

WARM-UP RATES AND BODY TEMPERATURES IN BEES: THE IMPORTANCE OF BODY SIZE, THERMAL REGIME AND PHYLOGENY

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Accepted 5 June 1989

Summary

1. We assess the importance of body mass and the minimum ambient temperature at which foraging occurs in determining the warm-up rates and thoracic temperatures in flight at an air temperature of 22°C of 55 species of bee (Hymenoptera: Apoidea) from six families adapted to a variety of thermal environments.

2. To control for the effects of taxonomic differences in the relationships between these variables, we use multiple regression incorporated in the phylogenetic regression method developed by Grafen (1989).

3. The prediction made by May (1976) that for very small heterotherms warm-up rate will correlate positively with body mass is confirmed when the effects of phylogeny and the thermal environment to which the bee is adapted have been controlled for. The relationship between warm-up rate and body mass within the Apoidea is thus not an extension to lower body masses of the relationship found for heterothermic vertebrates.

4. Having controlled for the effects of body mass in our analyses, we demonstrate that bees able to fly at lower ambient temperatures have higher thoracic temperatures and warm-up rates than bees adapted to warmer environments.

5. There is some suggestion that kleptoparasitic bees, being freed from the need to forage in order to provision cells, have lower warm-up rates than provisioning species.

6. The significance of these relationships in the ecology of bees is discussed in relation to studies of body temperatures and warm-up rates in bees and other insects.

Introduction

Many insects are capable of endothermic heat generation. Although activities involving endothermy include sound production in cicadas and katydids (e.g. Heath & Josephson, 1970), brood incubation in bumblebees (e.g. Heinrich, 1972*d*) and ball-rolling in dung beetles (Bartholomew & Heinrich, 1978),

words: thermoregulation, warm-up rates, body temperatures, Apoidea, comparative analysis.

endothermy has evolved most frequently in insects in association with flight (e.g. Bartholomew, 1981). It is to this use that we refer in this paper. Endothermic insects do not maintain elevated body temperatures at all times, and are thus heterotherms. Elevated body temperatures are often achieved partly by behavioural means in many endothermic insects (Casey, 1981*b*), but in the absence of alternative heat sources (e.g. solar radiation) each period of activity dependent on elevated body temperatures must be preceded by metabolic warm-up using the thoracic flight muscles (Josephson, 1981). We investigate the importance of both body mass and the ambient temperatures that the species experiences while it is active (or 'thermal regime') in determining warm-up rates and the levels of sustained thoracic temperatures within a single taxon – the bees (Hymenoptera: Apoidea).

Warm-up rates are determined by the balance between heat generation and loss. These two factors are differentially affected by changes in body mass. In all endothermic insects investigated, warm-up is thought to be achieved by rapid, simultaneous contractions of opposing sets of thoracic flight muscles, a process commonly referred to as shivering, or by substrate cycling by a pair of enzymes (Newsholme & Crabtree, 1973; Surholt & Newsholme, 1981). If thermogenic power output per unit mass of thoracic muscle is constant, and the mass of the thoracic musculature is a constant proportion of total body mass, then total thermogenic power output is a linear function of body mass.

If heat loss occurs mainly by convection over the animal's surface, then, since for a given body form surface area to volume ratios increase with decreasing size, specific rates of heat loss (measured in terms of conductance: joules per unit time per degree celsius above ambient temperature per unit body mass) increase with decreasing body mass. The negative correlation between conductance and body mass is well known for both vertebrate (McNab, 1970; Bradley & Deavers, 1980; Bartholomew, 1981) and insect endotherms (Bartholomew & Epting, 1975; May, 1976; Bartholomew, 1981).

The relationship between warm-up rate and body mass will be determined by the relative strengths of these two relationships. Among heterothermic vertebrates, metabolic rates per unit mass of tissue are not constant, but increase with decreasing body mass (Bartholomew, 1981). The greater thermogenic ability per unit mass of the smaller heterothermic vertebrates more than compensates for their higher rates of heat loss. Thus, for vertebrate heterotherms undergoing daily torpor, the relationship between body mass and warm-up rate is a highly significant negative correlation (Bartholomew, 1981), smaller endotherms warming more rapidly than large ones. Although warm-up rates for endothermic insects are compatible with an extension of the relationship for vertebrates to lower body masses (Heinrich & Bartholomew, 1971; Bartholomew, 1981), the form of the relationship within the insects remains uncertain. Some studies suggest that these two variables are not simply related (Heinrich & Bartholomew, 1971; Heinrich & Casey, 1973; Bartholomew & Epting, 1975; Dyer & Seeley, 1987), while other studies have found a positive correlation between the two (May, 1976; Morgan &

Heinrich, 1987). May (1976) and Bartholomew (1981) have suggested that, in the size range of endothermic insects, rate of heat loss will be the most important factor determining warm-up rates. If this is so, then larger insects, with lower surface area to volume ratios, should be able to warm up more rapidly and to sustain a higher temperature excess at a given ambient temperature. This assumes that, within the sample of species compared, heat loss is dependent simply on surface area and is not differentially modified between species by, for example, pubescence. It also assumes that, mass for mass, the thermogenic abilities of the tissues concerned are the same for the species compared, although there is some indication that these are relatively greater in smaller species (May, 1976; Bartholomew, 1981). Perhaps most importantly, it assumes that these purely physical characteristics are limiting for insect warm-up.

Although there are several interspecific comparisons of thoracic temperatures in flight in endothermic insects, no general conclusions on the importance of body mass have been established (see Discussion). The roles of several other factors in determining body temperatures independent of body mass have been investigated, particularly wing loading (Bartholomew & Heinrich, 1973; Bartholomew & Epting, 1975; Bartholomew & Casey, 1978; Casey, 1981a; Casey *et al.* 1981). In bees, wing loading is generally very high and we have assumed that the role of wing loading in determining differences in flight temperatures between species is relatively small in comparison to the roles of body mass and thermal environment (see below) (Bartholomew & Heinrich, 1973). It is, however, important to realise that, once the factors we investigate here have been controlled for, wing loading is likely to prove a further useful factor in the prediction of warm-up rates and body temperatures. Such an additional analysis is beyond the scope of this paper.

Although there is a considerable and growing literature on the effects of climate on body temperature in vertebrate endotherms (e.g. Chappell, 1980; Chappell & Bartholomew, 1981), we know of no study that has incorporated the effects of both body mass and the thermal regime to which the species is adapted on warm-up rates and body temperatures in insects. Such studies are hindered by the biased taxonomic distribution of previous studies, which focus on a few insect orders, and on a few families within these orders (see below). In this paper we present a comparative investigation of endothermy in a single insect group – the bees. In the past, interest has focused on particular families within this superfamily, particularly bumblebees of the genus *Bombus* (e.g. Heinrich, 1972a,b,c,d, 1974; Heinrich & Heinrich, 1983), the honeybee *Apis mellifera* (e.g. Heinrich, 1979; Cooper *et al.* 1985; Dyer & Seeley, 1987) and euglossine ‘orchid bees’ (May & Casey, 1983) in the family Apidae, and the large carpenter bees of the genus *Xylocopa* in the family Anthophoridae (e.g. Louw & Nicolson, 1983; Nicolson & Louw, 1982; Chappell, 1982; Baird, 1986; Heinrich & Buchmann, 1986; Willmer, 1988). We present new data on 28 species, and use published data for a further 27 species; Apidae (23 species), Anthophoridae (14 species), Megachilidae (10 species), Andrenidae (3 species), Colletidae (2 species) and Halictidae (3 species).

The interspecific relationships between body mass, body temperature in flight,

warm-up rate, and the thermal regime in which the bee is found and to which it is assumed to be adapted are examined. These relationships are considered intraspecifically for the solitary bee *Anthophora plumipes* (Anthophoridae). The hypothesis that in heterotherms as small as insects warm-up rate should increase with increasing body mass (May, 1976; Bartholomew, 1981) is tested.

Materials and methods

Thermal regime

It is impossible to use a single value to describe the average thermal conditions under which a species is active, and any value used will necessarily be an approximation open to criticism. An ideal measure would be similar to the standard operative temperature (T_{es}) used by Bakken (1976), Chappell (e.g. 1982) and others, which integrates the effects of air temperature (T_a), convection and radiation on body temperature, and would be integrated over the period during which the species is active. Although attractive, such a measure is probably impracticable. What interests us here are the differences between bees active in warmer or colder thermal regimes. One limit to a bee's endothermic ability can be estimated by the minimum temperature at which it is able to forage. Ideally, again we should use T_{es} minima, but in this study we use minimum air temperatures (MTA) as an approximation. In tropical or subtropical species with warm thermal regimes minimum air temperatures for foraging are generally encountered in the morning or evening. Minimum air temperatures for foraging in species active in low-temperature regimes may be obtained during sunny periods on cold days. Under such conditions the error between T_a and T_{es} would be more important for bees in cool than in warm thermal regimes (see Chappell & Bartholomew, 1981). For species for which we have collected data, MTA values are given for overcast days. When using data from published studies we have used the minimum quoted air temperatures at which foraging was recorded. Clearly the use of such data is far from ideal, but we feel that the strength of the resulting relationships justifies this approximation.

Laboratory investigations of warm-up rates

Bees used in experiments were captured and cooled to about 10°C before being restrained in a styrofoam-padded vice on a cooled steel stage. A hole was made mid-dorsally in the thorax with a tungsten needle mounted in a micromanipulator, so that the depth of penetration of the needle could be precisely controlled. A constantan-steel thermocouple with an external diameter of 0.2 mm, also mounted in a micromanipulator, was inserted 1 mm into larger species, and as shallowly as possible in smaller species so as to minimize damage to internal structures. For the smallest bees investigated (less than 75 mg, including *La. glossum smeathmanellum* Halictidae, 10 mg) we used a finer copper-constantan

couple (diameter 0.1 mm). We are aware of the potential of errors due to heat loss from the bees down the sensor wires, and give a simple treatment of the probable magnitude of these errors in the Appendix. Our assumption is that the errors involved are small, and do not seriously or systematically affect our data or analysis. In any measurements of insect body temperatures it is necessary to make an unavoidable compromise between two types of error. Measurement error, associated with the insertion of the thermocouple, is reduced by deep insertion into the thorax. A second error, which we might term physiological and behavioural error, stems from disturbance to the bee's normal behaviour and patterns of endothermy by damage to the tissues associated with insertion. It is our experience that the deeper the thermocouple is inserted, the more 'distressed' the bee becomes. Warm-ups become partial and disturbed, the bee making frequent attempts to pull itself free from the thermocouple, and rarely resting. Deep insertion frequently leads to slow death on release from the thermocouple. Warm-up rates and sustained thoracic temperatures recorded are higher, more uniform and easier to reproduce when measured using shallow insertion. This result is not predicted if errors of measurement determine our recordings, and we believe that physiological and behavioural errors are very important factors that should be minimized within the limits imposed by measurement. No bee was retained on the thermocouple for longer than 1 h, and all were released alive and seen to fly away. Data for any bees clearly harmed by insertion of the thermocouple were discarded. This procedure has proved sufficiently 'gentle' to allow warm-up rates in one recaptured bee (a marked male *Anthophora plumipes*, body mass 165 mg) to be examined three times over the period of a month. It is similar to those used by the other workers whose results we have cited.

The thermal conductivity of the thoracic tissue is at least 10–20 times that of the surrounding air. The thorax is almost completely occupied by the flight muscles, and thermogenesis is thought to occur throughout these tissues. The thoracic volume is small, and insulated by the cuticle, the head and abdomen and, in many cases, also by pubescence. It is unlikely, for these reasons, that there is a significant temperature gradient within the tissues of the thorax. We therefore assume that most of the temperature gradient between these endotherms and their environment exists at the body surface, so that shallow body temperatures can be replaced by core temperatures with little error. In the bees in this study, the thermocouple was inserted to a depth 5–7 times its diameter. For the reasons described above, deeper insertion was avoided. The thermocouple was secured to the dorsum of the thorax using a minimal amount of adhesive (Copydex, Unibond-Copydex Ltd, UK), which held the bee securely enough to allow the thermocouple to be the bees' sole support during tethered flight in even the largest species examined.

After the adhesive had hardened, the bee was released from the clamp and allowed to warm passively to room temperature before the experiment commenced. During warm-up, thoracic temperatures were recorded continuously using a thermocouple thermometer (P.I.8013, Portec Instruments, UK) and a

chart recorder (L6512, Linseis, West Germany). Bees often initiated warm-up without stimulation, but in some cases gentle tapping with forceps was necessary. Bees were given a small piece of styrofoam to grip in their tarsi to prevent flight attempts before warm-up was completed. Typically, bees warmed to a thoracic temperature at which the styrofoam was dropped and tethered flight initiated. As soon as wing movement ceased, the styrofoam was reintroduced to the bee's tarsi. Usually the bee then cooled to room temperature before attempting a further warm-up.

All the laboratory data we present here were obtained at an ambient temperature of 20–22°C in still air in the absence of any source of radiant heat. This choice of ambient temperature allows incorporation of data from several other studies. A major point in the subsequent analysis is that such an arbitrary standard temperature for comparison disregards interspecific differences in both the temperature range the bees are 'used to', and in the minimum thoracic temperatures required for flight. The thermal regime to which the bee is adapted is incorporated in our measurement of MTA (see above). When comparing the abilities of different species to fly at low ambient temperatures (T_a), it is important to consider the minimum thoracic temperature necessary for flight. This determines the minimum temperature excess the bee must generate over ambient temperatures, and is thus an important determinant of the energetic cost of warm-up. An absolute value is not easy to obtain. Thoracic temperatures at which bees cease to fly in the field are probably greater than the minima at which they will initiate tethered or free flight in the laboratory with sufficient provocation. Minimum thoracic temperatures for flight are important in the energetics of warm-up and we therefore need to know about them in order to relate the endothermic ability of a species to its environment. At present there is insufficient methodologically compatible data to allow a comparative analysis. However, a preliminary analysis of other variables is nonetheless revealing.

Definitions of terms

Mean warm-up rate (MWR). At a given air temperature, warm-up rates may depend on thoracic temperature, particularly at low ambient temperatures. In such cases, body temperature often rises exponentially with time, warm-up rate increasing with increasing body temperature. At an air temperature of 20–22°C, warm-up rates in many of the species we examined were independent of thoracic temperature, thoracic temperature increasing linearly with time. In some species, warm-up rate did increase with increasing thoracic temperatures. For such bees, we calculated linear approximations to 3°C sections of the warm-up curve and calculated the mean of these rates. Each bee used in our analysis performed several warm-ups, and where warm-ups were not simply linear we took care to ensure that measured warm-up rates were not biased to relatively low or relatively high thoracic temperatures. We assume that our measurements of average warm-up rate have not been seriously or systematically biased by differences between

species in the form of the warm-up curve. This is not to say that the form of the warm-up curves is unimportant, simply that while warm-up rate may depend on thoracic temperature, we are testing whether it depends also on body mass and thermal regime. Within each species, each bee contributes several warm-up rate data. Thus the potential error due to an unusual first warm-up after implantation of the thermocouple is reduced. Mean warm-up rates given for a particular species are the means of all the warm-ups for all the members of a particular species over a temperature range of 3°C or more.

Peak warm-up rate (PWR). This is the highest rate maintained over a 5°C temperature interval for the species.

Warm-up rates given in the literature, unless referred to as peak rates, are assumed to be mean rates. In two cases where warm-up rates have not been quoted, but figures showing a typical warm-up are presented, approximate rates have been calculated from the figure.

Field analyses of thoracic temperatures

We give data for thoracic temperatures of flying bees at ambient temperatures of 20–22°C. These were obtained using a standard ‘grab-and-stab’ technique, with a copper–constantan thermocouple mounted inside a hypodermic needle. While inserting the thermocouple, bees were not held, but restrained in the net against a flat styrofoam block. The process was carried out in the shade, and took a maximum of 5 s. In species for which 20–22°C lies at the lower limit of the ambient temperature range in which they were active, emphasis was put on sampling as many bees as possible within this temperature range. Where 20–22°C lies in the middle of the T_a range over which a species was active, an average thoracic temperature (T_{th}) was estimated either from data taken in the required T_a range or by extrapolation from a plot of T_{th} on T_a . In each case the number of values in the required ambient temperature range is given in parentheses in Table 1. Results from other studies are thoracic temperatures quoted for the temperature range 20–22°C, or mean values estimated from figures of thoracic temperature as a function of T_a , or values calculated from best-fit regression equations to the same figure. We recognize that there will be some variation in precisely what an ambient temperature of 22°C means – whether this is in the presence or absence of direct sunlight, for example, or of moving air. We assume, however, that such variation merely constitutes noise, and is unlikely to bias any statistical tests systematically. The errors involved in comparing grab-and-stab data between species where T_{es} data are not available will be to some extent paralleled by errors in the MTA data. Thus, when examining the relationship between body temperature and body mass, MTA can be used as an approximate control for the errors in grab-and-stab data. We assume that the errors associated with grab-and-stab measurement of thoracic temperature are small (Stone & Willmer, 1989) and independent of investigator, body mass and taxonomy.

For each species we present data for females, which are relatively long-lived and

feed on similar nectar diets. In the cases of *Bombus edwardsii* we use separate data for workers and for queens.

Statistical methods

Several studies have mentioned the considerable variation in warm-up rates in endothermic insects of similar body masses (e.g. May, 1976; Casey *et al.* 1981; Bartholomew, 1981), even among closely related species (Bartholomew, 1981). Warm-up rate and body temperature will be affected by factors other than body mass, and the relationships between warm-up rates and these other factors may well vary among taxa. When making interspecific comparisons of this type there is a clear risk of generating spurious across-species patterns due to differences between taxa that are independent of the variables being examined.

Several methods have been used to minimize such taxonomic artefacts (see Pagel & Harvey, 1988, for a recent review). Covariance in characters of fundamental biological importance within species, and the resulting interspecific relationships between these characters, should have arisen many times during the course of evolution (Ridley, 1983; Felsenstein, 1985; Huey, 1987; Pagel & Harvey, 1988). Thus among daughter taxa (families, genera, species) evolving from a single common ancestor in a higher taxon (order, family, genus), biologically important patterns should be repeated.

The statistical analysis used in this study is phylogenetic regression, developed by Grafen (1989), which uses multiple regression to analyse correlations between variables among all the daughter taxa of a higher taxon for all the higher taxa in a phylogeny. In this respect, phylogenetic regression is very similar to a model proposed by Felsenstein (1985). The relationships between the variables in each radiation from a higher taxon [rather than across all species as in a 'naive' (Grafen, 1989) interspecific analysis] become data points in the analysis. Each intra-taxon comparison is independent of the others because each taxon has only a single common ancestor, and an interspecific difference leading to the relationship in question has to re-evolve in each taxon. It is not necessary to know the exact phylogeny to use this analytical method. All that is necessary is that none of the groups used is polyphyletic. All the species within a genus are assumed to form a monophyletic group, and the same is assumed for genera within families and families within the superfamily. The degrees of freedom for the F ratios in the text are given by the number of within-taxon analyses contributing to the phylogenetic regression. In our analysis, Grafen's method has several advantages over alternative approaches (Pagel & Harvey, 1988). It allows maximal use of a limited data set, can control and test for as many variables as required, and does not require precise knowledge of the true binary phylogeny of the species concerned. To allow comparison with existing studies, we include 'naive' (Grafen, 1989), simple and multiple regression analyses where useful. When illustrating in multiple regression analyses the significance of one x variable having controlled for another, we plot the residuals of the y variable after simple regression on the first (controlled) variable as a function of the second (test) x variable. When

preliminary analysis indicates a logarithmic relationship between two variables, we have used logarithmically transformed data. Complete data sets are not available for all the species discussed here, leading to different sample sizes for each analysis.

When there is more than one source for a species, as for *A. mellifera*, we have used mean values among the various studies. This by no means implies that we are ignoring legitimate variations within a species. Our assumption, implicit in all interspecific comparisons, is that the intraspecific variation is considerably less than the interspecific variation.

Study sites

Data for *Anthophora plumipes*, *Anthophora quadrimaculata*, *Melecta albifrons*, *Andrena nigroaenea*, *Osmia rufa*, *Osmia laiana*, *Megachile willoughbiella*, *Megachile centuncularis*, *Colletes daviesanus*, *Lasioglossum smeathmanellum*, *Bombus terrestris*, *B. pascuorum*, *B. lapidarius* and *Psithyrus vestalis* were collected at Oxford between March and October 1988. Data for *Andrena clarkella*, *A. fulva* and *Colletes cunicularius* were collected at the Bee Research Unit, University College, Cardiff in April 1988. Data for *Creightonella frontalis*, *Xylocopa (Koptortosoma) spp.*, *Amegilla sapiens*, *Thyreus quadrimaculatus*, *Coelioxys spp.*, two *Megachile spp.*, and *Nomia spp.* were gathered while working at the Christensen Research Institute, Madang, Papua New Guinea in September and October 1987. Data for *Eucera spp. nov.* and *Chalicodoma sicula* and *C. montenigrense* were collected in the Mount Carmel region of Israel in 1986. The names used for the bumblebees in Table 1 are *sensu* Kloet & Hincks (1978) for the European species, and *sensu* Krombein *et al.* (1979) for the north American species.

Results

Mean warm-up rate

Fig. 1 shows the relationship between untransformed warm-up rate and body mass data. 'Naive' cross-species analysis reveals no significant correlation between $\log(\text{MWR})$ and $\log(\text{body mass})$ (Fig. 2A). A major contributing factor to the absence of any overall correlation is the fact that most of the larger bees active in warmer thermal regimes (e.g. *Xylocopa sp.*) have much lower warm-up rates than smaller species (e.g. *Osmia rufa*, see Table 1) adapted to cooler climates. Across all species there is a highly significant negative correlation between $\log(\text{MWR})$ and MTA (minimum ambient temperature for activity) ($N=28$, $r=-0.6$, $P<0.001$; Fig. 2B). 'Naive' multiple regression shows MTA to correlate negatively and significantly with $\log(\text{MWR})$ after controlling for $\log(\text{body mass})$ ($N=28$, $P<0.001$), while mass gives an insignificant positive correlation ($P=0.13$) having controlled for the effect of MTA (Figs 2C,D). Phylogenetic regression reveals that each of $\log(\text{body mass})$ ($F_{1,7}=8.65$, $P<0.025$, positive correlation) and MTA ($F_{1,7}=21.76$, $P<0.005$, negative correlation) correlate

Table 1. Summary of data for body mass, mean warm-up rate, thoracic temperature in flight and MTA

Species	Mean mass (g)	Mean warm-up rate ($^{\circ}\text{C min}^{-1}$)	Peak warm-up rate ($^{\circ}\text{C min}^{-1}$)	T_{th} at 22°C ($^{\circ}\text{C}$)	Minimum T_{a} for flight ($^{\circ}\text{C}$)	Source
APIDAE						
<i>Apis m. mellifera</i> L.	89 (7)	4.8 (34)	9.3	32.5	4.8	This paper
<i>Apis m. mellifera</i> L.	92.7			38	7	Heinrich (1979)
<i>Apis m. mellifera</i> L.	100.8			36	12	Cooper <i>et al.</i> (1985)
<i>Apis m. adansonii</i> Latreille	60.8				7	Heinrich (1979)
<i>Bombus lapidarius</i> (L.)	136 (12)	6.1 (83)	10.7		4	This paper
<i>B. pascuorum</i> (Scop.)	123 (8)	5.45 (64)	8.33		3	This paper
<i>B. terrestris</i> (L.)	250 (8)	8.8 (47)	12.5	40	2	Heinrich (1972c,d, 1975), Heinrich & Heinrich (1983)
<i>B. vosnesenskii</i> Rad. (queen)	550	12.3			2.5	Heinrich (1972c,d, 1975), Heinrich & Heinrich (1983)
<i>B. edwardsii</i> Cresson (queen)	400			42	2.5	Heinrich (1972c,d, 1975), Heinrich & Heinrich (1983)
<i>B. edwardsii</i> Cresson	120			37.5	2.5	Heinrich (1972c,d, 1975), Heinrich & Heinrich (1983)
<i>B. vagans</i> Smith	120			33	5	Heinrich (1972a), Heinrich & Heinrich (1983)
<i>B. terricola</i> Kirby	150			36.5	5	Heinrich (1972b), Heinrich & Heinrich (1983)
<i>Psithyrus vestalis</i> (Geoffroy)	195 (4)	6.3 (28)	9.6			This paper
<i>Euglossa variabilis</i> Friese	95	5.7			22.5	May (1976)
<i>E. igniventris</i> Friese	102	4.8				May (1976)
<i>E. imperialis</i> Cockerell	160	7		34.4	22.5	May (1976), May & Casey (1983)
<i>E. saphirina</i> Moure	70			32.3		May & Casey (1983)
<i>E. tridentata</i> Moure	110			35.5		May & Casey (1983)
<i>Exaerete smaragdina</i> (Guerin)	383	4.8			19	May (1976), May & Casey (1983)
<i>Exaerete frontalis</i> (Guerin)	680	6.2			19	May (1976), May & Casey (1983)
<i>Eulaema nigrita</i> Lep.	420	5.8			19	May (1976), May & Casey (1983)
<i>Eulaema meriana</i> (Olivier)	880	7			19	May (1976), May & Casey (1983)
<i>Eufriesia pulchra</i> (Smith)	460	7			19	May (1976), May & Casey (1983)
<i>Euplusia schmidtiana</i> (Friese)	460	6.9			19	May (1976)
ANTHOPHORIDAE						
<i>Xylocopa capitata</i> Smith	1300	4.5		37	23	Louw & Nicolson (1983), Nicolson & Louw (1982)

<i>X. californica</i> Cresson	590				40	12.5	Chappell (1982)
<i>X. virginica</i> L.	510				41	15	Baird (1986)
<i>X. varipuncta</i> Patton	673	2.25			37	12	Heinrich & Buchmann (1986)
<i>X. pubescens</i> (Spinola)	640	4.2			36	14	Willmer (1988)
<i>X. sulcatipes</i> Maa	420	3.2			34	19	Willmer (1988)
<i>Xylocopa (Koptortosoma)</i> spp.	260 (10)				38.6 (11)	16	This paper
<i>Centris pallida</i> Fox	197				39	25	Chappell (1984)
<i>Amegilla sapiens</i> (Cockerell)	117 (38)	3.75 (19)		6.5	33 (11)	18	This paper, Stone <i>et al.</i> (1988)
<i>Anthophora plumipes</i> (Pallas)	185 (32)	12.3 (136)		19.6	36.4 (24)	0.5	This paper
<i>A. quadrimaculata</i> (Panz)	90 (3)	5.1 (10)		7.0			This paper
<i>Thyreus quadrimaculatus</i> (Rad.)	100 (14)	1.75 (6)		2.1	28 (7)	26	This paper
<i>Melecta albifrons</i> (Fab.)	110 (6)	5.35 (55)		10.7		12	This paper
<i>Eucera</i> spp. nov. (teste Baker)	75 (6)	3.5 (6)			27.6 (8)	18	This paper
MEGACHILIDAE							
<i>Creightonella frontalis</i> (Fab.)	305 (59)	5.8 (29)		9	33 (10)	20	This paper
<i>Megachile</i> spp.	87 (14)				32.5 (9)		This paper
<i>Megachile</i> spp.	125 (8)				34 (8)		This paper
<i>Megachile willoughbiella</i> (Kirby)	121 (8)	6.3 (16)		10.4		16	This paper
<i>Megachile centuncularis</i> (L.)	64 (4)	3.7 (15)					This paper
<i>Coelioxys</i> spp.	90 (4)	1 (9)		1.4		26	This paper
<i>Osmia rufa</i> (L.)	85 (5)	10.5 (20)		12.2	33.5 (8)	5	This paper
<i>Osmia leatiana</i> (Kirby)	55 (6)	4.1 (10)					This paper
<i>Chalicodoma sicula</i> (Rossi)	190	4.2			32	17	Willmer (1986)
<i>C. montenigrense</i> (Dours)	128 (4)				28.9 (4)		This paper
ANDRENIDAE							
<i>Andrena clarkella</i> (Kirby)	85 (4)	6.2 (38)		7.7		8	This paper
<i>Andrena fulva</i> (Mulleer in Allioni)	81 (6)	4 (39)		6		12	This paper
<i>Andrena nigroaenea</i> (Kirby)	108 (4)	6.95 (21)		10.5		9	This paper
COLLETIDAE							
<i>Colletes cunicularius</i> (L.)	112 (8)	7.35 (121)		13.5		10	This paper
<i>Colletes daviesanus</i> Smith	36 (4)	3.8 (16)		6.0			This paper
HALICTIDAE							
<i>Nonia</i> spp.	43 (10)				28.5 (7)	20	This paper
<i>Nonia</i> spp.	45 (10)				30 (9)	20	This paper
<i>Lastiglossum smeathmanellum</i> Kirby	10 (4)	1.25 (12)		2.33			This paper

T_{th} , thoracic temperature; T_a , ambient temperature.

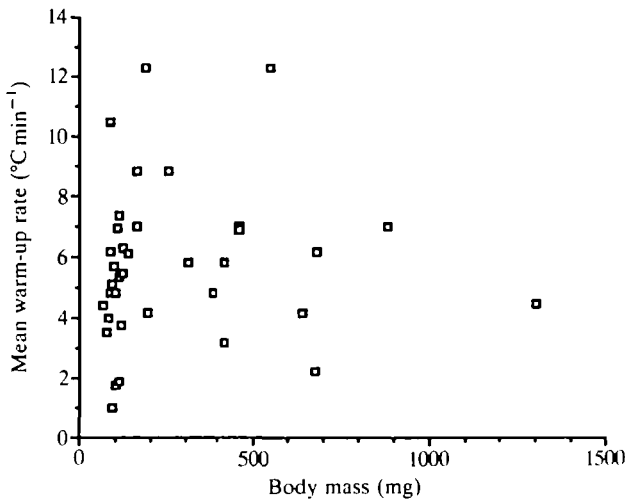


Fig. 1. Mean warm-up rate as a function of body mass.

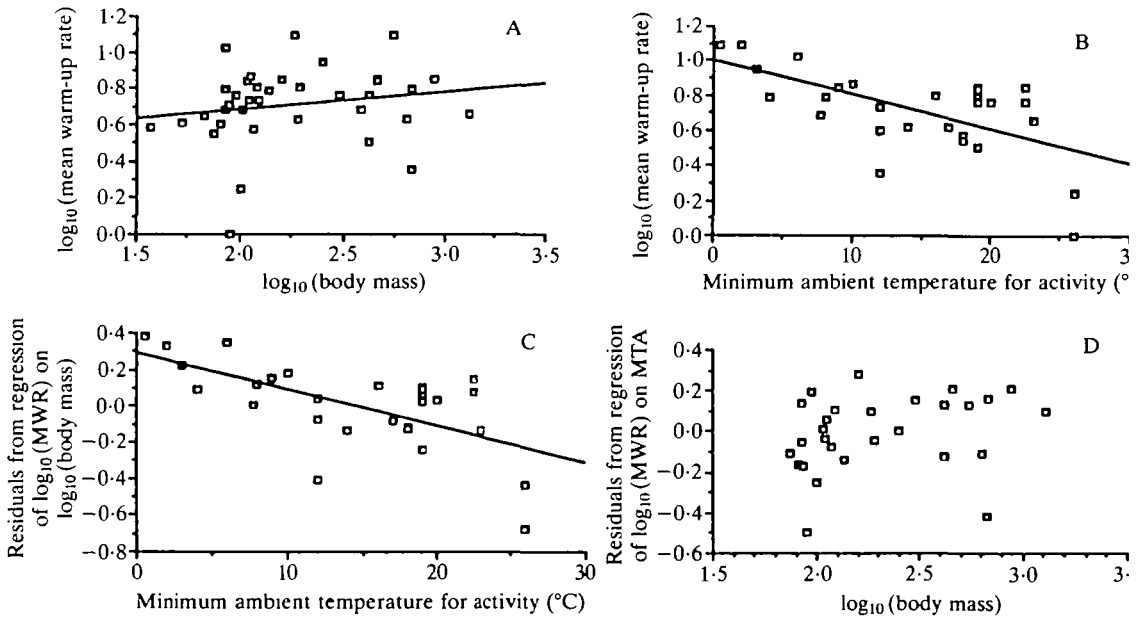


Fig. 2. (A) $\log(\text{mean warm-up rate})$ as a function of $\log(\text{body size})$ for all species ($y = 0.49 + 0.1x$; $r = 0.18$, $N = 36$, $P > 0.05$). (B) $\log(\text{mean warm-up rate})$ as a function of minimum ambient temperature for activity (MTA) for all species. (C) Residuals from regression of $\log(\text{mean warm-up rate})$ on $\log(\text{body mass})$ as a function of MTA for all species ($y = 0.3 - 0.02x$; $r = 0.63$, $N = 28$; $P < 0.001$). (D) Residuals from regression of $\log(\text{mean warm-up rate})$ on MTA as a function of $\log(\text{body mass})$ for all species.

significantly with $\log(\text{MWR})$ when the effect of the other is controlled for. The absence of an overall significant correlation between body mass and warm-up rate is thus, at least in part, due to differences in the form of the relationship between taxa. 'Naive' multiple regression shows $\log(\text{body mass})$, MTA and the interaction between the two to be significantly correlated with $\log(\text{MWR})$ in the Apidae [$N = 13$, $\log(\text{body mass}) P < 0.001$, MTA $P = 0.002$, interaction $P = 0.001$] and the Anthophoridae [$N = 11$, $\log(\text{body mass}) P = 0.01$, MTA $P = 0.005$, interaction $P = 0.01$]. This clearly shows the necessity of controlling for taxonomic effects in the overall interspecific analysis. The strong positive correlation between $\log(\text{MWR})$ and $\log(\text{body mass})$ in female *Anthophora plumipes* (mass range 140–220 mg) (Fig. 3), where MTA differences among individuals are small, illustrates the importance of body mass within this species ($N = 28$, $r = 0.56$, $P = 0.002$).

It is noteworthy that some of the warm-up rates for species adapted to cool conditions are very high. *Osmia rufa* has a high MWR of $10.5^\circ\text{C min}^{-1}$, with a peak rate of $12.2^\circ\text{C min}^{-1}$, while female *A. plumipes* have a very high mean rate of $12^\circ\text{C min}^{-1}$ and a peak rate of $18\text{--}19^\circ\text{C min}^{-1}$, the highest warm-up rate reported to date by a considerable margin. The smallest bee examined in this study was *Lasioglossum smeathmanellum* (Halictidae), with a body mass of about 10 mg. Although the errors involved in accurately determining warm-up rates in a species this small are assumed to prohibit the use of data for it in the analyses in this paper, despite having no apparent ability to maintain an elevated temperature during tethered flight, this species nevertheless elevated $T_{\text{th}} 2\text{--}3^\circ\text{C}$ above T_{a} before flight.

Females are forced to forage during less than optimal conditions if they are to minimize the time for which their cells are open to parasitism (Willmer, 1985a,b). Kleptoparasitic species, however, are freed from the need to forage and provision

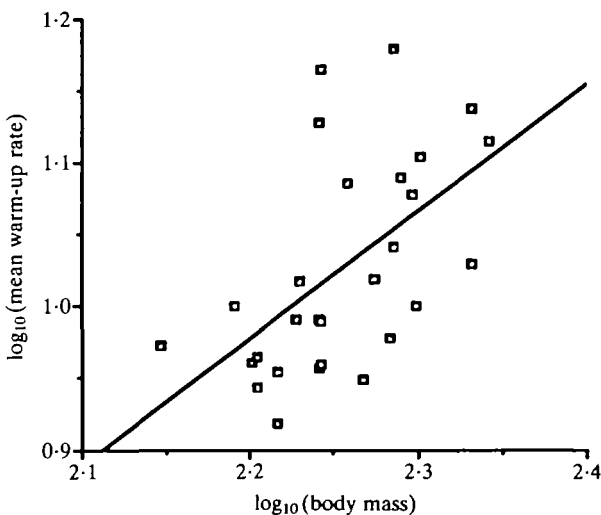


Fig. 3. $\log(\text{mean warm-up rate})$ as a function of $\log(\text{body mass})$ for female *Anthophora plumipes*.

cells during less than optimal climatic conditions, and we predict that these species should have lower warm-up rates for their mass and a higher MTA than females of provisioning species. Certainly the kleptoparasitic species in our data set (*Psithyrus*, Apidae; *Melecta* and *Thyreus*, Anthophoridae; *Coelioxys*, Megachilidae) all have low warm-up rates for their body mass. We have insufficient data to allow a conclusion on this point. A similar point could be made about males, although here the complication of the wide diversity of mating systems shown by bees precludes general predictions. There are very few data available concerning intraspecific male–female differences in endothermic physiology.

Thoracic temperatures during activity at 22°C

Fig. 4 shows the relationship between untransformed data for thoracic temperatures in flight and body mass. ‘Naive’ regression reveals a significant positive correlation between log (thoracic temperature at 22°C) and log (body mass) over the whole data set ($N = 34$, $r = 0.59$, $P < 0.001$ Fig. 5B), and a negative correlation with MTA ($N = 28$, $r = -0.43$, $P = 0.02$ Fig. 5A). ‘Naive’ multiple regression shows that each correlates significantly with log (thoracic temperature) when the other is controlled for [MTA: $P = 0.02$; log (body mass): $P = 0.001$ Fig. 5C,D). Controlling for taxonomic effects using phylogenetic regression confirms these results [MTA: $F_{1,7} = 13.8$, $P < 0.05$; log (body mass): $F_{1,7} = 7.19$, $P < 0.01$]. There is no significant interaction. Thus, for bees with a given minimum ambient temperature for activity, thoracic temperature in flight increases with mass. More tentatively (bearing in mind possible errors in MTA), for bees of a given body mass, those able to forage at lower air temperatures have higher thoracic temperatures at 22°C.

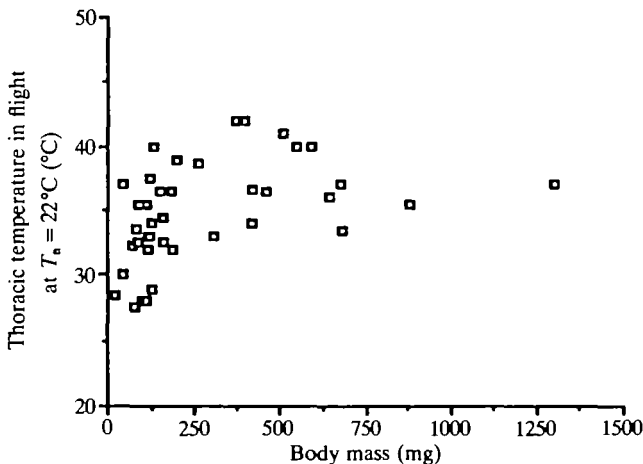


Fig. 4. Thoracic temperature in flight at 22°C as a function of body mass.

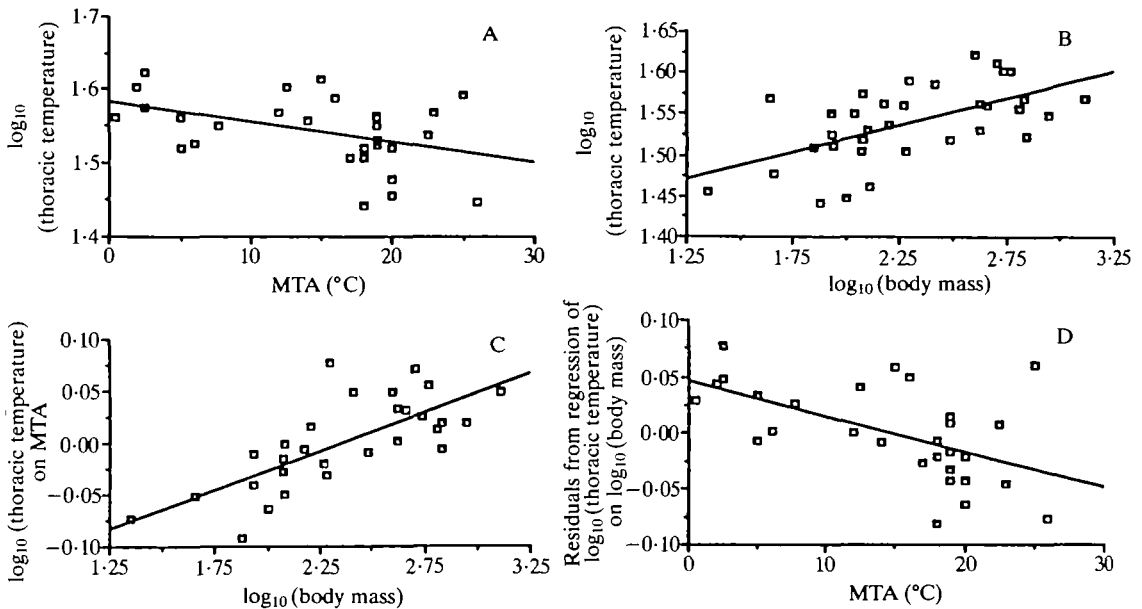


Fig. 5. (A) \log_{10} (thoracic temperature in flight at 22°C) as a function of MTA for all species. (B) \log_{10} (thoracic temperature in flight at 22°C) as a function of \log_{10} (body mass) for all species. (C) Residuals from regression of \log_{10} (thoracic temperature in flight at 22°C) on MTA as a function of \log_{10} (body mass) for all species ($y = -0.177 + 0.075x$; $r = 0.73$, $N = 29$, $P < 0.001$). (D) Residuals from regression of \log_{10} (thoracic temperature in flight at 22°C) on \log_{10} (body mass) as a function of MTA for all species ($y = 0.046 - 0.003x$; $r = 0.56$, $N = 27$, $P < 0.001$).

Discussion

Warm-up rate

There is no obvious simple relationship between body mass and mean warm-up rate. It is only when the variation in mean warm-up rates due to thermal regime and phylogeny is controlled for, using phylogenetic regression, that the relationship between body mass and MWR becomes clear. Furthermore, MTA and phylogeny are each important predictors of warm-up rate once other factors have been controlled for. The form of the relationship between body mass and warm-up rate within the Apoidea thus supports the predictions of May (1976) and Bartholomew (1981): it does seem to be true that, for the body mass range examined in this investigation, heat loss and surface area to volume ratios are important predictors (and probably major determinants) of warm-up rate. Thus, although warm-up rates in endothermic insects lie generally within the range predicted by a continuation to lower body masses of the relationship within vertebrate endotherms, the negative correlation between warm-up rate and body mass found for vertebrate heterotherms does not exist within the Apoidea.

The gradient of the best-fit 'naive' regression of \log (MWR) on \log (body mass)

is less than 1 over all species (Fig. 2A). This implies that overall smaller bees have a relatively higher warm-up rate per unit mass than larger bees. This is in accordance with studies by Bartholomew & Casey (1978) and Bartholomew *et al.* (1981) on hovering moths and Chappell (1982) on hovering *Xylocopa californica*, which report that mass-specific oxygen consumption per unit time decreases with increasing body mass, and the statement by May (1976) that heat production per gram body mass is higher in smaller euglossine bees than in larger species. However, it is clear from the scatter in the plot of $\log(\text{MWR})$ on $\log(\text{body mass})$ that mass is not a fundamental constraint across species. The gradient of the relationship between $\log(\text{MWR})$ and $\log(\text{body mass})$ for female *A. plumipes* (0.88 ± 0.26) approaches unity, implying that within a sex within a species endothermic abilities per unit mass may be more or less constant and further suggesting that warm-up rates are a property of the flight machinery of each particular species, and are not determined solely or simply by mass and surface area to volume ratios.

Thermal regime, represented in this analysis by the minimum ambient temperatures at which the species flies in the field, is also of major importance in determining warm-up rates. The importance of behavioural thermoregulatory mechanisms such as basking may differ among species of the same mass active at the same MTA; a bee species with a low metabolic warm-up rate may remain active under conditions favouring species with higher levels of endothermy by virtue of increased levels of basking. Such variation in the role of behavioural thermoregulation will cause noise in the relationship between warm-up rate and MTA which is not considered in this analysis. The results shown here suggest that there is nonetheless a relationship to explain. In thermoregulating endotherms, the temperature excess which must be generated, and thus the total energy expenditure in warm-up, is maximal at the lowest ambient temperatures at which warm-up occurs (e.g. Heinrich, 1975). The total time required for warm-up will also be maximal under these conditions (Bartholomew & Heinrich, 1973; Heinrich, 1975; Casey *et al.* 1981).

Several authors have suggested that the time taken to warm up should be minimized for a number of reasons, including minimizing the time during which the insect is exposed to predators without the ability to escape (Bartholomew & Heinrich, 1973) or the time for which foraging is impossible, and minimising the total energy expenditure associated with the warm-up. Insects which use endothermic flight musculature should therefore have thermogenic ability sufficient to achieve a minimum tolerable warm-up rate at the minimum ambient temperatures at which they fly. Of course, the time taken to complete warm-up depends not only on warm-up rate but also on the temperature excess which must be established. If we assume for the moment that thoracic temperature excesses at take-off are relatively constant across species, then part of the relationship between MWR and MTA shown in this study is explained. Bees adapted to a relatively warm thermal regime have a lower warm-up rate at 22°C than bees adapted to low temperatures, because 22°C is relatively closer to the minimum ambient tempera-

tures to which their thermogenic systems are adapted. This implies that were we to examine warm-up rates across species at the minimum ambient temperatures at which each species flies we would find similar warm-up rates (complicated by taxonomic considerations). It seems probable that were we to control for thermal regime most bees would have similar relationships between warm-up rate and ambient temperature. Certainly it is true that warm-up rates in most species examined to date are dependent on ambient temperature (e.g. Heinrich & Bartholomew, 1971; Bartholomew & Casey, 1973; Heinrich & Casey, 1973; Heinrich, 1975; Casey *et al.* 1981; Heinrich & Buchmann, 1986). Warm-up rates in bees whose MTA values are near 22°C are approximately 4–5°C min⁻¹ (Table 1). At an air temperature of 8°C the MWR for female *Anthophora plumipes* is 5–6°C min⁻¹, rather than the 12.3°C min⁻¹ shown at 22°C. It is probable that warm-up rates will approach 4°C min⁻¹ at $T_a = \text{MTA}$ for this species. Similarly, at ambient temperatures as far above their MTAs as 22°C is for some cold-adapted species, warm-adapted species may show far higher warm-up rates. For example, at an ambient temperature of 32°C (12–14°C above their MTAs) the tropical bees *Amegilla sapiens* (Anthophoridae) and *Creightonella frontalis* (Megachilidae) show mean warm-up rates comparable to those shown by cold-adapted species in this analysis (*A. sapiens*: 6.3 ± 0.8°C min⁻¹, $N = 12$; *C. frontalis*: 8.6 ± 0.3°C min⁻¹, $N = 14$). At 22°C their warm-up rates are much lower (*Amegilla sapiens* 3.75°C min⁻¹; *C. frontalis* 5.8°C min⁻¹).

Assumptions concerning temperature excesses generated at MTA values across species should therefore be modified. In general, among endothermic insects it appears that species capable of flight at very low ambient temperatures generate temperature excesses at their MTA which are larger than those generated by species with higher MTA values (e.g. Heinrich, 1987). For this reason we would predict greater endothermic abilities in cold-adapted species, even near their MTA, than in warm-adapted species, simply because they have further to warm up and can less afford the great inefficiency of slow warm-up for prolonged periods of time (Heinrich, 1987). In bees there is an indication that the temperature excesses which warm-regime bees sustain at their MTAs are relatively low compared with those generated by bees flying at very low ambient temperatures. For example, the 26°C temperature excess maintained at $T_a = 12^\circ\text{C}$ by 1–2 g *Xylocopa varipuncta* (Anthophoridae) from Arizona (Heinrich & Buchmann, 1986) is somewhat less than the 32°C excess maintained at a T_a of 4°C by the queens of *Bombus vosnesenskii* (Apidae) weighing only 0.25–0.6 g (Heinrich, 1975).

It is easy to accept that at the minimum air temperatures at which they are active all bees will have lower warm-up rates than they do at higher T_a . It is also predictable that bees generating high temperature excesses from low ambient temperatures should have low initial warm-up rates, particularly if they are small. It is harder, however, to see why large tropical bees should show such low warm-up rates at the relatively high ambient temperature minima which they experience. It seems certain that large tropical bees such as *Xylocopa* species could have evolved a higher warm-up rate if required, given that close relatives such as

Anthophora plumipes have extremely high warm-up rates. It may be that efficiency in warm-up, in terms of maximizing warm-up rate at low ambient temperatures, has been less of a selective pressure for warm-regime bees. Because of the high air temperatures at which some of these species fly, and the very high thoracic temperatures which are generated in some of the larger species such as *Xylocopa* spp. (e.g. Chappell, 1982; Heinrich & Buchmann, 1986), a more important selective pressure for warm-regime bees must have been tolerance of high ambient and body temperatures. Species capable of warm-up at very low ambient temperatures may become heat stressed at relatively low air temperatures, and thus cannot remain active at high T_a (e.g. Heinrich, 1987): warm-up at very low T_a and activity at high T_a are not compatible. It is possible that a flight system tolerant of extremely high working temperatures in warm-regime bees [up to 48°C in female *Creightonella frontalis* at an ambient temperature of 35–38°C; a similar upper limit has been reported by Chappell (1982) for the desert-living *Xylocopa californica*] is capable of warm-up only at low rates even at relatively high ambient temperatures.

There are two compatible solutions to thermoregulation at low ambient temperatures – an increase in thermogenic ability, and/or a reduction in the minimum tolerated body temperature necessary for the activity concerned. Our analysis suggests that the former has occurred within the Apoidea, and that there is considerable ability to adjust the setting of the ‘thermogenic thermostat’ over evolutionary time in response to environmental conditions. It should be noted that even for species of similar mass and MTA there is variation in warm-up rate and temperature excesses generated. For example, *Osmia rufa* (Megachilidae: mean mass 85 mg, MTA 5°C) at 22°C warms up at a mean rate of 10.5°C min⁻¹ and generates a mean thoracic temperature excess of 13.6°C before take-off at $T_a = 22^\circ\text{C}$, whereas *Andrena clarkella* (Andrenidae: mean mass 85 mg, MTA 8°C) has a much lower mean warm-up rate of 6.2°C min⁻¹ and generates a much lower mean thoracic temperature excess of 4.2°C at take-off. All the *Andrena* species examined here have relatively low warm-up rates, and this not only prompts questions about the evolution of different thermal strategies in bees living under similar conditions but also emphasizes the need for an awareness of phylogeny.

The generally higher warm-up rates in cold-regime bees could be due either to a reduction in conductance or to an increase in metabolic heat generation. The species in our analysis with the lowest MTA values have extremely dense insulating pile (particularly *Bombus* spp., *Anthophora plumipes* and *Osmia rufa*). Since the form and distribution of pubescence tends to be similar in closely related species, an analysis of changes in conductance in response to thermal regime would have to control for taxonomic effects. Other studies have supported the suggestion that it is variation in metabolic heat production, rather than differences in conductance, that causes differences in warm-up rates between different endothermic insects (e.g. Casey *et al.* 1981). It is probable, therefore, that within the Apoidea variation in metabolic rate during warm-up is a major response to differing thermal regimes.

Thoracic temperature in flight

Maintenance of a given thoracic temperature excess during flight at a given ambient temperature becomes relatively more expensive per unit of body mass the smaller you are, other things being equal, owing to an increasing surface area to volume ratio and relatively greater rates of convective heat loss (Bartholomew & Heinrich, 1973). We might expect small endotherms to make concessions to the cost of endothermy by reducing the temperature excess they maintain at a given T_a . This appears to be the case among mammals (McNab, 1970), where sustained body temperatures are a function of body mass up to a 'critical mass' above which body temperature is independent of body mass. Bartholomew & Heinrich (1973) demonstrated a similar non-linear relationship between body mass and thoracic temperatures when moths of several families were considered together. However, analysis of this relationship within families gave significant positive correlations for only two of the six families considered. Thoracic temperatures in flight were found to correlate positively with wing loading in all six families. Thus, the positive correlation between body mass and thoracic temperature found overall and in the two families may be due to inter-family and within family variation in wing loading. The importance of controlling for taxonomic effects is shown by their comment that, although thoracic temperatures correlate with wing loading within a family, species in different families with the same wing loading can have very different thoracic temperatures. Heinrich & Casey (1973) found no significant correlation between body mass and thoracic temperature for sphingid moths of 13 species over the mass range 0.3–3.5 g. Heinrich & Heinrich (1983) report that for workers and queens of a variety of *Bombus* species over the mass range 100–750 mg there was no overall correlation between body mass and thoracic temperature while foraging. Our data reveal a clear positive correlation between body mass and thoracic temperature in flight once the effects of thermal regime and taxonomy have been controlled for. As Bartholomew & Heinrich's study suggested, within the Apoidea the relationship is non-linear, and most pronounced at low body masses. The data presented by Heinrich & Heinrich (1983) showing no correlation between mass and thoracic temperature were gathered over a wide range of ambient temperatures (2.5–22°C). Their data concerned both large queens and smaller workers, and they mention that queens were able to forage at somewhat lower ambient temperatures than workers. This suggests to us that, although at higher ambient temperatures there was indeed no relationship between body mass and thoracic temperature for the species they examined, at ambient temperatures near the lower limit tolerated by workers there may well have been a relationship between the two.

Thoracic temperatures in flight, like warm-up rates, appear to be affected by thermal regime. Having controlled for the effects of body mass and taxonomy, there is a significant negative correlation between thoracic temperature in flight at 22°C and MTA. Bees adapted to cooler regimes fly hotter at a given T_a . Although the nature of our statistic describing thermal regime necessitates caution in making conclusions, clearly the ambient temperatures to which a species is adapted are a

factor that must be considered in comparative analyses. It appears to be true that, as McNab (1970) states for mammals, the levels of regulated body temperatures are capable of some variation independent of conductance and body mass in a manner adaptive to climate. We can now make two important conclusions.

First, body mass correlates positively with (and is probably an important determinant of) both warm-up rates and thoracic temperatures during flight in the Apoidea, confirming the predictions of May (1976) and Bartholomew (1981). Thus, within the Apoidea, although smaller bees show higher warm-up rates (and thus metabolic rates) per unit mass, the strong negative correlation between conductance and body mass negates this effect and leads to slower overall warm-up rates.

Second, it is clear that correlations with body mass alone are insufficient to explain all of the observed variation in warm-up rate and thoracic temperatures in flight between species. Indeed, the relationship between body mass and warm-up rate only becomes apparent when the considerable effects of thermal regime and phylogeny have been controlled for. Species active at lower temperatures have both higher warm-up rates and higher thoracic temperatures in flight.

As Dyer & Seeley (1987) state: 'general scaling relationships based on body mass alone may fail to predict qualitative physiological differences even within a closely related group of species'. This study shows that it is essential to take into account both phylogenetic and ecological differences between the species involved. Warm-up rates appear to have been very susceptible to selective change within the absolute constraints imposed by size. There can be no doubt that warm-up rates have evolved to match physiologically average conditions in which the insect is active. We predict that warm-up rates in kleptoparasitic bees, which are freed from the need to forage during sub-optimal conditions, will be lower than those in related bees of similar mass. When physiological and activity pattern data become available for more male Apoidea an interesting comparative analysis linking endothermic abilities, body size, thermal regime and mating system will be possible. Differences in mating systems among species and higher taxa can be expected to have exerted different selective pressures on the endothermic machinery of males of different species, although we should bear in mind that just as female warm-up rates may be phylogenetically related, so male warm-up rates may be phylogenetically linked to female warm-up rates. Answers to this sort of questions must await more extensive and detailed data.

Appendix

The problem of heat loss to the sensor and along its leads

We are not aware of any discussion of the magnitude of these problems in the published literature, and what follows is an attempt at a very simple 'order of magnitude' investigation of them. The warm-up rate of a bee at any time will be the result of the following: (metabolic heat production) minus (convective and other body surface area heat losses) minus (heat losses *via* sensor and wires). If we

can show that heat losses *via* wires are small compared with other cooling effects, and that losses *via* wires are small compared with the total power generated by the bee's endothermic mechanism, and that, though this error will vary with body mass, its magnitude is insufficient to explain the observed effect, then we can suggest that the observed pattern of increasing warm-up rate with increasing body size among bees of a given thermal regime is not due to such errors.

It is possible to estimate the proportion of the bee's generated power that is required to heat the thermocouple rather than the bee. We can consider this first in terms of heat capacities of bee and sensor, the energy required to heat the bee and thermocouple through the same unit temperature increase. The heat capacity of a body is given by its mass multiplied by its specific heat capacity. The sensor in our experiments consisted of a steel tube 0.2 mm in external diameter through which was threaded a constantan wire <0.1 mm in diameter. Wire and tube were soldered at the tip. For the sake of approximation in a worst-case scenario, we consider the thermocouple to consist of solid steel wire 0.2 mm in diameter. Both the thermal conductivity and the specific heat capacity of this approximation to the thermocouple are thus overestimates. The thermocouple is mounted in a resin block such that 1.0 cm of wire is exposed between the bee and the resin. We consider the resin to be an infinite heat sink at ambient temperature. Returning to heat capacities:

heat capacity of wire = mass \times specific heat capacity of steel ,

$$\text{mass} = \pi r^2 h \times \text{density} = 3 \times 10^{-6} \text{ kg} \quad (\pi = 3, \\ r = 10^{-4} \text{ m}, h = 10^{-2} \text{ m}, \text{density} = 10^4 \text{ kg}^{-3}) ,$$

specific heat capacity of steel = $0.5 \text{ J kg}^{-1} \text{ K}^{-1}$,

heat capacity of wire = $1.5 \times 10^{-6} \text{ J K}^{-1}$.

Consider an isolated bee thorax of mass 100 mg (10^{-4} kg):

specific heat capacity = $3.4 \text{ J kg}^{-1} \text{ K}^{-1}$ (Heinrich, 1975) ,

heat capacity of bee = $3.4 \times 10^{-4} \text{ J K}^{-1}$.

Thus the thermal loading of the thermocouple on a bee of thorax mass 100 mg is negligible. For a bee of thorax mass 25 mg, the heat capacity is $8.5 \times 10^{-5} \text{ J kg}^{-1}$. Thus, even for small bees the heat required to warm the sensor is only 2 % of the heat required to warm the bee. Now we need to consider heat loss by conduction along the wire.

A simple model

Consider the bee as a sphere, suspended by the thermocouple. Heat is evenly distributed throughout the sphere's volume. The physiological impact of thermocouple insertion does not vary with body size, and all bees are equally stressed. The specific heat capacity of all bees is the same at $3.4 \text{ J kg}^{-1} \text{ K}^{-1}$. Because we want to use data for power generated from Heinrich's (1976) work on *Bombus vosnesenskii*, we shall use the same temperature conditions as he gives for his data.

So, we assume that all bees have a 10°C temperature excess over ambient (for *B. vosnesenskii* the figures were thoracic temperature 31°C and ambient temperature 20°C). What we are now considering is the fraction of the total power generated by the bee that is lost down the wires. This requires estimates of the power generated by bees of different masses at this ambient temperature. Here it is necessary to use approximations in the absence of precise data. Heinrich (1976) states that a *B. vosnesenskii* queen maintaining a steady temperature excess under the conditions given above expends energy at a rate of 23 J g⁻¹ min⁻¹, or 400 W kg⁻¹.

Our data show that, even with errors, small bees warm up more rapidly per unit mass than large bees. Thus small bees must generate a higher power per unit mass than larger bees. We have assumed that heat production varies with mass raised to a power between 0.6 and 0.85 (G. A. Bartholomew, personal communication). For the purpose of illustration we take the power to be 0.7. Then mass-specific power outputs are proportional to mass raised to the power -0.3. From this relationship we have calculated mass-specific and total power outputs for hypothetical *Bombus* species with a range of body masses in Table 2. Total outputs for bees of the given thoracic masses are obtained by multiplying the mass-specific power outputs by the mass of the thorax.

The thermocouple

We assume that at the point where the thermocouple wire enters the resin block it is at ambient temperature, so that the gradient from bee temperature (30°C) to ambient temperature (20°C) occurs along the 10 mm of exposed steel. We assume also that the significant heat loss through the wire occurs by conduction along it, and that convective loss from the wire is minimal by comparison. Given the low conductivity of air, the small surface area of exposed wire, the low temperature excess involved, and the absence of forced convection, this is a reasonable assumption. Heat loss *via* the wire (Q_{wire}) in this simplified model is then given by:

$$Q_{\text{wire}} = KAdT/dx ,$$

Table 2. *Power generation per unit mass, total power generated and the proportion of that power lost via the thermocouple for hypothetical Bombus species over a range of body masses*

Thorax mass (kg)	Mass-specific power output (W kg ⁻¹)	Total power generated (W)	% total power lost <i>via</i> sensor
2.5 × 10 ⁻⁵	788	0.020	9
5.0 × 10 ⁻⁵	640	0.032	5.6
7.5 × 10 ⁻⁵	567	0.043	4.2
1.0 × 10 ⁻⁴	519	0.052	3.5
2.0 × 10 ⁻⁴	422	0.084	2.1
2.4 × 10 ⁻⁴ (<i>B. vosnesenskii</i>)	400	0.096	2.0

where K is the conductivity of steel ($60 \text{ W m}^{-2} \text{ K}^{-1}$), A is the cross-sectional area of the wire, and dT/dx is the temperature gradient along it (K m^{-1}). $A = \pi r^2 = 3 \times 10^{-8} \text{ m}^2$; dT/dx is 10 K in $1 \text{ cm} = 1000 \text{ K m}^{-1}$. Thus $Q_{\text{wire}} = 1.8 \times 10^{-3} \text{ W}$, whatever the size of the bee.

Table 2 shows the estimated power generated by bees of given mass using the assumptions given above, and the fraction of this power that is lost along the wire. The proportion of heat generated that is lost down the wires in this simplest model increases with decreasing thorax mass, and at a thoracic mass of 25 mg reaches about 9% of the total heat generated. In the case of the *B. vosnesenskii* being studied by Heinrich (1976), the bee was in thermal equilibrium, and thus the vast majority (97.9% in our model) of the generated heat must have been lost by body surface effects, mostly by convection. The change in the proportion of generated heat that is being converted into a rise in thoracic temperature and being dissipated by other means by our model is from 91% at a thoracic mass of 25 mg to 98% at a thoracic mass of 240 mg. It is unlikely, even if our assumptions are only approximately acceptable, that errors due to heat loss along sensor wires could explain any more than a small proportion of the correlation between warm-up rate and body size. Cooling down sensor wires could, however, become significant at the smallest body sizes we investigated. If data for the smallest bees examined (<50 mg total body mass) are eliminated, the observed relationship between body mass and warm-up rate remains significant. The discovery of endothermy in smaller bees is certainly of interest, and warm-up rates should be presented, but their use in comparative analysis should be suspended until more accurate assessment of the errors involved becomes possible.

We would like to thank Alan Grafen, Paul Harvey, Andrew Read, Mark Pagel, Anne Keymer and Daniel Promislow for all their patient help with the techniques of comparative analysis; George Bartholomew, Peter Miller and Steve Simpson for their constructive criticism of early drafts of the manuscript; and Ron Hill and Charles Ellington for their thermodynamics advice. We thank Mike Dolan, Dick Cheney, Tony Price and Terry Barker for their technical assistance, and Chris O'Toole for his help in identification. GNS would particularly like to thank Dr Robert Paxton for his considerable time and support in Cardiff, Dr Brian Thistleton for the same at Mount Hagen, New Guinea, and Lisa Meredith and Jenny Vernon for everything. The work in New Guinea was made possible by generous support from the Christensen Research Institute, Madang, and from the SERC (GNS). Work in Israel (PGW) was supported by the Royal Society. This is contribution number 27 of the Christensen Research Institute, box 305, Madang, Papua New Guinea.

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