

ENDOTHERMY IN THE SOLITARY BEE *ANTHOPHORA PLUMIPES*: INDEPENDENT MEASURES OF THERMOREGULATORY ABILITY, COSTS OF WARM-UP AND THE ROLE OF BODY SIZE

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Summary

1. This study examines variation in thoracic temperatures, rates of pre-flight warm-up and heat loss in the solitary bee *Anthophora plumipes* (Hymenoptera; Anthophoridae).

2. Thoracic temperatures were measured both during free flight in the field and during tethered flight in the laboratory, over a range of ambient temperatures. These two techniques give independent measures of thermoregulatory ability. In terms of the gradient of thoracic temperature on ambient temperature, thermoregulation by *A. plumipes* is more effective before flight than during flight.

3. Warm-up rates and body temperatures correlate positively with body mass, while mass-specific rates of heat loss correlate negatively with body mass. Larger bees are significantly more likely to achieve flight temperatures at low ambient temperatures.

4. Simultaneous measurement of thoracic and abdominal temperatures shows that *A. plumipes* is capable of regulating heat flow between thorax and abdomen. Accelerated thoracic cooling is only demonstrated at high ambient temperatures.

5. *Anthophora plumipes* is able to fly at low ambient temperatures by tolerating thoracic temperatures as low as 25°C, reducing the metabolic expense of endothermic activity.

6. Rates of heat generation and loss are used to calculate the thermal power generated by *A. plumipes* and the total energetic cost of warm-up under different thermal conditions. The power generated increases with thoracic temperature excess and ambient temperature. The total cost of warm-up correlates negatively with ambient temperature.

Introduction

The majority of studies of endothermy in bees in temperate and cool climates have been on social species in the family Apidae, particularly in the genera *Apis* (e.g. Heinrich, 1979; Cooper *et al.* 1985; Dyer and Seeley, 1987; Coelho, 1991; Underwood, 1991) and *Bombus* (e.g. Heinrich, 1972a,b, 1976; Prys-Jones, 1986; Surholt *et al.* 1990; Esch and

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Goller, 1991). Among solitary bees most studies have been on relatively large species active in warm or tropical climates, particularly the carpenter bees of the genus *Xylocopa* (Anthophoridae) (e.g. Chappell, 1982; Nicolson and Louw, 1982; Louw and Nicolson, 1983; Baird, 1986; Heinrich and Buchmann, 1986; Willmer, 1988; Surholt *et al.* 1990). Comparisons across species show that body mass alone is not a good indicator of endothermic ability (May, 1976) and small species adapted to cold thermal regimes are capable of high rates of warm-up and high thoracic temperatures (Stone and Willmer, 1989b). Endothermy is widespread among small solitary bees active in cool climates and is known in the families Andrenidae, Anthophoridae, Colletidae, Halictidae and Megachilidae (Stone and Willmer, 1989b). Do small solitary species have thermoregulatory abilities comparable with the better known social species active in similar environments? How do their responses to changes in ambient temperature, in terms of the thermal power generated and the total energetic cost of warm-up, compare to those of *Bombus*, the best known endothermic bees? This study addresses these questions through detailed study of a small anthophorid solitary bee, *Anthophora plumipes*, active in a cold thermal regime.

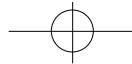
Anthophora is a large genus of fast-flying, robust bees occurring on all continents except Australia and South America. They are often extremely furry and all members of the genus examined to date are extremely endothermic (G. Stone, in preparation). In Britain, the commonest species is *Anthophora plumipes*, whose geographic range extends as far as Israel in the east. In Britain, *A. plumipes* flies from March until May, and in Israel from February until April. Throughout its range it is active in the spring when weather conditions and ambient temperature (T_a) fluctuate widely. This variation creates a situation in which some degree of endothermic thermoregulation has advantages over activity that is governed solely by dependence on unpredictable environmental conditions.

An important variable in studies of thermal physiology is body mass because, for organisms of a constant form, body mass determines surface area to volume ratios and hence the balance between mass-specific rates of heat generation and loss (May, 1976; Bartholomew, 1981; Heinrich and Heinrich, 1983). Across species, body mass is an important variable both in heterothermic insects (Stone and Willmer, 1989b; Coelho, 1991) and heterothermic mammals (Stone and Purvis, 1992). This study examines in detail the role of body size in warm-up rates and body temperatures in a single species.

Materials and methods

Field measurements of body temperature

The 'grab-and-stab' techniques used in this study are as described by Stone and Willmer (1989a). Grab-and-stab measurements were made at feeding and nesting sites in the Botanical Gardens, Oxford, and in the grounds of Merton College and University College, Oxford, during 1987, 1988 and 1989. Laboratory measurements of body temperature were made at Oxford University Department of Zoology over the same period and at the Botany Department of the Hebrew University, Givat Ram, Jerusalem, in February and March 1989. In Israel, bees were collected from an artificial mediterranean



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plant community established at Beit Jala (Har Gilo) in the Occupied Territories of the West Bank to the south of Jerusalem.

Laboratory measurement of warm-up rates and body temperatures

During warm-up and tethered flight, the bee was suspended from a fine thermocouple implanted shallowly in the thoracic flight muscles, as described by Stone and Willmer (1989b). In bumblebees (Heinrich, 1972, 1976) and carpenter bees (Heinrich and Buchmann, 1986), the temperature of the thorax is controlled by regulation of heat transfer from the thorax in the form of hot haemolymph passing down the petiole into the abdomen. At low T_a , *Bombus* minimises heat loss from the thorax to the abdomen by operation of a countercurrent heat exchange system in the petiole (Heinrich, 1976). Continuous measurement of abdominal temperature (T_{ab}) in *A. plumipes* was achieved using a flexible copper–constantan thermocouple (diameter 0.1mm) inserted through a small hole in the second abdominal tergite. The thermocouple was inserted dorso-laterally to avoid damage to the dorsal heart, to a depth of approximately 1mm, and secured in place with adhesive. The temperature at which a bee initiated tethered flight is referred to as its voluntary flight temperature (VFT). After flight for a period of 60s or so, body temperature usually stabilised at a value termed the stable flight temperature (SFT) (Stone and Willmer, 1989a). After each experiment, bees were released, apparently unharmed, at the site of capture. Laboratory investigations of thermogenesis were carried out at four ambient temperatures (T_a): 9, 16, 21 and 29°C.

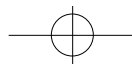
After a number of warm-ups over the full range of thoracic temperature (T_{th}) from T_a to VFT, bees showed general lowering of warm-up rates. This apparent fatigue could be dramatically ‘cured’ by feeding the bee with a solution of sucrose. Shortly after feeding had been initiated, there was a marked increase in abdominal pumping and a rapid increase in T_{th} . The bee warmed to levels in excess of those in previous warm-ups and ceased feeding shortly before flight. This increase in apparent thermogenic ability remained for several subsequent warm-ups. The major effect of feeding was an increase in VFT and in the power of tethered flight. This suggests that observed levels of endothermy could be dependent on the energy reserves carried by the bee at the time of capture. Both male and female *A. plumipes* collect nectar to the exclusion of all other flight activities during the early part of their flying period (Stone, 1989). Bees were therefore collected during the later stages of this period to minimise the probability that they might be limited during warm-up by low levels of nectar in their crops. Each bee was also allowed only five periods of tethered flight before release.

Conductance

The rate at which a body cools depends on how rapidly heat is lost per unit area from its surface (its conductance, C) and on the temperature difference that exists between the body and its surroundings (for bees, the thoracic temperature excess, $T_{th} - T_a$, abbreviated to T_{ex}). This relationship is expressed algebraically as:

$$dT_{th}/dt \propto CT_{ex}.$$

Conductance values can be calculated by multiplying the cooling constant [the gradient



of a regression of cooling rate (y) on T_{ex} (x)] determined by analysis of the cooling curve of each bee by the specific heat capacity of tissue (taken as $3.4 \text{ J g}^{-1} \text{ degree}^{-1}$; Heinrich, 1975; Coelho, 1991).

In order to exclude the possibility of physiological modification of cooling rates, cooling constants were obtained for freshly killed dead bees. The bee was attached to a thermocouple in the normal way and its thorax heated with a microscope lamp (48W, Vickers, UK) situated 10cm from the bee. Heating of head and abdomen was minimised by shading them with pieces of polished sheet steel, acting both as shading screens and heat sinks. The bee was enclosed in a Perspex chamber to minimise the cooling effects of air currents in the room. When the bee's thorax had been warmed to, and stabilised at, the required temperature, it was allowed to cool passively until it had equilibrated with room air temperature. Each bee was warmed and allowed to cool three times. These three coolings were used to calculate a mean value of the cooling constant for each individual. Total body mass and thoracic mass were determined on an electric balance (Mettler AE160).

Statistical methods

When analysing the effects of more than one continuous variable (such as T_a and body mass) on another continuous variable (such as T_{th}), multiple regression has been used. Utilisation of this technique is only valid if all the data are statistically independent. When each data point comes from a different individual, this assumption is probably justified. When each individual contributes a different number of values to the data set it may not be. If there are differences between individuals (such as damage due to insertion of a thermocouple) that are not due to the variables being examined, individuals for which more data were obtained will bias the analysis towards this unknown variable. To control for this effect, each individual must contribute the same weight to the analysis. To achieve this, mean values of the variables being investigated were obtained for each individual and are referred to as individual means (e.g. individual mean warm-up rate, etc.). These values are then used in a normal multiple regression analysis. Comparisons between Israeli and British populations were made by using country of origin as a categorical variable in analyses.

Results

Field measurements of body temperature

During free flight in the field T_{th} increased from an average of approximately 25°C at $T_a=5^\circ\text{C}$ to 39°C at $T_a=26^\circ\text{C}$. The gradient of the least-squares regression of T_{th} on T_a is 0.62 (95% confidence limits 0.587–0.656; $N=81$, $r^2=0.93$, $P<0.001$) and for T_{ab} on T_a it is 0.96 (95% confidence limits 0.916–1.015; $N=81$, $r^2=0.92$, $P<0.001$). As T_a increases, the gradients of both T_{ab} and T_{th} on T_a decrease and a better fit for both T_{th} and T_{ab} is obtained using polynomial regressions (Fig. 1). There is a strong positive correlation between body mass and T_{th} , controlling for the effect of T_a ($N=80$, $r^2=0.96$, $P<0.001$).

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Laboratory measurements of warm-up rate, voluntary flight temperatures and stable flight temperatures

Mean warm-up rates and body temperatures obtained at the different ambient temperatures are summarised in Table 1.

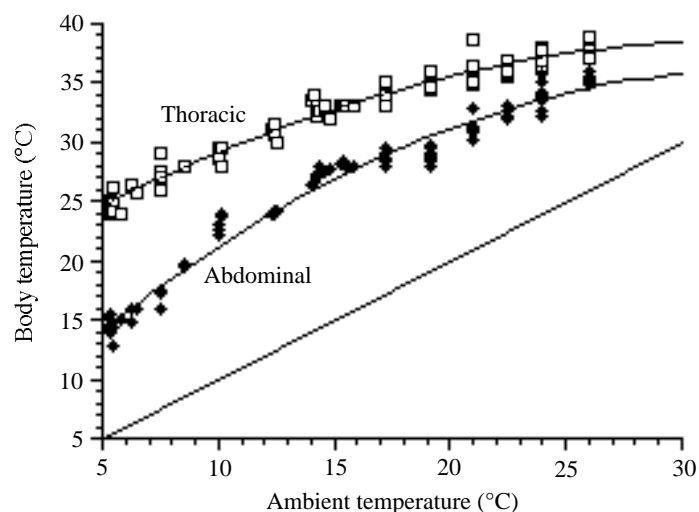
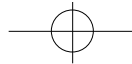


Fig. 1. (A) Thoracic and abdominal temperatures in male and female *Anthophora plumipes* as functions of ambient temperature (T_{th} : $y=19.17+1.18x-0.02x^2$, $r^2=0.970$; T_{ab} : $y=5.83+1.81x-0.03x^2$, $r^2=0.940$).

Table 1. Warm-up rates, voluntary flight temperatures and stable flight temperatures in male and female *Anthophora plumipes*

Ambient temperature (°C)		Mean warm-up rate (degreesmin ⁻¹)	Voluntary flight temperature (°C)	Stable flight temperature (°C)
$T_a=9^{\circ}\text{C}$	Males	3.4 ± 0.2 (17)	31.6 ± 0.5 (8)	27.5 ± 0.5 (5)
	Females	4.2 ± 0.3 (14)	32.7 ± 0.4 (8)	29.9 ± 0.6 (4)
$T_a=16^{\circ}\text{C}$	Males	7.5 ± 0.9 (4)	31.5 ± 0.3 (4)	29.0 ± 0.2 (4)
	Females	9.9 ± 1.0 (4)	34.0 ± 0.3 (4)	32.2 ± 0.2 (4)
$T_a=21^{\circ}\text{C}$				
Britain	Males	8.8 ± 0.4 (21)	32.3 ± 0.5 (17)	30.8 ± 0.3 (20)
	Females	12.3 ± 0.6 (28)	34.4 ± 0.6 (11)	34.6 ± 0.6 (12)
Israel	Males	9.7 ± 0.6 (4)	34.3 ± 0.3 (4)	32.6 ± 0.4 (4)
	Females	11.05 ± 0.4 (4)	35.7 ± 0.4 (4)	34.1 ± 0.3 (4)
$T_a=29^{\circ}\text{C}$				
	Males	12.3 ± 0.5 (6)	34.8 ± 0.3 (3)	37.4 ± 0.3 (3)
	Females	15.2 ± 0.4 (3)	36.5 ± 0.3 (3)	38.6 ± 0.2 (3)

Each value given is the mean of the individual means obtained for each sex at each $T_a \pm 1$ standard error, with the number of individual means in parentheses.



Warm-up at an ambient temperature of 21°C

Acceptable warm-up traces were obtained from 21 male and 28 female *A. plumipes* at $T_a=21^\circ\text{C}$. A typical warm-up trace is shown in Fig. 2. During warm-up there was no audible buzzing, and no vibration of the thorax was visible through a dissecting microscope (magnification $30\times$). In almost all cases, the first warm-up from T_a was markedly curvilinear, warm-up rate increasing with T_{th} and sometimes decreasing slightly just before flight temperatures were reached. Thereafter, rates of warm-up became more linear as a result of increased rates of warm-up at low T_{th} .

Individual mean warm-up rate correlates positively with both individual mean T_{th} and body mass (Fig. 3A,B). When individual mean warm-up rate is regressed against both individual mean T_{th} and body mass, the significant effect of body mass disappears ($N=48$, $r^2=0.3$, $T_{th} P<0.001$, body mass NS). There is no significant difference between warm-up rates in males and females once the effects of T_{th} and body mass have been controlled for. At high T_{th} , the warm-up rates in large females reached more than $19^\circ\text{C min}^{-1}$, among the highest rates in any heterotherm.

There is a strong positive correlation between the rate of abdominal pumping and T_{th} , as shown in Fig. 4. Furthermore, at a given T_{th} , smaller bees have higher rates of abdominal pumping and, at a given temperature and body mass, males have lower rates of pumping than females (multiple regression: $N=236$, $r^2=0.67$, $T_{th} P<0.001$, body mass $P<0.001$, sex $P<0.001$).

At $T_a=21^\circ\text{C}$, the temperature at which flight was initiated by the bee (VFT) was somewhat higher than the temperature that it sustained during tethered flight (SFT) (Table 1). Larger bees warmed to a higher VFT than smaller bees (Fig. 5A) and maintained a higher SFT (Fig. 5B).

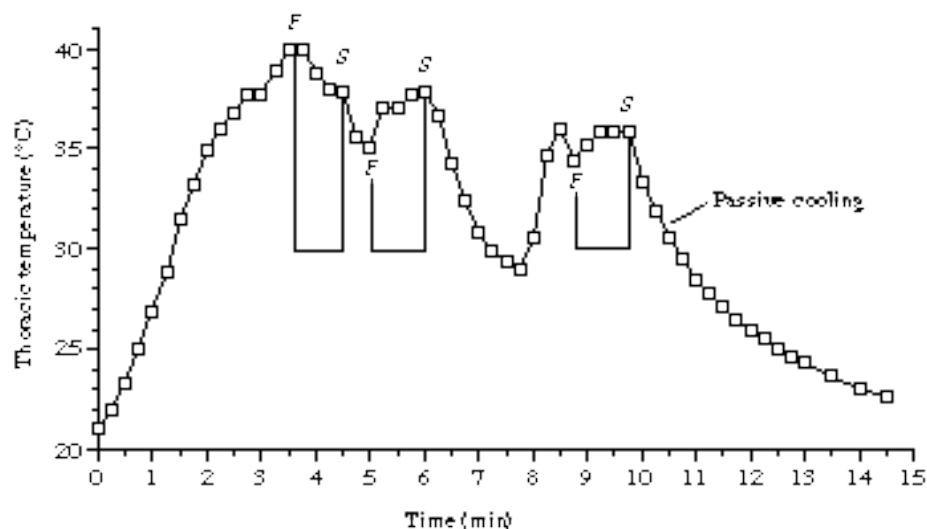


Fig. 2. Thoracic temperature over time for a female *A. plumipes* during warm-up at $T_a=21^\circ\text{C}$. Initiation of flight is indicated by *F* and cessation of flight by *S*.

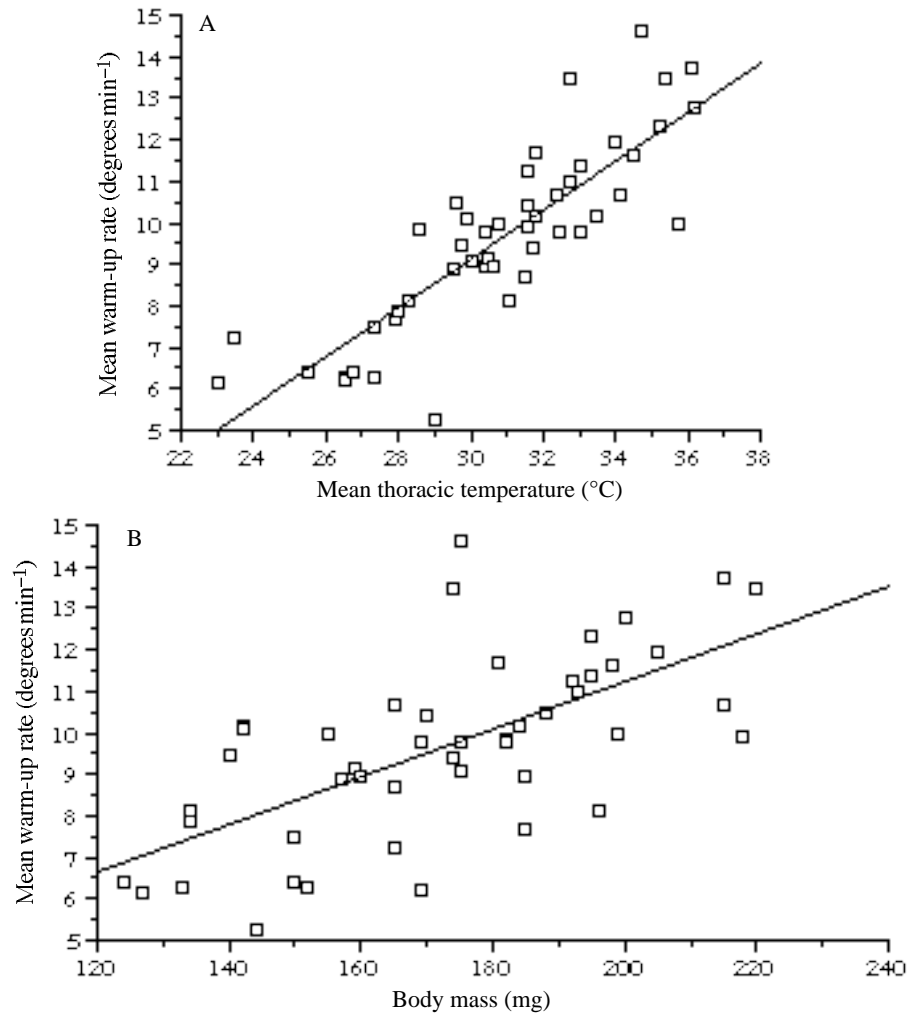


Fig. 3. (A) Individual mean warm-up rate as a function of individual mean thoracic temperature in *A. plumipes* at $T_a = 21^\circ\text{C}$ ($y = -8.6 + 0.59x$, $r^2 = 0.722$, $P < 0.001$). (B) Individual mean warm-up rate as a function of body mass for *A. plumipes* at $T_a = 21^\circ\text{C}$ ($y = -0.21 + 0.06x$, $r^2 = 0.422$, $P < 0.001$).

Warm-up at ambient temperatures of 9 and 29°C

Initial rates of warm-up by all bees at 9°C were very low. Four out of 14 females and 9 out of 17 males failed to reach a T_{th} high enough for flight. Even brief interruption of flight by the bee, leading to cooling of the thorax by more than 2–3°C, made it impossible for flight to be resumed without warm-up. There was a strong positive correlation between ability to warm up to flight temperatures and body mass (Fig. 6). Despite low initial warm-up rates, *A. plumipes* generated a thoracic temperature excess (T_{ex}) of 22–24°C at this T_a [individual mean male excess $22.6 \pm 0.5^\circ\text{C}$, ($N=8$); individual mean

female excess $23.7 \pm 0.4^\circ\text{C}$ ($N=8$), $5\text{--}7^\circ\text{C}$ more than the average T_{ex} at take-off at $T_{\text{a}}=21^\circ\text{C}$.

Warm-up rates at $T_{\text{a}}=29^\circ\text{C}$ were uniformly high (Table 1), although the maximum recorded warm-up rate ($19.2^\circ\text{Cmin}^{-1}$ for a 201mg female) was not higher than the maximum recorded at $T_{\text{a}}=21^\circ\text{C}$. The T_{ex} at which those *A. plumipes* that could be induced to fly flew was only $7\text{--}8^\circ\text{C}$ (Table 1) and, when tethered flight was initiated, T_{th} rose rapidly. Although T_{th} approached an asymptotic SFT value, in only three males and three females were flights of over 15s in duration recorded. Prolonged flight would lead to the generation of far higher T_{th} values. In all cases, flight ceased once T_{th} approached $38\text{--}40^\circ\text{C}$.

At $T_{\text{a}}=21^\circ\text{C}$ there was no rise in T_{ab} associated with a simultaneous decrease in T_{th} at cessation of tethered flight for any of the five *A. plumipes* examined. At $T_{\text{a}}=29^\circ\text{C}$,

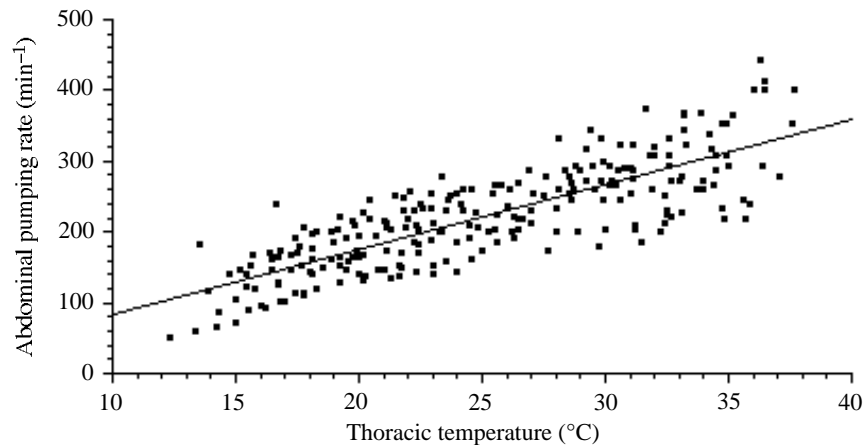


Fig. 4. Abdominal pumping rate as a function of thoracic temperature in male and female *A. plumipes* at $T_{\text{a}}=9^\circ\text{C}$ and $T_{\text{a}}=21^\circ\text{C}$ ($y=-7.93+9.17x$, $r^2=0.673$).

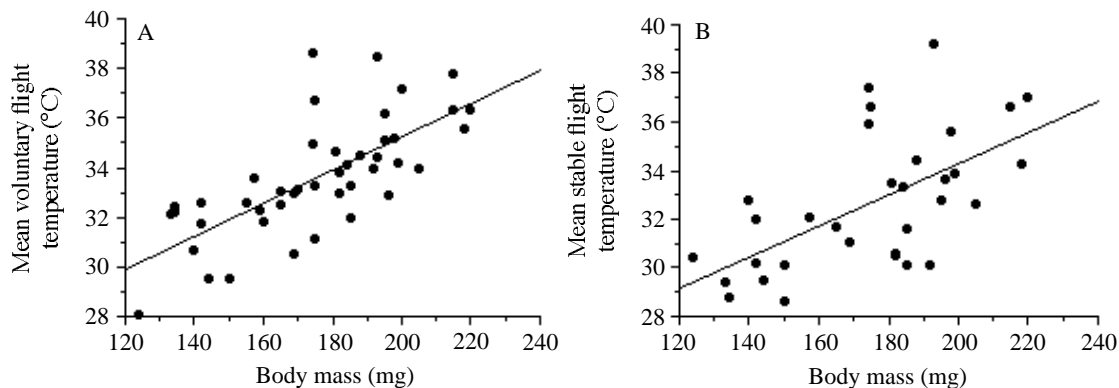


Fig. 5. (A) Mean individual VFT as a function of body mass in *A. plumipes* at $T_{\text{a}}=21^\circ\text{C}$ ($y=21.9+0.07x$, $r^2=0.518$, $P<0.001$). (B) Mean individual SFT as a function of body mass in *A. plumipes* at $T_{\text{a}}=21^\circ\text{C}$ ($y=21.6+0.06x$, $r^2=0.360$, $P<0.01$).

however, T_{th} rose rapidly during flight to 38–40°C, and at the end of flight there was a rapid rise in T_{ab} (Fig. 7).

The effect of ambient temperature on warm-up in A. plumipes

Warm-up rates and flight temperatures. Warm-up rate correlates positively with T_a (Fig. 8). Relationships between VFT, SFT and T_a give an indication of the thermoregulatory ability of *A. plumipes* independent of the conclusions based on 'grab-and-stab' data. For both males and females, gradients of both VFT and SFT on T_a are significantly less than 1 (mean \pm standard errors): male VFT, 0.16 ± 0.06 ; female VFT,

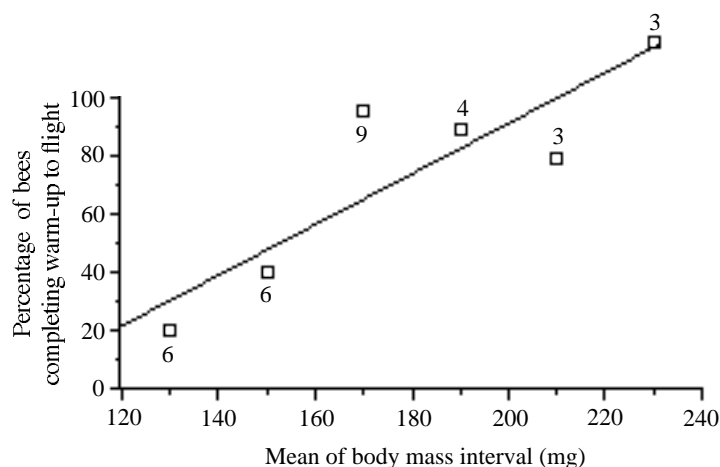


Fig. 6. The percentage of *A. plumipes* attempting warm-up which reach flight temperatures at $T_a=9^\circ\text{C}$ as a function of body mass ($N=6$, $y=-69.6+0.73x$, $r^2=0.774$, $P=0.02$). The number of bees in each mass interval is shown next to the data point.

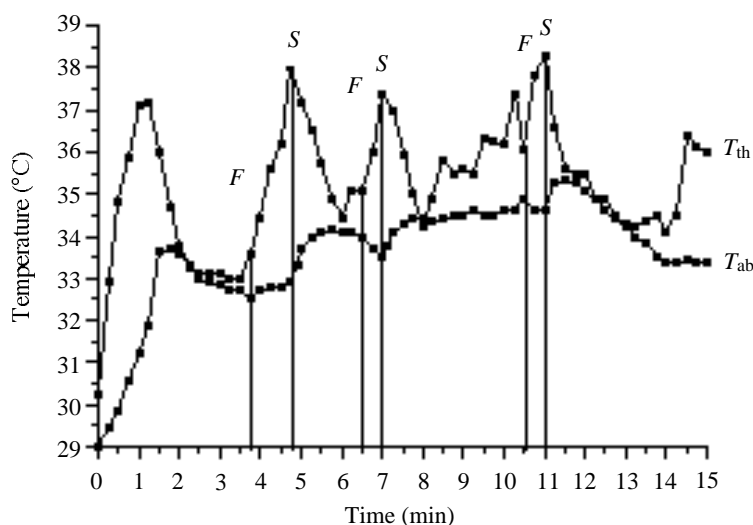


Fig. 7. Thoracic and abdominal temperatures over time for a female *A. plumipes* at $T_a=29^\circ\text{C}$. F and S indicate the beginning and end of tethered flight.

0.19±0.03; male SFT, 0.49±0.11; female SFT 0.44±0.03). For all four data sets a better fit is given by polynomial functions (Fig. 9). For both sexes at low T_a , VFT>SFT, while the relationship is reversed at higher T_a . Fig. 9 suggests that no temperature change with initiation of tethered flight (i.e. VFT=SFT) should occur at an ambient temperature of approximately 24.5°C for males and 20.0°C for females.

Time required to complete warm-up. The total time required to complete warm-up to flight temperature in *A. plumipes* is also dependent on T_a , as shown in Fig. 10. While at

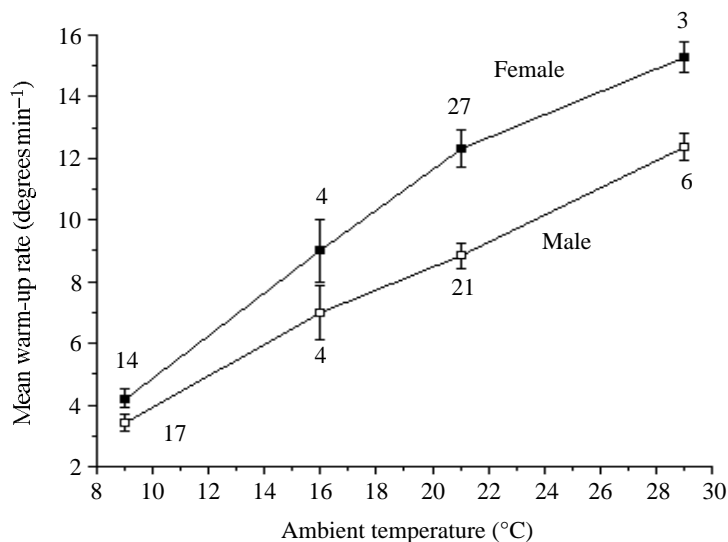


Fig. 8. Mean warm-up rate (\pm S.E.M.) as a function of ambient temperature for male and female *A. plumipes*. The number of individual mean warm-up rates contributing to the overall mean at each ambient temperature is shown beside each data point.

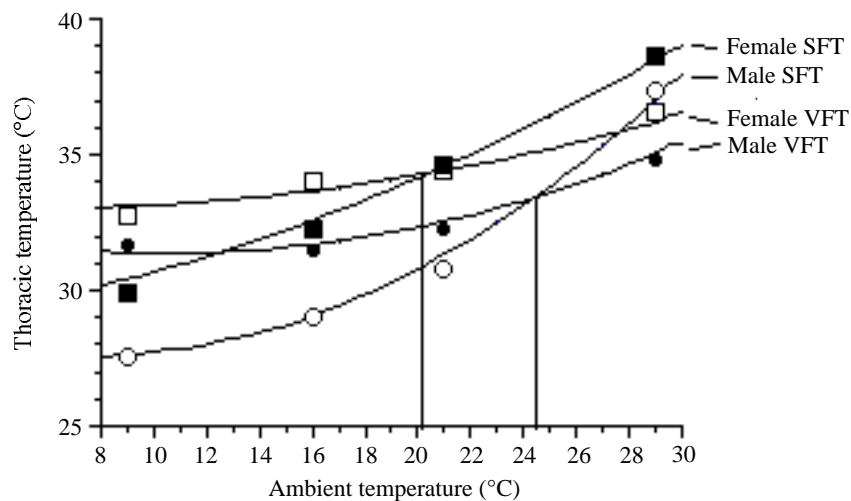


Fig. 9. VFT and SFT as functions of T_a for male and female *A. plumipes*. The mean of the individual means for each sex is plotted at each T_a and in each case the curve is fitted to the individual means. Vertical lines show VFT=SFT for males and females (see text).

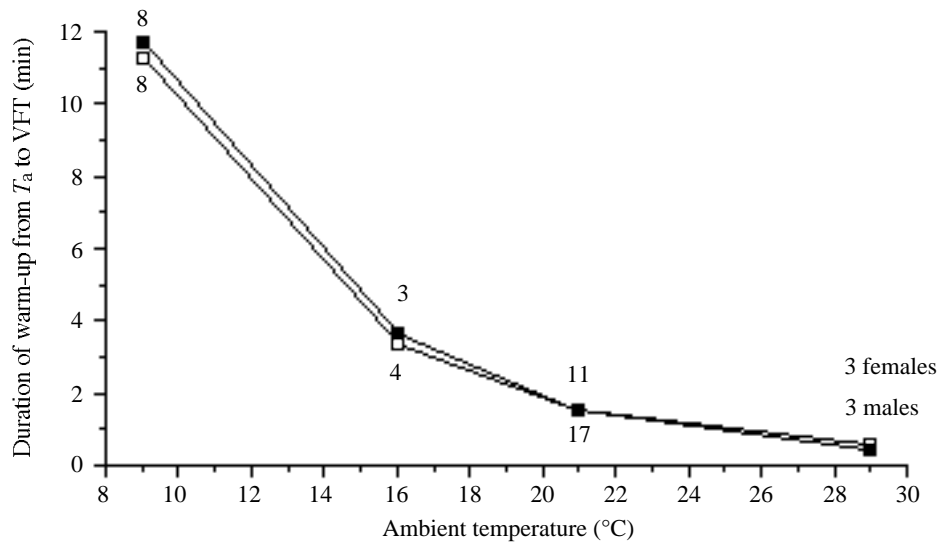


Fig. 10. Mean duration of warm-up from ambient temperature to VFT as a function of ambient temperature for female (■) and male (□) *A. plumipes*. In both figures the number of individual means contributing to the overall mean at each ambient temperature is shown beside each data point.

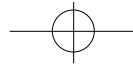
$T_a=21^\circ\text{C}$, warm-up took a mean of $1.6\pm0.1\text{min}$ for both males ($N=17$) and females ($N=11$), warm-up at $T_a=9^\circ\text{C}$ took a mean of $11.2\pm0.6\text{min}$ ($N=11$) for males and $11.7\pm0.6\text{min}$ ($N=9$) for females. Larger bees warm up more rapidly than small bees (which reduces warm-up time), but also warm up further than small bees (which tends to extend warm-up). Thus, whether large bees take longer or shorter periods to complete warm-up depends on the balance between these effects. At T_a of both 9°C and 21°C these effects seem to cancel each other out – there was no significant effect of individual mean warm-up rate, body mass or individual mean VFT on warm-up duration.

Conductance

Conductance values were obtained for 14 *A. plumipes* (8 males and 6 females) at an ambient temperature of 21°C . The rate of heat loss correlates positively with T_{ex} (Fig. 11A). The mean cooling constant for *A. plumipes* is 0.53min^{-1} , giving a mean thermal conductance of $0.03\text{Wg}^{-1}\text{degree}^{-1}$. The cooling constant (and therefore the thermal conductance) of *A. plumipes* decreases significantly with increasing thoracic mass; small bees lose heat more rapidly than large bees do (Fig. 11B). If total body mass is used rather than thoracic mass, males also lose heat more slowly than females do ($N=14$, body mass $P=0.002$, sex $P=0.01$).

Comparisons between Israeli and British populations of *A. plumipes*

Warm-up data at an ambient temperature of 21°C were obtained for four male and four female *A. plumipes* from Jerusalem. Although both males and females of the Israeli population have a lower mean body mass than the British population, they have higher



mean VFT and SFT at 21°C, and males have higher warm-up rates than their British counterparts (Table 1). Having controlled for the effects of thoracic temperature and body mass, Israeli bees have a higher individual mean warm-up rate (multiple regression: $N=56$, $r^2=0.73$, body mass $P=0.065$, T_{th} $P<0.001$, country $P=0.04$) and higher VFT values, having controlled for the effect of body mass (multiple regression: $N=49$, $r^2=0.47$, body mass $P<0.001$, country $P=0.006$).

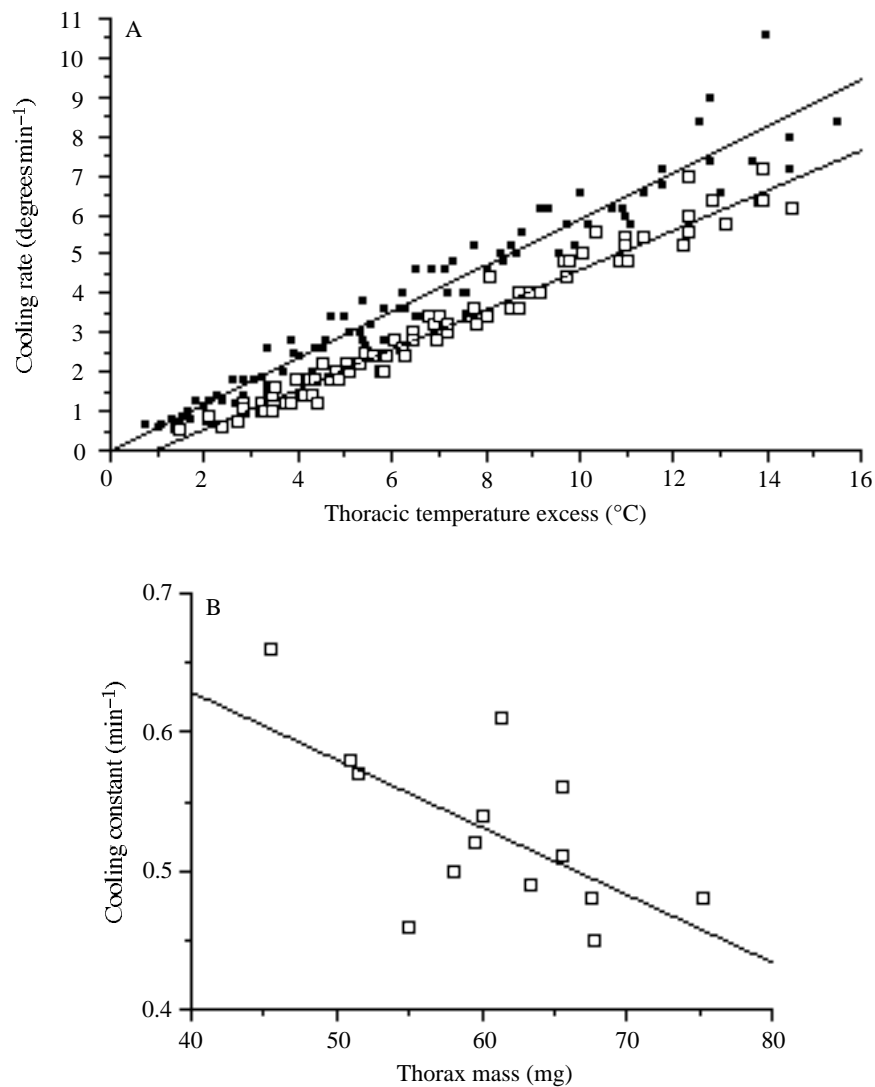


Fig. 11. (A) Cooling rate as a function of thoracic temperature excess in two female (190 and 194mg) (\square) ($y = -0.46 + 0.51x$, $r^2=0.960$, $P<0.001$) and three male (100, 115 and 121mg) (\blacksquare) ($y = -0.025 + 0.6x$, $r^2=0.941$, $P<0.001$) *A. plumipes*. (B) The cooling constant as a function of thorax mass (both sexes) in *A. plumipes* ($N=14$, $y = 0.82 - 0.005x$, $r^2=0.530$, $P<0.01$).

Discussion

Comparison of grab-and-stab and laboratory data

Table 2 shows mean SFT values at the ambient temperatures used in the laboratory together with mean grab-and-stab estimates for the same ambient temperatures taken from Fig. 2. The two methods agree well in their estimation of T_{th} in flight at high and at low T_a , although at moderate T_a grab-and-stab estimates are higher than the

Table 2. *A comparison between stable flight temperature and 'grab-and-stab' data*

	Ambient temperature (°C)			
	9	16	21	29
Stable flight temperature (°C)	28.5	31	32	38
'Grab-and-stab' estimate (°C)	28	33	35	39

SFT are mean values at the ambient temperatures used in the laboratory and 'grab-and-stab' estimates are taken from Fig. 2.

Table 3. *Calculation of rates of heat generation in the thorax by male Anthophora plumipes*

Ambient temperature (°C)	Thoracic temperature (°C)	Thoracic excess (°C)	Warm-up rate (degrees min ⁻¹)	Cooling rate (degrees min ⁻¹)	Power generated (W g ⁻¹ thorax)
21	21	0	4.80	0.00	0.26
21	24	3	6.30	1.75	0.45
21	27	6	7.80	3.50	0.63
21	30	9	9.35	5.30	0.81
21	33	12	10.90	7.10	1.00
21	36	15	12.40	8.85	1.18
21	39	18	13.90	10.60	1.37
9	10	1	0.10	0.57	0.04
9	12	3	0.60	1.75	0.13
9	15	6	1.40	3.50	0.27
9	18	9	2.20	5.30	0.42
9	21	12	2.95	7.10	0.56
9	24	15	3.70	8.85	0.70
9	27	18	4.50	10.60	0.84
9	30	21	5.30	12.40	0.99
9	33	24	6.10	14.16	1.13

The following regression equations (all significant at $P < 0.001$) are used to calculate rates of warm-up and cooling at the given thoracic temperatures and thoracic temperature excesses.

Males: cooling rate (degrees min⁻¹) = $0.591[\text{thoracic temperature excess (°C)}] - 0.025$. Warm-up rate at $T_a = 21^\circ\text{C}$ (degrees min⁻¹) = $0.508[\text{thoracic temperature (°C)}] - 5.89$. Warm-up rate at $T_a = 9^\circ\text{C}$ (degrees min⁻¹) = $0.259[\text{thoracic temperature (°C)}] - 2.49$.

Females: cooling rate (degrees min⁻¹) = $0.508[\text{thoracic temperature excess (°C)}] - 0.459$. Warm-up rates for females are given by the same expressions as those for males.

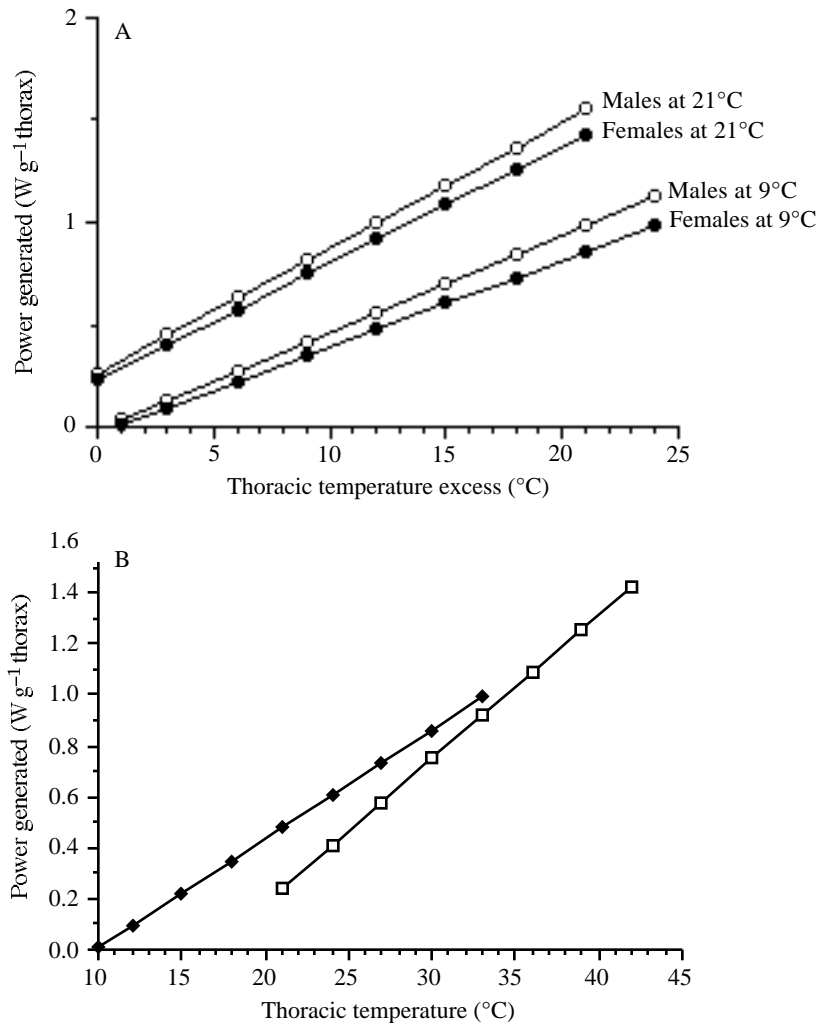
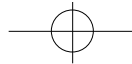


Fig. 12. (A) Power output as a function of thoracic temperature excess and ambient temperature in male and female *A. plumipes*. (B) Power output as a function of thoracic temperature for female *A. plumipes* at $T_a=9^\circ\text{C}$ (◆) and $T_a=21^\circ\text{C}$ (□).

corresponding SFT values. The reasons why SFT values are probably under-estimates and grab-and-stab over-estimates of true T_{th} have already been discussed (Stone and Willmer, 1989a). Laboratory and field data agree that 25°C is very close to the minimum T_{th} at which this species flies and 39°C close to the maximum.

Power generation during warm-up

During warm-up, energy is expended both in movement of the musculature and in generation of heat. Here only the thermal power generated is considered and this will be an underestimate of the actual power generated (Bartholomew, 1981). The thermal power generated at a given T_{ex} is the sum of the rate of heat storage in the thorax and the rate of

passive heat loss. This can be expressed as: rate of heat generation at a given T_{ex} = (warm-up rate \times specific heat capacity of tissue \times thoracic mass) + (passive cooling rate \times specific heat capacity of tissue \times thoracic mass), if heat losses from other body tagmata are ignored (Heinrich and Bartholomew, 1971). If it is assumed that, during warm-up, all the heat generated is sequestered in the thorax, then rates of passive heat loss depend only on T_{ex} (as long as there is no significant variation in factors such as air movement around the bee). It is therefore possible to calculate such rates of heat loss at any T_{ex} for any T_{a} from best-fit regressions of rate of cooling as a function of T_{ex} , such as those shown in Fig. 5A. As shown above, there are strong correlations between warm-up rate and T_{th} at a given T_{a} . From these relationships it is possible to calculate the mean warm-up rate for *A. plumipes* at a given T_{th} at a specific T_{a} , and thus at a given T_{ex} . From the relationships and quantities described above, the power generated at a specified T_{th} and T_{a} can be calculated. Table 3 shows steps in the calculation of the rate of heat production during

Table 4. Calculation of the total energy required to complete warm-up at four ambient temperatures

Ambient temperature (°C)	VFT (°C)	Time taken to warm from T_{a} to VFT (min)	Area under warm-up curve (min°C)	Total energy for warm-up (J)
9	31.7	10.75	87.2	14.0
16	34.0	3.80	43.5	9.0
21	36.0	2.10	29.8	6.1
29	38.0	0.42	5.9	2.6

The figures given are values for an average female (body mass 190–200 mg).

The specific heat capacity of tissue is taken as $3.4 \text{ J g}^{-1} \text{ °C}^{-1}$ and the thoracic mass as 0.065 g.

CA is a constant of value $0.10 \text{ J °C}^{-1} \text{ min}^{-1}$.

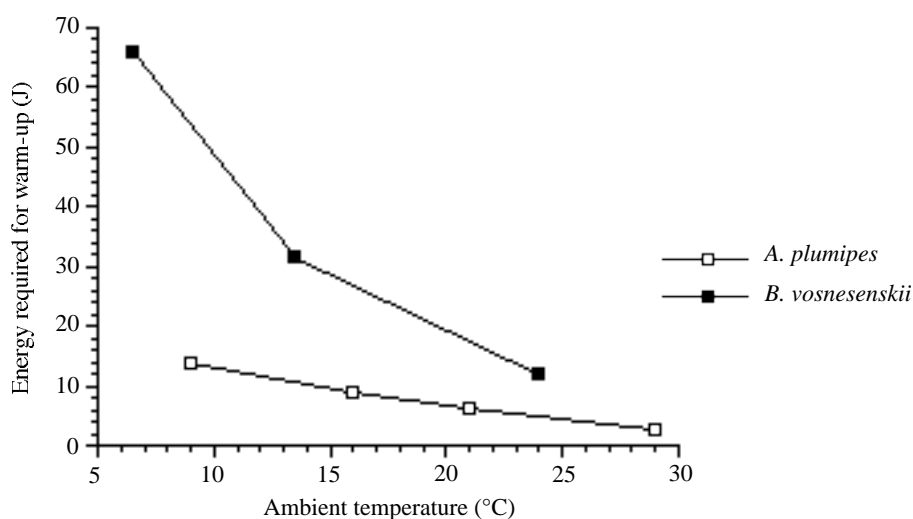


Fig. 13. The total energy required to complete warm-up from ambient temperature to VFT in *Bombus vosnesenskii* and female *A. plumipes* as functions of ambient temperature.

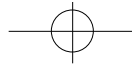


Table 5. *Gradients of regressions of thoracic temperature on ambient temperature, at take-off and/or during flight, in endothermic insects*

Species	Family	Gradient before flight	Gradient during flight	Stated regression or estimated gradient	Source
Bees					
<i>Anthophora plumipes</i>	Anthophoridae	0.20 (VFT)	0.52 (SFT)	Stated	1
			0.62 (G+S)	Stated	1
<i>Amegilla sapiens</i>	Anthophoridae	0.61 (VFT)	0.98 (SFT)	Stated	2
			0.54 (G+S)	Stated	3
<i>Creightonella frontalis</i>	Megachilidae	0.46 (VFT)	0.87 (SFT)	Stated	2
			0.68 (G+S)	Stated	2
<i>Apis mellifera</i>	Apidae	0.00 (G+S)	0.37 (G+S)	Estimate	4
		0.00 (G+S)	0.55 (G+S)	Estimate	5
Moths					
<i>Malacosoma americanum</i>	Lasiocampidae	0.11 (G+S)	0.60 (G+S)	Estimate	6
Beetles					
<i>Pachnoda</i> sp.	Scarabeidae	0.00 (G+S)	0.70 (G+S)	Estimate	7
<i>Popillia japonica</i>	Scarabeidae	0.27 (G+S)	0.74 (G+S)	Stated	8

All the gradients stated are from statistically significant regressions. In the cases indicated, gradients have been estimated from figures.

VFT and SFT indicate measurements obtained during tethered flight, as used in the text.

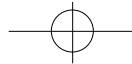
G+S indicates gradients obtained using 'grab-and-stab' techniques.

Sources are indicated by the following numbers: (1) This study. (2) Stone (1989). (3) Stone and Willmer (1989a). (4) Cooper *et al.* (1985). (5) Heinrich (1979). (6) Casey *et al.* (1981), Casey (1981). (7) Heinrich and McClain (1986). (8) Oertli and Oertli (1990).

warm-up for *A. plumipes* at 9 and 21°C. Power output for males and females as a function of T_{ex} is shown in Fig. 12A.

Power output increases linearly with T_{ex} and at a given T_{ex} power output at 21°C is higher than that at 9°C. Although the rate of heat loss depends only on the T_{ex} , the rate of heat generation depends on T_{th} (Fig. 12B) (Heinrich, 1975, 1987). At $T_a=9^\circ\text{C}$ (Table 3) and with a T_{th} of 15°C (a T_{ex} of 6°C), the mean power generated by *A. plumipes* is 0.27W, and the rate of heat loss 0.19W. 70% of the estimated generated heat is lost through passive cooling. At $T_a=21^\circ\text{C}$ and with a T_{th} of 27°C (the same T_{ex} of 6°C), while the rate of passive heat loss is still 0.19W, the total power generated is 0.63W. At the higher T_a , passive heat loss accounts for only 30% of the total power generated.

The power generated during warm-up is strikingly similar to that generated by queen bumblebees (Heinrich, 1975). At a T_{ex} of 20°C, queen *Bombus vosnesenskii* produce 0.28–0.35 W g⁻¹ thorax (Heinrich, 1975). Table 3 shows that at $T_a=21^\circ\text{C}$ male *A. plumipes* produce 0.26–1.37 W g⁻¹ thorax, depending on the T_{th} . The maximum power output produced by *A. plumipes* (1.37 W g⁻¹ thorax at a T_{th} of 39°C at $T_a=21^\circ\text{C}$) is somewhat higher than the maximum rate reported by Heinrich (1975) for *B. vosnesenskii* (1.05 W g⁻¹ thorax) and cuculiine moths (Heinrich, 1987, maximum rates almost identical to those of *B. vosnesenskii*). Using the common approximation that 1ml of



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oxygen liberates 20.1J (e.g. Weis-Fogh, 1967; Casey *et al.* 1981), *A. plumipes* uses approximately 247ml O₂ g⁻¹ thorax h⁻¹ (or 84.5ml O₂ g⁻¹ total body mass h⁻¹), somewhat higher than rates recorded for other endothermic insects (Kammer and Heinrich, 1974; Bartholomew *et al.* 1981; Casey, 1981; Casey *et al.* 1981; Morgan, 1987). The oxygen consumption of *A. plumipes* is comparable with rates determined for flying honeybees (Hocking, 1953) and bumblebees (Heinrich, 1975; Bertsch, 1984; Surholt *et al.* 1990; Ellington *et al.* 1990). This illustrates the fact that, in terms of metabolic power output, high rates of warm-up are compatible with flight. The greater the T_{ex} that the bee is maintaining, the higher its rate of heat production must be to counter heat losses and the greater the required rate of oxygen supply to the tissues (Bartholomew and Barnhart, 1984), explaining the positive correlation between abdominal pumping rate and thoracic temperature. Body mass probably correlates negatively with pumping rate because small bees cool faster and have to expend more energy in maintaining the same T_{ex} (Bartholomew and Casey, 1978).

The total energetic cost of warm-up

The expression for the rate of heat generation given in the preceding section can be written as follows (Heinrich, 1975):

$$dHp/dt = (WSdT_{th}/dt) + (CAT_{ex}), \quad (1)$$

where dHp/dt is the rate of heat generation, W is the mass of the thorax, S is the specific heat of tissue, dT_{th}/dt is the warm-up rate at a given T_{th} , C is the conductance and A is the surface area of the thorax exposed to heat losses.

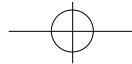
A is difficult to measure alone, and it has been suggested (Heinrich, 1975) that it is best to calculate CA using known estimates for the other variables. When a bee is maintaining its T_{th} at a steady value, $dT_{th}/dt=0$ and $dHp/dt=CAT_{ex}$. When a dead bee is cooling passively, $dHp/dt=0$ and $WSdT_{th}/dt+CAT_{ex}=0$. Because dT_{th}/dt is negative, this can be rewritten as $WSdT_{th}/dt=CAT_{ex}$ and $CA=(WSdT_{th}/dt)$ divided by T_{ex} . W , S and T_{ex} are easy to measure and dT_{th}/dt is the rate of passive cooling at the T_{ex} that is being maintained, determined from Fig. 11A. For a female *A. plumipes*, thermoregulating at $T_{th}=36^{\circ}\text{C}$ at $T_a=21^{\circ}\text{C}$, $CA=(0.065\text{ g}\times 3.4\text{ J g}^{-1}\text{ degree}^{-1}\times 7\text{ degrees min}^{-1})/(36-21)=0.1\text{ J degree}^{-1}\text{ min}^{-1}$, slightly lower than the value given by Heinrich (1975) for queen *Bombus vosnesenskii* ($0.18\text{ J degree}^{-1}\text{ min}^{-1}$).

The total energy expended during a warm-up is given by the integral of equation 1 over the total time required for warm-up, tf . Thus:

$$Hp = WS(VFT - T_a) - CA tf + CA \int_0^{tf} T_{th} dt.$$

(the area under the warm-up curve).

With an estimate of CA , the total energy required to warm-up at any T_a can be calculated once the area under the warm-up curve has been measured. Table 4 gives the values required to calculate the total energy required to warm up at four values of T_a . The results for *A. plumipes* are compared with data obtained in the same way by Heinrich (1975) for queen *Bombus vosnesenskii* in Fig. 13. It is clear from Table 4 and Fig. 13 that the lower the T_a and the longer it takes to raise T_{th} to flight temperatures, the more



expensive the warm-up becomes. The total energy required by a female *A. plumipes* is rather less than that required by queen *B. vosnesenskii*. The mean mass of the thorax of queen *B. vosnesenskii* is 0.210g, over three times greater than that of female *A. plumipes* (0.065g), and the bumblebee therefore needs to expend more energy in order to raise the temperature of its thorax by 1°C than *A. plumipes* does. *B. vosnesenskii* is also a better thermoregulator before flight than *A. plumipes* is – at low T_a values, the former generates a rather higher T_{ex} than the latter and reaches a T_{th} of near 36°C whatever the T_a (Heinrich, 1975). *A. plumipes* could be said to reduce the total energy required to warm up by sacrificing its ability to regulate T_{th} within such narrow bounds.

The inability of some of the smaller *A. plumipes* to warm up at $T_a=9^\circ\text{C}$ indicates that the period for which the required metabolic expenditure must be sustained, and the total T_{ex} that must be generated, clearly place constraints on the conditions under which flight is possible.

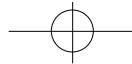
Variation in the form of warm-up curves at a given ambient temperature

There is a change in the form of the warm-up curve over time at $T_a=21^\circ\text{C}$ in *A. plumipes* from a curvilinear first warm-up to more or less linear warm-ups thereafter. This change suggests that during the first warm-up the bee's endothermy is in some way modified, resulting in higher metabolic rates at lower T_{th} during subsequent warm-ups. It is possible that such an effect might be caused by release of a modulating hormone such as octopamine. Octopamine levels have been shown to rise during the first few minutes of flight in locusts (Goosey and Candy, 1980) and cockroaches (Bailey *et al.* 1983), resulting in increased rates of carbohydrate metabolism (Candy, 1978; Whim and Evans, 1988) and increases in the force generated by the flight muscles (Whim and Evans, 1988). Endothermy occurs in the flight muscles and involves very high rates of metabolism, and octopamine release during the first warm-up could produce the observed changes in patterns of warm-up.

Falls in the VFT and warm-up rates obtained for a given animal at $T_a=21^\circ\text{C}$ are probably the results of exhaustion. Wigglesworth (1949) implicated substrate depletion as a cause of flight exhaustion in blowflies, and feeding with glucose rapidly restores flight ability (Hudson, 1958; Clegg and Evans, 1961). In bumblebees, the flight fuels are mono- and disaccharides stored in the gut (Surholt and Newsholme, 1983; Surholt *et al.* 1988), rather than carbohydrates mobilised from the fat body as in some other endothermic insects (Ziegler and Schultz, 1986; Joos, 1987). Radiolabelled glucose appears in the blood of blowflies less than 30s after ingestion (Clegg and Evans, 1961) and absorbed sugars are rapidly incorporated into the transport sugar trehalose (Treherne, 1957; Clegg and Evans, 1961; Friedman, 1967). It is therefore quite possible that the recovery of endothermic performance shown by *Anthophora plumipes* in response to feeding was due to availability of renewed energy sources, and that poor performance prior to feeding may have been due to low energy supplies.

How good a thermoregulator is A. plumipes?

If the gradient of the regression of T_{th} on T_a is used as the indicator of thermoregulatory



ability (May, 1976; Stone and Willmer, 1989a), then it is clear that the thermoregulatory ability of *A. plumipes* depends on whether T_{th} before or during flight is used. Comparison of VFT on the one hand and SFT and 'grab-and-stab' results on the other indicates that regulation of T_{th} is better prior to flight than it is during flight. Table 5 summarises data for endothermic bees, moths and beetles. In every case where T_{th} both before and during flight have been recorded, thermoregulation before flight is far better than it is during flight. This result shows that although these endothermic insects are clearly able to regulate T_{th} in still air before flight, they are unable to compensate entirely either for the high rates of convective cooling during flight at low T_a or for the heat generated by flight muscle activity at high T_a . Achievement of higher thoracic temperatures than can be maintained in flight may have independent selective advantages. If higher muscular power and levels of sensory coordination are required for take-off than for normal flight, then higher values of T_{th} at take-off may be selected for regardless of the cooling that follows. It is also possible that higher values of T_{th} in non-flying *A. plumipes* at low T_a have advantages independent of flight; they may contribute to a greater ability to detect mates or predators in resting males or to digging ability while excavating nests in females (Stone, 1989).

Comparison of the gradients of best-fit regressions of T_{th} on T_a for insects sampled during flight shows that, compared to other endothermic insects, *Anthophora plumipes* is an average thermoregulator. It cannot match the levels of thermoregulation shown by bumblebees (Heinrich, 1972a,b, 1975) or by the much larger carpenter bees in the genus *Xylocopa* (Heinrich and Buchmann, 1986; Baird, 1986; Willmer, 1988). *A. plumipes* shows a similar gradient to those of *Apis mellifera* (Cooper *et al.* 1985; Heinrich, 1979) and the euglossine bees investigated by May and Casey (1983). The gradient of T_{ab} on T_a does not differ significantly from one, indicating that there is no regulation of abdominal temperature. *A. plumipes* nonetheless manages to fly over a wide range of T_a values and, in particular, down to very low temperatures. This is at least in part due to the low minimum T_{th} this species will tolerate in flight. Minimum values of T_{th} in flight of about 25°C are well below the minimum T_{th} for flight recorded for *Apis mellifera* (Cooper *et al.* 1985) and the bumblebee species investigated to date (e.g. 30°C for *Bombus edwardsii*, Heinrich, 1975). The cuculiine moths of the genera *Lithophane* and *Eupsilia*, which are able to warm up from temperatures near 0°C and have a similar body mass to *A. plumipes*, maintain a minimum T_{th} of around 30°C in flight at $T_a=0^\circ\text{C}$ (Heinrich, 1987). It appears that, through evolving a low minimum T_{th} for flight, *A. plumipes* has compromised on the high cost of maintaining a high T_{ex} at low T_a .

Simultaneous measurement of T_{th} and T_{ab} in *A. plumipes* suggests the presence of physiological regulation of heat flow between thorax and abdomen. A petiole countercurrent system is known from larger anthophorid carpenter bees in the genus *Xylocopa* (Heinrich and Buchmann, 1986). This study extends the evidence for such a physiological mechanism to smaller anthophorids. In *A. plumipes* flushing of heat to the abdomen appears only to occur at relatively high ambient temperatures; during most of its spring flight period this species rarely experiences such thermal stress.

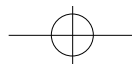
The role of body mass in thermoregulation

VFT, SFT and temperatures during free flight all correlate positively with body mass in *A. plumipes*. At low T_a , high body mass is also advantageous in the generation of a sufficient thoracic temperature excess to allow flight. Females have a significantly higher mean body mass [Britain $185 \pm x$ mg ($N=x$), Israel 177 ± 5 mg ($N=6$)] than males [Britain $160 \pm x$ mg ($N=x$), Israel 141 ± 20 mg ($N=5$)], and these correlations with body mass should therefore generate mean sexual differences in physiological responses to changing T_a . Mass differences probably explain why female *A. plumipes* are able to fly to lower minimum ambient temperatures than males (Stone and Willmer, 1989b). If both females and males have similar upper tolerance limits for thoracic temperature, females will be forced to cease flight activity at a lower T_a than males. This effect of difference in mass between the sexes is demonstrated by the observation that females cease cooling with the onset of flight at a lower T_a than males do. These conclusions on the role of body mass agree with other studies of hymenopteran thermoregulation (Willmer, 1985a,b; Larsson, 1989a,b; Coelho, 1991). Considerable variation in warm-up rates and body temperature exists between bee taxa that is not explained by variation in body mass (G. Stone and Willmer, 1989b). The differences between Israeli and British populations suggest that physiological adaptation can occur within a species independently of differences in body size. Similar differences between populations of the same species have been demonstrated in *Amegilla sapiens*, a close relative of *Anthophora plumipes* (Stone, in preparation). Because no comparable measurements of thermal conductance were obtained for Israeli bees it is impossible to establish whether the higher VFT and warm-up rates of Israeli *A. plumipes* are due to higher rates of heat production or lower rates of heat loss per unit mass.

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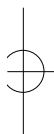
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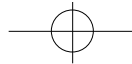


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