of insects flying in the field. Our model has allowed us to estimate the relative importance of convective and evaporative cooling for honey bees flying at high ambient temperatures commonly occurring in the desert (Table 3).

Foraging bees

Low ambient temperature flight

The model of heat transfer indicates that honey bees will have a net heat loss during flight at low T_a . The field data support this prediction as bees returning to the hive at ambient temperatures below 27°C are cooler than departing bees. Continuous flight at ambient temperatures below 20°C will result in thoracic

Fig. 3. Body temperatures of *Apis mellifera caucasica* arriving and departing from a standard Langstroth hive plotted against air temperature in the shade. (A) Head temperatures, T_h ; (B) thoracic temperatures, T_{th} ; (C) abdominal temperatures, T_{abd} . Means \pm confidence interval. Numbers of bees in parentheses. \circ , arriving bees; \bullet , departing bees.

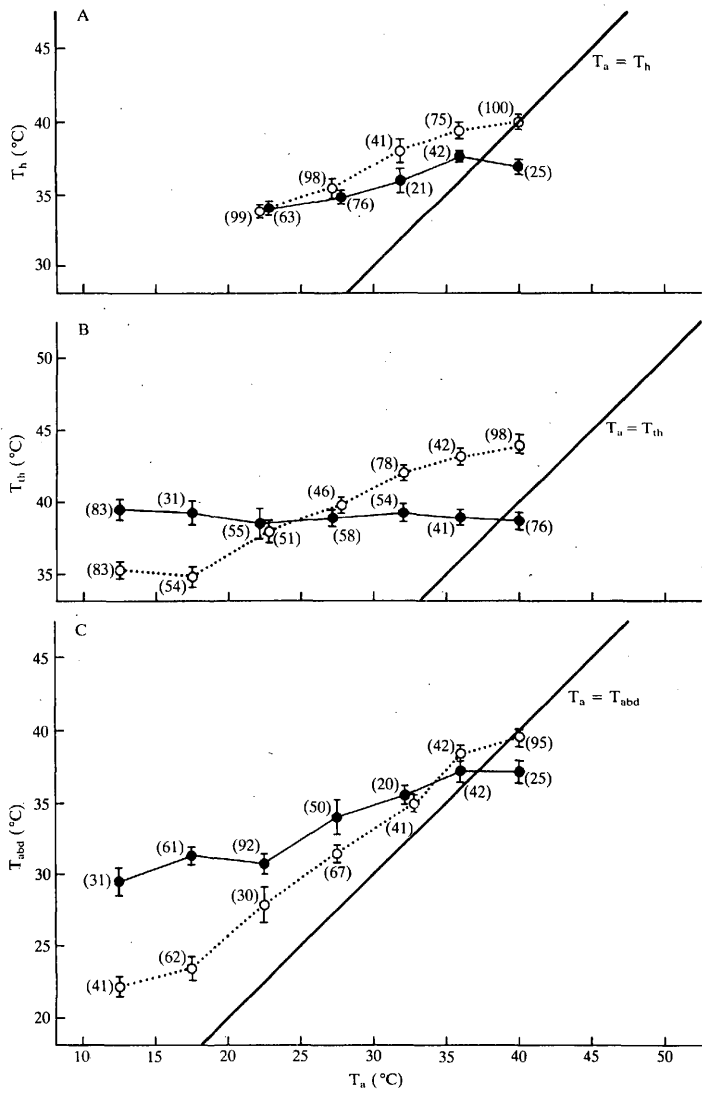


Fig. 3

Table 3. *Influence of pollen and regurgitation on temperatures of arriving Caucasian honey bees*

T _a (°C)	NPNF*			PNF*		
	N	\bar{X}	95 % CI	N	\bar{X}	95 % CI
Head						
20-25	51	33.69†	0.6	0	—	—
25-30	21	36.93	0.8	0	—	—
30-34	9	39.81	1.3	1	40.10	—
34-38	18	39.72†	0.8	1	42.30†	—
38-42	73	40.28†	0.4	24	38.94†	0.7
Thorax						
20-25	47	37.71	0.7	0	—	—
25-30	26	40.66	0.8	0	—	—
30-34	31	42.02†	0.7	3	41.73	4.2
34-38	120	42.69†	0.3	11	41.80†	1.1
38-42	50	44.18†	0.6	39	43.22†	0.7
Abdomen						
20-25	41	29.25	0.6	0	—	—
25-30	25	32.82	0.8	0	—	—
30-34	14	36.39	1.0	0	—	—
34-38	12	37.51†	1.0	1	42.40	—
38-42	67	39.60†	0.6	25	38.21†	1.0

Statistical differences relative to NPNF temperatures.

Mean and 95 % confidence interval.

* NPNF, no pollen, no fluid; NPF, no pollen, fluid on proboscis; PNF, pollen, no fluid.

† $P < 0.05$; ‡ $P < 0.10$.

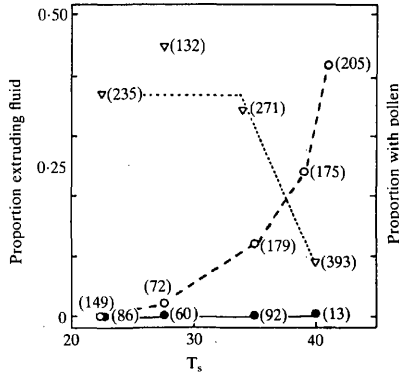


Fig. 4. Proportion of returning honey bees extruding a droplet of fluid on the tongue. Proportion increases with air temperature in the shade (T_s) for nectar and water collectors (hollow circles). Pollen gatherers (solid circles) almost never regurgitated fluid. Proportion of bees returning with pollen (triangles) declines for T_s exceeding 38°C. Values determined from pooling data for 5° intervals between 20 and 30°C, 8° intervals between 30 and 38°C and the 4° interval between 38 and 42°C. Lines fitted by eye.

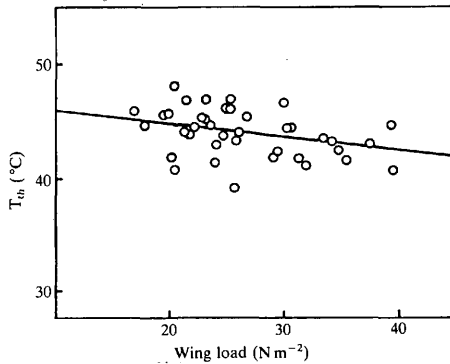


Fig. 5. Relation between thoracic temperature and wing-loading for bees flying at temperatures between 35 and 40°C under clear sky conditions. Line fitted by least squares regression $T_{th} = 47.22 - 0.123 (WL)$, $r = 0.415$, $N = 40$. Slope significantly different from zero ($t = 2.81$, $df = 38$, $P < 0.01$).

temperatures dropping below the minimum temperature of 33°C necessary to produce lift (Esch, 1976). Bees leaving the hive with a thoracic temperature of 35°C would be able to fly only for 35–40 s before thoracic temperatures fell 5°C. Slower flight would reduce the rate at which bee temperature falls below the critical temperature for flight (Fig. 2). Esch (1976) suggests that honey bees can change the body angle for flight and could sacrifice flight velocity for additional lift and thus fly at lower thoracic temperatures, although we never observed this, and indeed the

increased metabolism associated with slower flight speed (Pennycuik, 1972) may preclude this possibility. More reasonably, bees could alternate between flying and warming-up as Heinrich (1979b) suggested, permitting foraging at lower temperatures.

High ambient temperature flight

We have observed foraging activity at ambient temperatures above 40°C. Although a high rate of evaporative water loss is predicted for body temperature maintenance (127% body weight h^{-1}) at 40°C from our model, foraging does not appear to be limited at 40°C. However, the rate at which heat can be lost by evaporative cooling may be limited either by availability of fluid or by the ability of bees to extrude fluid. Increased cloud cover and lower energy gain from direct solar radiation would reduce heat input rate and thus lessen the required rate of evaporative cooling, thereby extending foraging time.

Ambient temperatures above 40°C curtail pollen collection (Fig. 4). Pollen carriers have the highest temperatures measured for returning foragers. Since bees carrying pollen do not have significantly higher flight metabolic rates than the other foragers, it is reasonable to conclude that the differences in body temperature result from the lack of fluid available for evaporative cooling.

Bees can tolerate body temperatures of 50°C for short periods without lethal effects (Lensky, 1964), and we have measured thoracic temperatures of pollen carriers exceeding 50°C. Without fluid available, bees could fly for 45 s at $T_a = 40^\circ\text{C}$ before body temperature increased from 40 to 50°C. Assuming a flight speed of 5 m s^{-1} , and a 'beeline' flight, a foraging radius of only 225 m would be possible. Evaporation of 1.58 mg H_2O over the 45-s flight would prevent any increase in body temperature. Returning foragers in June 1981 carried 8–10 mg of nectar with a concentration of between 35 and 40% total dissolved solids (unpublished data). Thus, even in these conditions, 3–4 mg H_2O were available for evaporative cooling, permitting a further 120 s of flight time before body temperature began increasing.

Bees collecting pollen at high ambient temperatures are more susceptible to increased body temperatures since they do not carry nectar during the hottest periods of summer. The observed higher temperatures of pollen gatherers may also reflect increased wing-loading as a result of heavier payloads (mean mass of pollen collectors was 110.1 mg compared to 95.8 mg for other foragers in June) and possibly increased parasite drag associated with forward flight and the location of pollen on the legs.

Wing-loading does appear to influence thoracic temperature in nectar- and water-collecting bees, but bees with the highest wing-loads have the lowest thoracic temperatures, instead of the expected higher temperatures (Heinrich, 1979c). The lower thoracic temperatures can be explained if bees with heavier nectar or water loads exhibit a greater proclivity to cool evaporatively, and the relation between body weight and regurgitation is consistent with this hypothesis. The relation between thoracic temperature and body weight is in contrast to the measurements of Heinrich (1979b) for *A.m. adansonii*. His measurements were done at relatively

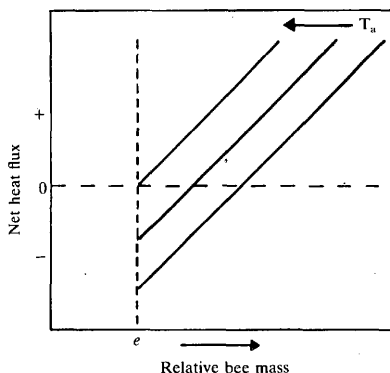


Fig. 6. Relationship between net heat flux, relative bee mass (loaded mass/unloaded mass) and ambient temperature for honey bees flying in the desert under clear sky conditions. Honey bees with no load represented by vertical dashed line through point *e* of abscissa. Heat balance (gain = loss) represented by horizontal dashed line. Angled lines represent isoclines of temperature, with ambient temperature increasing from right to left. Highest temperature isocline bisects intersection of heat balance and empty bee weight lines indicating that bee would always be gaining heat when flying in these conditions.

low temperatures when honeybees would be losing heat during flight and this might prevent observation of any effects of foraging load on thoracic temperatures.

Foraging for nectar and water does not appear to be limited by normal temperatures in the Sonoran desert. Pollen foraging may be limited at high T_a . However availability of pollen may also be low during the hottest periods of the day, as most anthers dehisce either in the morning or evening. If bees overheat, they can quickly land and cool off in favourable microclimates which occur on plants (see above). Thus 'resting bees' discussed in a previous paper (Schaffer *et al.* 1979) may actually be overheated, rather than out of energy. Although bees began flying again when given a 25 % sugar solution, they might have done this if only water had been imbibed.

Body weight, heat balance and ambient temperature can be tentatively integrated in Fig. 6. The ambient temperature isoclines increase in temperature from right to left. The critical temperature is the ambient temperature when empty bees (no fluids in honey stomach) are gaining heat during flight (point where dotted lines intersect). At lower temperatures, unladen bees actually lose heat during flight, as indicated by the intersection of temperature isoclines at progressively more negative points on the empty bee line. Bees loaded with nectar or water are able to fly and maintain body temperature by evaporative cooling at temperatures when empty bees of the same mass begin to increase body temperature.

Pollen-carriers are represented on the graph as empty bees. By eliminating the possibility of evaporative cooling, any increase in weight would automatically result in an increase in net heat gain. This response is what we believe is observed in the increased body temperatures of pollen collectors.

This study is consistent with the previous suggestion (Schaffer *et al.* 1979) that

honey bees stop foraging on *Agave schottii* above 35°C, not as a result of individual thermoregulatory problems, but rather in response to the increased requirements for fluid necessary for hive thermoregulation. Our calculations indicate that a single bee could continue to forage at profit, with respect to both energy and fluid, on the agaves. Possibly the response of hive bees to bees bringing in relatively small loads is decreased at high temperature. If bees switch to foraging on flowers with either more dilute nectar or which contain greater quantities of nectar, the rate of fluid and/or energy brought into the hive would be increased. Studies on artificially heated hives and colonies indicate that at high temperatures both nectar foraging and water foraging increase (unpublished data), suggesting that if nectar is available in large quantities, foraging would be stimulated to increase the rate at which it enters the hive. Thus the reduced foraging on *Agave schottii* at high temperatures may reflect the colony requirements for resources, and not a simple individual bee thermoregulatory response.

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