

Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology

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Summary

1. The thermoregulatory capabilities of 18 species of Alaskan bees spanning nearly two orders of magnitude of body mass were measured. Thoracic temperature, measured across the temperature range at which each species forages, was regressed against operative (environmental) temperature to determine bees' abilities to maintain relatively constant thoracic temperatures across a range of operative temperatures (thermoregulatory performance).

2. Previous studies on insect thermoregulation have compared thoracic temperature with ambient air temperature. Operative temperature, which integrates air temperature, solar radiation and effects of wind, was estimated by measuring the temperature of a fresh, dead bee in the field environment. It is suggested that this is a more accurate measure of the thermal environment experienced by the insect and also allows direct comparisons of insects under different microclimate conditions, such as in sun and shade.

3. Simple regression analysis of species and family means, and analysis of phylogenetically based independent contrasts showed thermoregulatory capability, ability to elevate thoracic temperature, and minimum thoracic temperature necessary for initiating flight all increased with body size.

4. Bumble-bees were better thermoregulators than solitary bees primarily as a consequence of their larger body size. However, their thermoregulatory abilities were slightly, but significantly, better than predicted from body size alone, suggesting an added role of pelage and/or physiology. Large solitary bees were better thermoregulators than small solitary bees apparently as a result of body-size differences, with small bees acting as thermal conformers.

Key-words: Apoidea, body size, operative temperature, thermoregulation

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Introduction

Insects of high latitudes and high elevations face thermal constraints during foraging in the summer as well as over-wintering (see Kingsolver 1983; Barnes *et al.* 1996). While insects with low levels of activity (e.g. walking and sitting still) or of very small body size and light wing loading can operate with relatively low thoracic temperatures (T_{th}), large flying insects must generally have higher T_{th} (Heinrich 1974). Flying insects that can elevate T_{th} can forage with some independence of environmental temperature (Heinrich & Heinrich 1983a). In contrast, flying insects with T_{th}

conforming to environmental temperature are spatially and temporally restricted to habitats that are warm enough to allow adequate T_{th} for flight.

Bee species richness varies widely among habitats in interior Alaska (Armbruster & Guinn 1989). Warm, open, sunny habitats such as south-facing bluffs, river bars and roadsides have relatively rich solitary bee faunas compared with shaded forests and cool alpine habitats, even though the habitats are similarly rich in appropriate nectar-producing host plants (W. S. Armbruster & J. A. Bishop, unpublished data). Bumble-bees (*Bombus* spp., Apidae), however, are almost equally diverse in all habitats of interior Alaska. It thus appears that bumble-bees (18 species in interior Alaska) inhabit sites of various thermal regimes while solitary bees (58 species in interior Alaska) are restricted to warm, open habitats. This suggests that there may be fundamental differences in

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the abilities of bumble-bees and solitary bees to regulate T_{th} and forage at cool temperatures (see reviews in Heinrich 1979, 1993). Differences between thermoregulatory abilities of bumble-bees and solitary bees in subarctic Alaska (and elsewhere) may result from inherent differences in physiology, pelage, colour, size or some combination of these factors. (Differences in the nesting biology of solitary bees and bumble-bees could also contribute to this pattern, but are not analysed here.) The purpose of this study was to explore the role of size vs other factors in determining these thermoregulatory differences.

The ability to elevate and regulate T_{th} has been documented for bumble-bees (Heinrich 1972a, 1972b, 1975), honey-bees (Cooper, Schaffer & Buchmann 1985; Dyer & Seeley 1987) and a few large solitary bees (Chappell 1982, 1984; Nicolson & Louw 1982; Heinrich & Buchmann 1986; Baird 1986). Less is known about thermoregulation in smaller bees. Stone & Willmer (1989b) have shown that elevation of T_{th} over air temperature increases with size in bees once the effects of thermal regime and phylogeny have been removed. Very few studies, however, have reported on the abilities of solitary bees to regulate T_{th} over a range of environmental temperatures (but see Stone 1993a,b), and none has employed integrated measures of the thermal environment ('operative temperature'; Bakken 1992;).

OPERATIVE TEMPERATURE

Ambient air temperature (T_a) is often an inaccurate measure of the thermal environment experienced by insects because the thermal environment is also influenced by radiation load and convective effects of wind (Chappell 1982a). T_a , solar radiation and convective effects of wind can be integrated into a single measure by directly estimating the operative (environmental) temperature (T_e ; Bakken 1976, 1980, 1992). The best measure of T_e is the temperature of a physical model that approximates the thermal properties and position of the study organism in the field environment. T_e for insects can be estimated by mounting a freshly killed insect on a thermocouple lead and placing it in the field environment (Parker 1982; Bakken 1992; Casey 1992; O'Neill & Kemp 1992). A dead-insect thermometer cannot, of course, estimate the convective effects of flight and wing movement. Black-globe measurements have also been used to approximate environmental temperature of insect (e.g. Corbet *et al.* 1993) and this method can give quite similar estimates to dead-insect thermometers (W. S. Armbruster, R. Matsuki & M. Lee, unpublished data). The advantages of dead-insect thermometers are that they equilibrate to the thermal environment more quickly and respond thermodynamically more like the living insect. Disadvantages relative to the black-globe thermometer include unwanted variance due to variation in arrangement of body parts (e.g. abdomen, legs, wings)

and orientation of the insect relative to the sun. On balance, if care is used in deployment, the advantages of fresh insects as a T_e thermometer outweigh their disadvantages (Parker 1982; Bakken 1992; O'Neill & Kemp 1992).

THERMOREGULATORY CAPABILITIES OF INSECTS

It is suggested that an insect's thermoregulatory capability comprises two major, interacting components: (1) the ability to maintain a relatively constant T_{th} over a wide range of T_e ; and (2) the ability to elevate T_{th} above T_e when T_e is relatively low. These are related to the slope and elevation, respectively, of the relationship between T_{th} and T_e . Both components may be influenced by body mass in insects (Bartholomew & Heinrich 1973, 1978; Heinrich 1974, 1989; Bartholomew 1981; Casey & Joos 1983; Heinrich & Mommsen 1985; Stone & Willmer 1989b; Stone 1993a,b). The magnitude of T_{th} elevation over T_e in insects is determined by the input (metabolic heat) minus output (convective, evaporative and radiative heat loss) (Bartholomew 1981; Porter *et al.* 1994). Note that radiative heat gains to the insect, as well as the effects of T_a and convection, are included in its T_e (Bakken 1976, 1980, 1992). Metabolic rate and the rate of convective heat loss both increase (per unit mass) as the size of the insect decreases; however, the latter increases more rapidly with decrease in body size (May 1976; Bartholomew 1981; Porter *et al.* 1994). Because heat loss is proportional to surface area and metabolic heat production is proportional to thoracic volume, at small body sizes above a critical surface-area to volume ratio, convective heat loss becomes so great that production of metabolic heat is insufficient to elevate T_{th} over T_e . The influence of size on both components (1 and 2 above) of thermal performance was examined.

Small insects that occur in cool environments and are unable to elevate temperature before or during flight may evolve the capability of flying at lower T_{th} than larger insects that can elevate T_{th} (e.g. Heinrich & Mommsen 1985). Bumble-bees must have a T_{th} of at least 29–30 °C to fly (Krogh & Zeuthen 1941; Sotavalta 1954), but almost nothing is known about minimum T_{th} of small solitary bees in flight. The first analysis of the relationship in bees between body size and minimum T_{th} necessary for flight is presented here.

Materials and methods

FIELD SITES

Fieldwork was conducted in interior Alaska between May and July of 1990 and April and July of 1991. Interior Alaska has a continental climate with cold winters and warm summers. Bees start foraging in early to mid-April. Most species cease activity in late

July or early August (Armbruster & Guinn 1989). The study sites in 1990 were Bonanza Creek Bluff, 25 km south-west of Fairbanks, Alaska (64°42'N, 148°18'W) and Moose Creek Bluff, 35 km south-east of Fairbanks, Alaska (64°44'N, 147°14'W). The study site at Bonanza Creek Bluff was a patch of roadside vegetation dominated by two legumes, *Hedysarum boreale* and *Hedysarum alpinum* (Fabaceae), at the base of the south-facing bluff. The bee fauna and pollination interactions of the site have been described by Armbruster & Guinn (1989), Armbruster & McGuire (1991) and McGuire (1993). The Moose Creek Bluff study site was a south-facing river bluff with predominantly azonal subarctic steppe vegetation (described by McGuire & Armbruster 1991). Fieldwork in 1991 was done at Kathul Mountain near the confluence of Washington Creek and the Yukon River, ≈ 80 km north-west of Eagle, Alaska (65°22'N, 142°16'W). Habitats in which bees were caught included riverbanks, steppe on south-facing slopes, and alpine tundra (see Edwards & Armbruster 1989; Lloyd, Armbruster & Edwards 1994). Additional information on the taxonomy of bees in interior Alaska (including authors of species) can be found in Armbruster & Guinn (1989).

PASSIVE COOLING RATES

Cooling curves for females or workers of 10 species, and both males and females of one species were measured to determine the relative importance of convective heat loss. Freshly killed bees were mounted on a 29-gauge thermocouple probe (Physitemp MT-29/2; Physitemp Instruments Inc., Clifton, NJ) ventrally inserted to the middle of the thorax, and placed next to a gasoline lantern (Coleman 285–700; Coleman Camping Equipment Inc., Wichita, KS), which served as a radiant heat source. When the temperature of the thorax of the mounted bee (T_{th}) reached 22 °C above T_a , the lantern was removed, and T_{th} was recorded every 5 s until the bee temperature reached ambient air temperature (generally ≈ 10 °C or less). Completely eliminating air currents was impossible because all measurements were done in a tent at the field site. However, if a draught was felt during a recording session, the measurement was not included. Each recording session lasted a maximum of 5 min, and T_a never changed more than 1 °C in the tent during a run. Cooling rates were measured for three individuals of each 'size group' (caste or sex partitioned by species, e.g. female *Anthophora bomboidea*, vs male *A. bomboidea*, vs female *Osmia bucephala*, vs queen *Bombus sylvicola*).

Cooling curves were log-transformed to obtain a linear relationship. The slope of the log-linearized relationship is the cooling constant, a measure of the passive cooling rate (cf. Wathen, Mitchell & Porter 1971). These thoracic cooling rates are probably very close, but not identical, to those experienced by live bees that warm endothermally, because the heads and abdomens were also heated by the experimental

warming process (whereas only the thorax is warmed endothermally). However, cooling rates should approximate the cooling rates of more ectothermal bees whose heads and abdomens warm along with thoraces during basking. The mean cooling constants were regressed against $\ln(\text{mean dry mass})$.

MEASUREMENT OF THORACIC TEMPERATURE

During the course of the bees' flight seasons, field sites were visited each day before bees started foraging, and T_{th} was measured during most of the diel period of bee activity. In this way it was possible to obtain, for each common species, accurate estimates of minimum T_e of flight and a full range of T_{th} under a range of thermal environments. Uncommon species were therefore not included in the analyses.

Most studies of thermoregulatory capability of insects have measured T_{th} of insects in flight (Heinrich 1975; Chappell 1982, 1984; Heinrich & Buchmann 1986). In this study, however, T_{th} at which a bee can take off was measured. This was chosen for two reasons: (1) T_{th} at takeoff is more easily measured in a consistent way (just as the insect takes off) and likely to be less variable than T_{th} during flight (the latter is affected by flight speed and prior activity levels); and (2) achieving minimum T_{th} necessary for flight at takeoff is probably a critical challenge to foraging in cool weather. Although bees can sometimes take off but not maintain flight (G. Stone, personal communication), this was not observed at our study sites (or if it did occur, it resulted in bees moving between flowers in a normal foraging pattern). Because bees were not disturbed prior to takeoff, we believe they generally initiated flight under conditions that allowed them to maintain flight for ecologically meaningful periods of time. Bees often allow T_{th} to drop while feeding on flowers and warm up just prior to flight (Heinrich & Heinrich 1983b; Waddington 1990). Thus, it was not assumed that a bee on a flower could fly, and bees were captured only after a successful foraging visit and voluntary takeoff.

Thoracic temperatures of live bees were measured in 21 'size groups' (as defined above: caste or sex partitioned by species), representing 18 species of solitary and social bees in interior Alaska. Different castes (queens and workers) of bumble-bees of the same species were treated separately because of the differences in body mass. Male and female solitary bees were also treated separately because of differences in size and potentially in thermoregulatory ability. Bees were sampled over the entire range of environmental temperatures at which they were found foraging on flowers.

T_{th} was measured under field conditions for each bee captured in the field. Bees were captured with an insect net immediately upon takeoff from flowers and immobilized against a gloved finger. A 29-gauge thermocouple probe (Physitemp MT-29/2; time constant =

0.025 s) was immediately inserted into the middle of the thorax and the temperature was read to the nearest 0.1 °C on a digital thermometer (Omega Model HH-72T; Omega Engineering Inc., Stamford, CT). To minimize the potential for inaccurate readings because of convective cooling or to heat production from the flight muscles caused by agitation, the bee was not used if T_{th} could not be measured within 7 s of capture (see Stone & Willmer 1989a). The temperature of the flight muscle of honey-bees has been shown to be fairly constant throughout the muscle (Feller & Nachtigall 1989), and the gradient from the core to the surface is expected, on theoretical grounds, to be very small in small insects (W. P. Porter, personal communication). Therefore, inadvertent variation in placement of the probe within the flight muscle was probably not a source of much error. Each specimen was retained for later identification.

One concern was that the thermal mass of the probe would influence the T_{th} reading from smaller bees. To assess the severity of this problem, dead *Evyllaenus comagenensis* (Halictidae), one of the smallest bees (fresh mass \approx 10 mg), were placed in a 5 °C walk-in refrigerator and allowed to equilibrate to T_a . To determine the effect of probe temperature on T_{th} , a probe that had been in a warm water bath was inserted into the bee's thorax. When the probe was 30 °C warmer than the dead bee, T_{th} read only 0.5 °C warmer than actual T_{th} . Because T_{th} was altered so little by a bee-probe temperature differential that was greater than that experienced in the field, we considered the effect of probe temperature on T_{th} of small bees to be negligible (see also Stone & Willmer 1989a).

T_e was measured at the time of capture by measuring T_{th} of a recently killed bee mounted on a thermocouple (which Bakken 1992 has termed a T_e thermometer). The bee used as a thermometer was the same size group (species/caste/sex) as the live bee under study and was positioned in as a natural a posture as possible (e.g. wings partially spread), oriented horizontally and placed next to the flower on which the bee was foraging.

To determine whether the time since collection of the bee used for the T_e thermometer introduced variance in the T_e reading, T_e measured with five freshly killed honey-bees was compared with T_e measured with five honey-bees killed 3 days previously. The T_e readings were identical (to the nearest 0.1 °C) across all bees, and therefore small differences in age of T_e carcasses were not considered to be a source of significant error.

SIZE VARIABLES

Body dry mass was measured from specimens mounted on preweighed pins. The bees were dried for two months under ambient laboratory conditions ($T_a \approx$ 23 °C, relative humidity \approx 15%). The remote field location precluded measurement of fresh mass. The dry mass/fresh mass ratio was calculated for a total of

22 individuals from six species in the Anthophoridae and Apidae to allow estimation of fresh mass. Average dry mass was 36.8% (standard deviation = 4.7%) of fresh mass.

Thoracic volume was calculated using the equation for an ellipsoid:

$$V = 4/3\pi abc \quad \text{eqn 1}$$

where a = length/2, b = width/2 and c = depth/2. Thoracic volume values are means of four randomly selected specimens of each size group.

Wing loading was calculated by dividing dry mass by wing surface area. Wing surface area was measured with a video digitizer interfaced with a desktop computer.

Only mean values of size variables were used in further statistical analyses. Means differed significantly among all size groups. The standard deviations were small relative to the means and are therefore not reported in Table 1.

THERMOREGULATORY PERFORMANCE

The thermoregulatory performance index was defined as the slope of the relationship between T_{th} and T_e and was calculated for each species using ordinary least-squares regression on individuals within a size group (species and caste/sex). A slope of 0 indicates that T_{th} is independent of T_e and a slope of 1 indicates thermal conformance. The relationship between T_{th} and T_e was not significantly different from linear across the observed T_e range for all size groups investigated in this study, allowing use of simple linear regression. Although least-squares regression assumes no error in the x -values (and there was sampling as well as measurement error in our size measurements), it is in wide use for studies such as these (Neter, Wasserman & Kutner 1985). There are two reasons for this. Alternatives, such as Type-II (major axis) regression, have not been developed as thoroughly, have their own statistical problems, and tend not to deviate very much from least squares when the relationship is reasonably strong (Neter *et al.* 1985; Pagel & Harvey 1988). If least-squares regression introduced a bias, it would probably have accentuated slightly the differences between thermoregulators and conformers, by underestimating the slope for the former but not for the latter (see Pagel & Harvey 1988). We think this problem is minor, but it should be borne in mind.

THORACIC TEMPERATURE ELEVATION AND MINIMUM TEMPERATURE FOR TAKEOFF

The T_{th} elevation index is a measure of the ability of each species to elevate T_{th} above T_e and was defined as the difference between T_e and the expected value of T_{th} (calculated from the T_{th}/T_e regression equation) at the lowest air temperature at which bees were observed foraging. Although functionally similar to the y -inter-

cept, this value was used instead because it was considered biologically more relevant. This index is preferable to the average $T_{th} - T_e$ value for all bees measured because the maximum attainable difference at low temperatures is an indication of the thermal constraints placed on behaviour. The minimum T_{th} at which bees were observed to be able to take off was assessed from the range of measured T_{th} for each size group.

STATISTICAL ANALYSES

Thermoregulatory performance index, elevation of thoracic temperature and minimum thoracic temperature at takeoff were regressed 'naïvely' (see Grafen 1989) against the natural log of mean dry mass, thoracic volume and wing loading for all bee size groups (as defined above). The size measures were too highly intercorrelated to use in multiple regression. Body dry mass appeared to be the best general measure of size and is most widely used; it alone was used in the more detailed analyses. In all the analyses, mass was natural log-transformed to linearize relationships with the y variables.

Most size groups comprised female bees. However, measurements were also made on male and worker bees and treated as different size groups. These additional size groups were included in our analyses to increase the sample size and size range. Although

there is a risk of obscuring or creating patterns by pooling heterogeneous data, inspection of the data and residuals suggested that including females, males and workers in the same analysis would not cause statistical problems. To test this assumption, all analyses were repeated without males and workers. The results were very similar; the correlation coefficients changed by less than 10% in all cases, and therefore only the results of analyses of the full data set are reported.

The statistical estimates of relationships based on data pooled from species belonging to several higher taxa (or clades) represent a blend of within- and among-group (clade or taxon) relationships (Armbruster 1988, 1992, 1996; Bell 1989; Harvey & Pagel 1991). Furthermore, species are not independent observations but rather structured by phylogeny; hence the phylogeny of species being compared should be incorporated in the analysis of comparative data (Felsenstein 1985; Harvey & Pagel 1991; Armbruster 1992). Two additional analyses were conducted to deal with these problems. To assess the seriousness of the first problem, the among-species relationships were compared with the among-family relationships between thermoregulatory parameters and mean dry mass. Generic means were used in calculating family means to prevent genera with several sampled species from biasing family means.

Table 1. Thermoregulatory and size data for bee taxa of interior Alaska. Abbreviations: f = females, m = males, q = queens, w = workers. Taxa for which cooling constants were calculated are denoted with an asterisk. 95% confidence intervals of the thermoregulatory performance index are shown in parentheses

Taxon	<i>N</i>	Thermoregulatory performance index	Thoracic temp. elevation index	Mean thoracic vol. (mm ³)	Mean dry mass (g)	Est. mean fresh mass (g)	Lowest flight T_e	Lowest takeoff T_{th}
Colletidae								
<i>Hylaeus ellipticus</i> (f)*	25	0.96 (0.89–1.56)	3.7	12.4	0.0042	0.0120	16.2	23.0
Halictidae								
<i>Dialictus ruidosensis</i> (f)	27	0.88 (0.66–0.01)	3.6	9.2	0.0031	0.0089	17.5	20.0
<i>Evyllaes comagenensis</i> (f)*	29	0.88 (0.68–1.02)	1.9	14.0	0.0069	0.0197	17.0	17.0
Andrenidae								
<i>Andrena thaspia</i> (m)	11	0.87 (0.61–1.14)	3.8	15.1	0.0079	0.0226	18.5	21.2
<i>Andrena frigida</i> (f)*	12	0.68 (0.49–0.88)	7.8	22.1	0.0252	0.0721	11.3	17.9
Megachilidae								
<i>Megachile giliae</i> (f)*	37	0.42 (0.29–0.54)	14.0	25.0	0.0357	0.1021	16.8	29.6
<i>Megachile melanophaea</i> (f)	15	0.54 (0.28–0.79)	11.1	25.2	0.0365	0.1044	17.8	27.0
<i>Hoplitis albifrons</i> (f)*	13	0.88 (0.19–1.47)	4.4	21.2	0.0236	0.0675	22.7	27.1
<i>Osmia</i> sp. nov. (f)*	28	0.60 (0.24–0.88)	7.2	17.2	0.0160	0.0458	22.2	26.2
<i>Osmia bucephala</i> (f)*	14	0.70 (0.044–0.91)	9.6	29.4	0.0703	0.2011	22.6	33.0
Anthophoridae								
<i>Anthophora bomboidea</i> (f)*	14	0.41 (0.24–0.58)	14.9	31.6	0.0596	0.1705	17.3	31.5
<i>Anthophora bomboidea</i> (m)*	8	0.61 (0.38–0.84)	12.6	26.2	0.0339	0.0970	17.4	27.5
Apidae								
<i>Bombus flavifrons</i> (q)	20	0.24 (0.03–0.44)	21.3	25.8	0.0969	0.2771	14.4	32.3
<i>Bombus flavifrons</i> (w)	6	0.59 (–0.02–1.20)	13.6	26.0	0.0280	0.0801	21.0	32.2
<i>Bombus frigidus</i> (q)	14	0.12 (–0.02–0.26)	31.1	40.6	0.0899	0.2571	6.0	35.7
<i>Bombus frigidus</i> (w)	14	0.30 (0.19–0.40)	20.1	27.9	0.0453	0.1296	12.6	33.1
<i>Bombus sylvicola</i> (q)*	11	0.37 (0.03–0.58)	22.3	38.5	0.0969	0.2771	12.0	34.2
<i>Bombus mixtus</i> (q)	8	0.63 (0.38–0.94)	18.0	35.4	0.0844	0.2421	17.0	35.1
<i>Bombus alboanalis</i> (w)	19	0.13 (0.09–0.34)	17.5	25.8	0.0372	0.1064	15.7	30.8
<i>Bombus occidentalis</i> (q)	9	0.23 (0.10–0.35)	27.0	63.4	0.01760	0.4750	9.0	33.9
<i>Bombus occidentalis</i> (w)	13	0.43 (0.05–0.72)	15.2	35.4	0.0740	0.2116	18.2	29.7

To deal with the problem of phylogenetic structure in the data, Pagel's (1992) modification of Felsenstein's (1985) method of analysing independent contrasts, as operationalized by Purvis & Rambaut (1995) in their computer program CAIC, was employed. Phylogenetic relationships were inferred from taxonomic information presented in Michener,

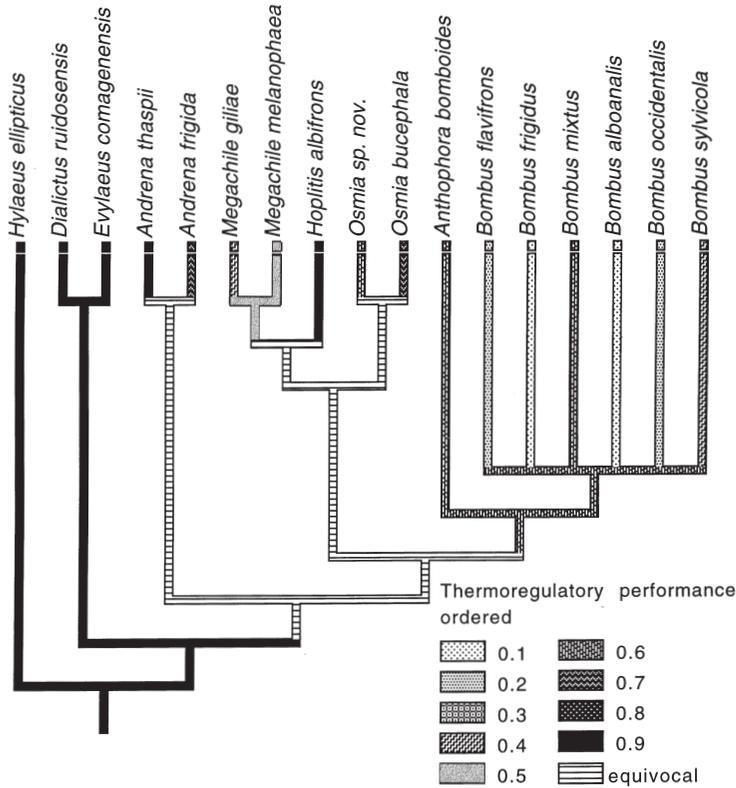


Fig. 1. Inferred phylogeny of bee genera used in independent-contrasts analysis, based on taxonomic information presented in Michener *et al.* (1994) and the phylogeny presented in Michener (1974), as modified for Anthophoridae/Apidae by Roig-Aisina & Michener (1993). The thermoregulatory performance index was mapped onto the phylogeny using ordered-state parsimony (Maddison & Maddison 1992) to illustrate the apparent evolutionary lability of this trait.

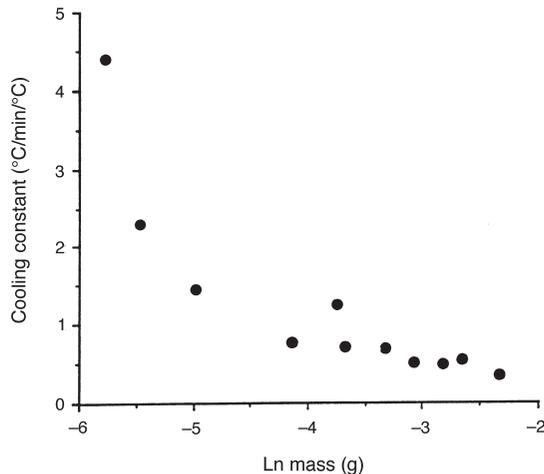


Fig. 2. Cooling constant vs ln(dry mass) for 11 bee size groups (species/sexes) in interior Alaska. The taxa used in this analysis are denoted by an asterisk in Table 1.

McGinley & Danforth (1994) and the phylogeny presented in Michener (1974), as modified for Anthophoridae/Apidae by Roig-Aisina & Michener (1993) (Fig. 1). For this analysis branch lengths were assumed equal. Males and workers were not included in the analysis except in two cases where female/queen data were unavailable for the species (*Andrena thaspia*, *Bombus alboanalis*). This analysis calculates, for each variable, the differences between the values of paired sister taxa in the phylogeny. It also calculates differences between estimated values of phylogenetically paired ancestors. The variables are related to one another by regressing the values of the paired differences for one variable on the corresponding values of the other variable, with the regression constrained through the origin (see Purvis & Rambaut 1995).

To test whether bumble-bees are better thermoregulators than solitary bees after the effect of size has been removed, analysis of covariance of thermoregulatory performance, thoracic temperature elevation and minimum T_{th} at takeoff was conducted, using body mass as a covariate. Similar analyses were conducted to look for size-corrected thermoregulatory differences between worker and queen *Bombus*. Because bumble-bees generally cluster at the upper end of the size range, there is the potential for accelerating non-linearity of the size-thermoregulatory ability relationship to cause overestimation of bumble-bee thermoregulatory ability and mistaken rejection of the null hypothesis. However, consideration of basic biophysical principles suggests that any non-linear relationship is more likely to be decelerating (i.e. thermoregulatory ability improves asymptotically with size) and thus overestimation of bumble-bee thermoregulatory ability is unlikely. Another weakness of the ANCOVA approach is that the covariate is estimated 'naïvely', that is without benefit of phylogenetic information. For reasons discussed below, we do not consider this a serious problem, but it should be kept in mind.

Results

COOLING CURVES

Cooling curves for individuals of all species showed exponential decay (T_{th} vs time). Across the species studied, the cooling constants (the slopes of the log-linearized cooling curves) decrease approximately exponentially with increasing mean dry body mass (Fig. 2). Thus, small bees lose heat very quickly and large bees lose heat comparatively slowly as would be expected from biophysical principles (e.g. Wathen *et al.* 1971; Porter *et al.* 1994). No size group showed a conspicuous departure from this trend.

THERMOREGULATORY PERFORMANCE INDEX

The regression of T_{th} against T_e for each species shows

how well it regulates T_{th} . The relationship between T_{th} and T_e is depicted in Fig. 3 for a small solitary bee, *Hylaeus ellipticus* (dry mass = 0.0042 g, fresh mass \approx 0.012 g), a moderate-size solitary bee, *Megachile gilliae* (dry mass = 0.0357 g, fresh mass \approx 0.102 g), and a large social bee, *Bombus frigidus* (queen; dry mass = 0.0899 g, fresh mass \approx 0.257 g). The slope of the line described by T_{th} vs T_e for each species is used as its thermoregulatory performance index (recall that near 1.0 is poor regulation, near zero is good regulation). The thermoregulatory performance index is 0.96 for

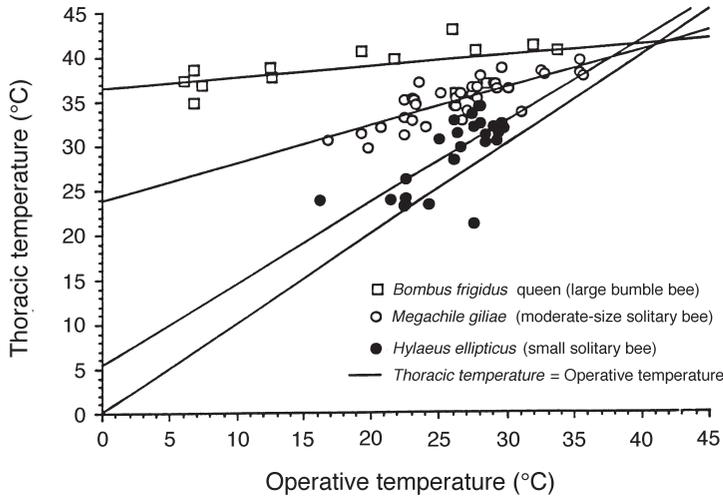


Fig. 3. Thoracic temperature vs operative temperature for three representative bee species. Each point represents a measurement on an individual bee. Thermoregulatory capabilities are shown for a small bee, a moderate-size bee and a large bee. The isothermal line ($T_{th} = T_e$) is included for reference.

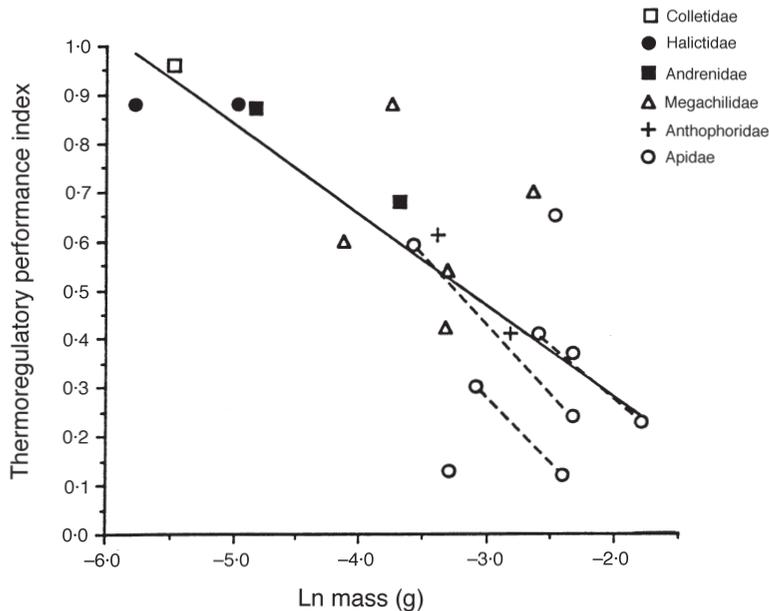


Fig. 4. Thermoregulatory performance index vs Ln dry mass. Each point represents a size group. The thermoregulatory capability is associated with size ($Y = -0.187x - 0.095$, $r^2 = 0.60$, $P = 0.0001$). Queen and worker bumble-bees of the same species are connected by dashed lines.

Hylaeus ellipticus, 0.42 for *Megachile gilliae*, and 0.12 for *Bombus frigidus* (see Fig. 3). The thermoregulatory performance indices for *Bombus frigidus* and *Hylaeus ellipticus* are the lowest and highest, respectively, of the 21 taxa measured (Table 1).

'Naïve' regression analyses across species and families and analysis of independent contrasts all showed significant negative relationships between the thermoregulatory performance index and dry mass (Table 2, Figs 4 and 5), and the estimated slopes of the relationships did not differ significantly across methods (Table 2). The thermoregulatory performance index was also significantly negatively correlated with thoracic volume ($r^2 = 0.59$, $P < 0.001$, $N = 21$) and wing loading ($r^2 = 0.49$, $P < 0.001$, $N = 21$). These results indicate that body size alone explains much of the variation in bee thermoregulatory ability (with and without the effects of phylogeny being removed) and that large bees are generally better at regulating body temperature than small bees.

ELEVATION OF THORACIC TEMPERATURE

T_{th} elevation indices ranged from 1.9 °C to 31.1 °C (Table 1). 'Naïve' regression analyses across species and families and analysis of independent contrasts all showed significant positive relationships between the elevation of thoracic temperature and dry mass (Table 2, Figs 6 and 7). Furthermore, the estimated slopes of the relationships were generally similar and not statistically different across analyses (Table 2). The T_{th} elevation index was also significantly positively correlated with thoracic volume ($r^2 = 0.73$, $P < 0.001$) and wing loading ($r^2 = 0.60$, $P < 0.001$). These results indicate that body size alone explains much of the variation in bees' ability to maintain thoracic temperature above the environmental temperature and that large bees are generally better at maintaining elevated thoracic temperature than small bees.

MINIMUM MUSCLE TEMPERATURE FOR TAKEOFF

The minimum T_{th} at flight initiation for each group ranged from 17.0 to 35.7 °C (Table 1). 'Naïve' regression analysis across species and families and analysis of independent contrasts all showed significant (or nearly significant) positive relationships between dry mass and the minimum observed T_{th} at which bees were observed to take off (Table 2, Figs 8 and 9). Furthermore, the estimated slopes of the relationships were generally similar and not statistically different across analyses (Table 2). Minimum T_{th} for flight initiation was also significantly positively correlated with thoracic volume ($r^2 = 0.69$, $P < 0.001$) and wing loading ($r^2 = 0.65$, $P < 0.001$). These results indicate that body size can explain much of the variation in minimal thoracic temperature at which bees can fly and that small bees can generally fly with a lower T_{th} than large bees.

Table 2. Comparison of results of 'naïve' among-species and among-family regressions and analyses of phylogenetically based independent contrasts

Analysis	r^2	n	P	Regression coefficient (95% confidence interval)
Thermoregulatory performance index vs dry mass				
Among size groups	0.60	21	<0.001	-0.186 (-0.259 to -0.114)
Among families	0.92	6	0.002	-0.190 (-0.265 to -0.114)
Independent contrasts	0.39	11	0.029	-0.129 (-0.228 to -0.030)
Temperature elevation of thorax vs dry mass				
Among size groups	0.71	21	<0.001	6.25 (4.33 to 8.16)
Among families	0.83	6	0.012	5.29 (1.95 to 7.70)
Independent contrasts	0.52	11	0.009	4.29 (1.73 to 6.85)
Minimum thoracic temperature at takeoff				
Among size groups	0.69	21	<0.001	4.35 (2.96 to 5.73)
Among families	0.75	6	0.025	4.10 (0.86 to 7.70)
Independent contrasts	0.30	11	0.064	2.51 (0.15 to 4.87)

THERMOREGULATION BY BUMBLE-BEES VS SOLITARY BEES

Bumble-bees fell generally on or below the regression of thermoregulatory performance on dry mass (Fig. 4), and thus tended to be slightly better thermoregulators than predicted by size. There was no evidence that the slopes of the thermoregulatory performance-mass relationships differed between solitary bees and bumble-bees ($F_{1,17} = 0.40$, $P = 0.54$). Analysis of covariance (ANCOVA) indicated a small but significant difference in thermoregulatory ability of bumble-bees and solitary bees after the effect of size was removed ($F_{1,18} = 4.55$, $P = 0.047$). Thus bumble-bees appear to be slightly better thermoregulators (as measured by this index) than solitary bees, even after

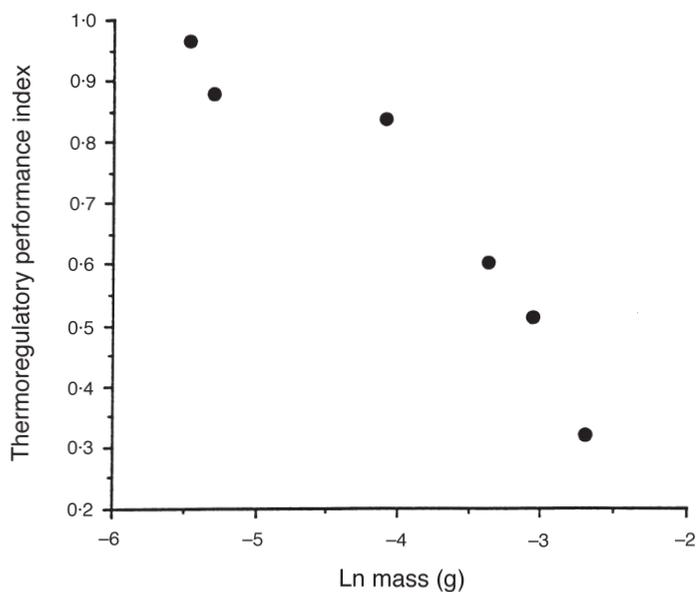


Fig. 5. Thermoregulatory performance index vs Ln dry mass at the family level. Each point represents the means of one family. The ability to regulate T_{th} is correlated with mass at the family level (Kendall's tau = 1, $z = -2.82$, $P = 0.002$).

the effect of size differences has been removed. There were no apparent differences in the slopes of relationships between mass and thermoregulatory performance for worker and queen bumble-bees ($F_{1,5} = 0.12$, $P = 0.89$), nor in their size-corrected thermoregulatory abilities (see Fig. 3; ANCOVA, $F_{1,6} = 1.73$, $P = 0.21$).

Bumble-bees fell generally above the regression of T_{th} elevation on dry mass and thus appeared to be better temperature elevators than predicted by size (Fig. 6). The slopes of the regression of T_{th} elevation on dry mass for bumble-bees and solitary bees were not significantly heterogeneous ($F_{1,17} = 1.56$, $P = 0.23$), and ANCOVA indicated that bumble-bees were better at maintaining elevated thoracic temperature than solitary bees, even after the effect of larger body size had been removed ($F_{1,18} = 12.59$, $P = 0.002$). There were no apparent differences in the slopes of the mass-temperature elevation relationships for worker and queen bumble-bees ($F_{1,5} = 1.25$, $P = 0.31$), nor in their size-corrected ability to elevate thoracic temperature ($F_{1,6} = 1.04$, $P = 0.37$).

Bumble-bees had more positive than negative residuals off the regression of minimum takeoff T_{th} on dry mass (Fig. 8). ANCOVA showed the trend toward higher T_{th} than predicted by size to be marginally significant ($F_{1,18} = 3.68$, $P = 0.07$; the slopes of the mass-takeoff T_{th} relationships were not significantly heterogeneous; $F_{1,17} = 1.95$, $P = 0.18$). There were no apparent differences in the slopes of the mass-takeoff T_{th} relationships ($F_{1,5} = 0.27$, $P = 0.77$) or in the size-corrected takeoff T_{th} of worker and queen bumble-bees ($F_{1,6} = 0.26$, $P = 0.77$).

Discussion

Both measures of bee thermoregulatory capability (the slope and the elevation of the relationship

between thoracic temperature and environmental temperature) were correlated with the three measures of size (dry body mass, thoracic volume and wing-loading). These correlations were apparent in species comparisons, family comparisons and analysis of independent contrasts. Large bees had generally better thermoregulatory capabilities than smaller bees. The minimum observed muscle temperature at takeoff was also positively correlated with body mass. This corre-

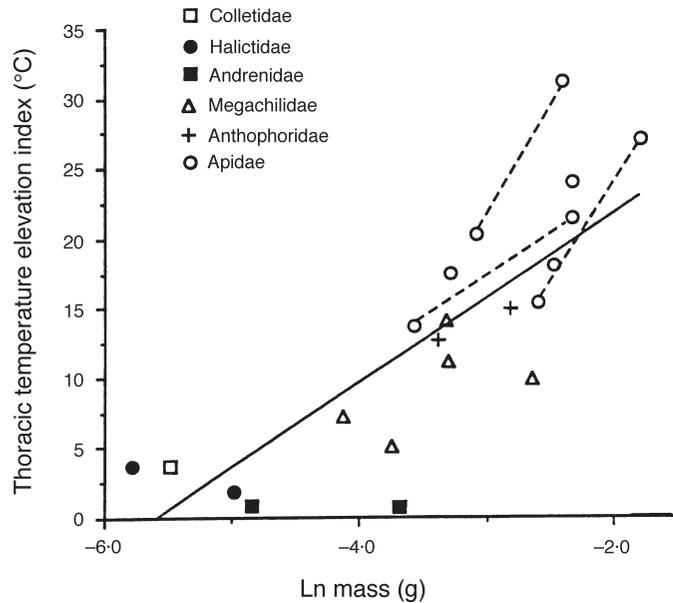


Fig. 6. Thoracic temperature elevation index vs Ln dry mass. Each point represents a size group. The ability to elevate T_{th} is significantly associated with the natural log of mass ($Y = 5.98x + 33.72$, $r^2 = 0.67$, $P = 0.0001$). Queen and worker bumble-bees of the same species are connected by dashed lines.

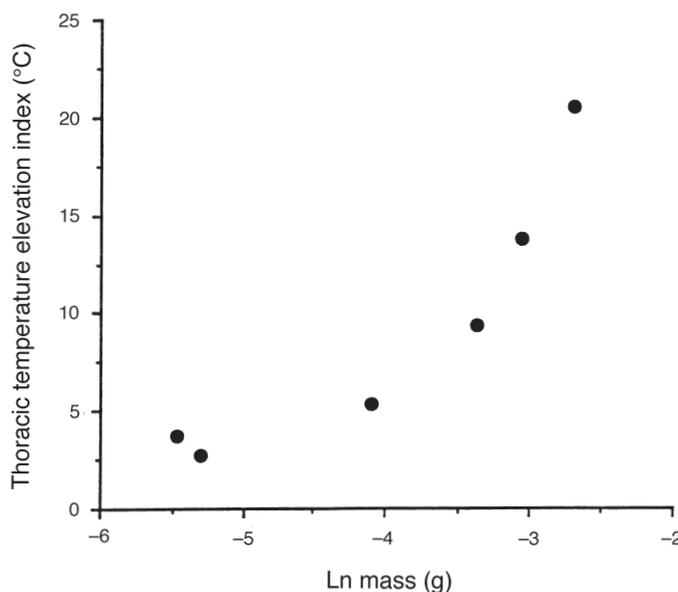


Fig. 7. Thoracic temperature elevation index vs Ln dry mass at the family level. Each point represents the means of one family. The ability to elevate T_{th} is significantly associated with the natural log of mass (Kendall's tau = 0.87, $z = 2.44$, $P = 0.02$).

lation was also significant at species and family levels, and marginally significant in the independent-contrast analysis. In general, small bees could initiate flight at lower thoracic temperatures than large bees.

Some of these results could be predicted from simple biophysical models that incorporate rate of heat loss and gain in relation to pelage and thoracic shape and diameter of each bee species (see Wathen *et al.* 1971; Kingsolver 1979, 1983; Porter *et al.* 1973, 1994; Grant & Porter 1992; Helmuth 1998). However, one difficulty with this approach is deciding whether to model bees as basically endothermic or ectothermic (compare, for example, Porter *et al.* 1994 and Helmuth 1998). Our results indicate that bees display continuous variation in degree of endothermy, ranging from endothermy in bumble-bees to ectothermy in the smallest solitary bees; more refined biophysical models would need to address this variation.

RELATIONSHIP BETWEEN THERMOREGULATORY CAPABILITY AND SIZE

The observed relationship between thermoregulatory performance index and body mass shows a continuum between good thermoregulators and thermal conformers (see Fig. 3). Bumble-bees showed the greatest ability to regulate T_{th} of any bees in interior Alaska. Several intermediate-size bees (e.g. *Megachile* spp., *Anthophora bomboides*, *Osmia* spp.) showed intermediate abilities to regulate T_{th} . *Osmia* sp. nov. was the smallest bee to show appreciable ability to regulate T_{th} (thermoregulatory performance index = 0.60, mean dry mass = 0.016 g). Bees smaller than 0.015-g dry mass (e.g. *Evylaeus comagenensis*, *Hylaeus ellipticus* and *Dialictus ruidosensis*) showed no appreciable ability to regulate T_{th} . These results are largely in agreement with previous studies (e.g. Stone & Willmer 1989b; Stone 1993a,b).

The ability to elevate T_{th} was used as another measure of thermoregulatory capability. The positive relationship between T_{th} elevation index and size in bees is consistent with studies in beetles (Bartholomew & Heinrich 1978) and moths (Bartholomew & Heinrich 1973). Also, values for T_{th} at $T_a = 22$ °C in this study were similar to values of similar sized bees in other parts of the world (Stone & Willmer 1989b). The positive relationship between T_{th} elevation and mass is also consistent with the negative relationship between the thermoregulatory performance index and mass.

It appears that bumble-bees are better thermoregulators than solitary bees mostly because of their larger size. The amount of variance explained by the covariate (size) in the ANCOVAs was much greater than that explained by class (bumble-bee vs solitary bee). Size within class explained 31% of the variance in thermoregulatory performance index, whereas class explained only 14%. Size within class explained 39% of the variance in elevation of thoracic temperature, whereas class explained 25%. ANCOVA of both measures

of thermoregulation provided evidence that thermoregulatory abilities of bumble-bees are significantly further enhanced by morphological (including insulative), physiological or behavioural features, or some combination of these. These could include greater thermogenic abilities, better heat conservation in the circulation system, and longer and denser pelage (Heinrich 1979, 1993). Differences may reflect a long history of specialization to cold climates by *Bombus*, and explain their greater abundance and diversity in colder climates and cooler microclimates

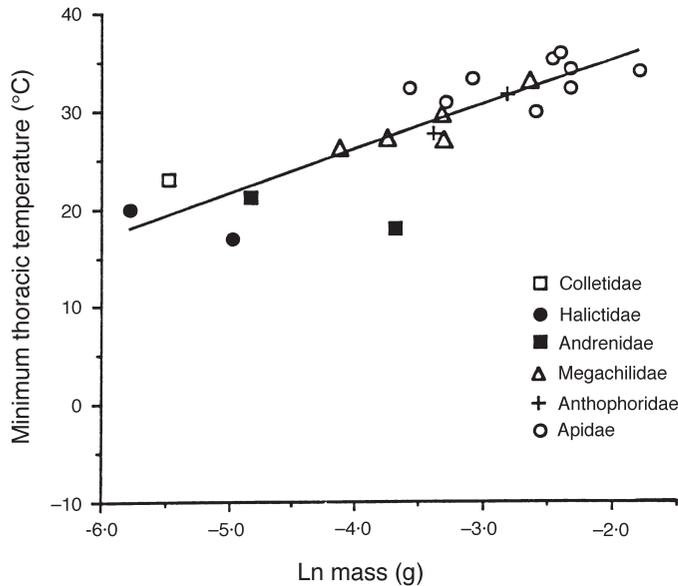


Fig. 8. Minimum T_{th} for flight vs \ln dry mass. Each point represents a size group. The minimum T_{th} at which bees were observed to fly increases with the natural log of body mass ($Y = 5.98x + 33.72$, $r^2 = 0.67$, $P = 0.0001$).

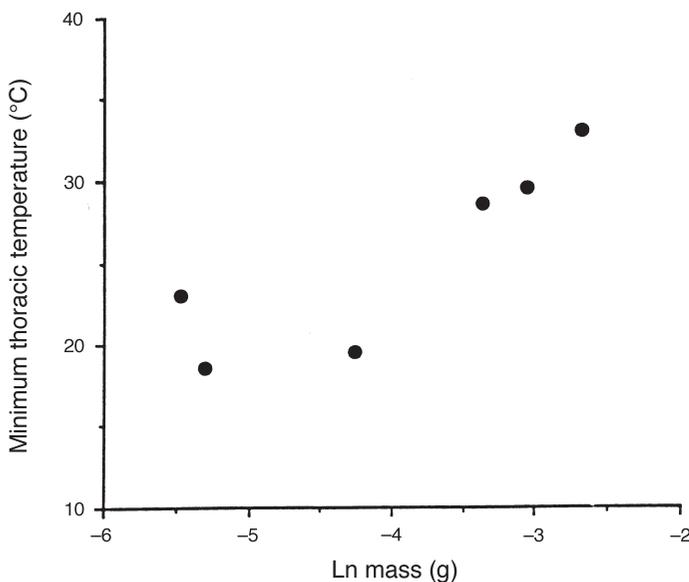


Fig. 9. Minimum T_{th} for flight vs \ln dry mass at the family level. Each point represents the means of one family. The minimum T_{th} at which bees were observed to fly increases with the natural log of body mass (Kendall's tau = 0.73, $z = 2.07$, $P = 0.032$).

in interior Alaska, and at high latitudes and elevations in general.

T_{th} regulation, T_{th} elevation and minimum T_{th} for takeoff by queens and workers of three *Bombus* species were measured (see Figs 4 and 6). Queens regulated and elevated T_{th} better than workers, and required a higher T_{th} for flight in all three species studied (*Bombus frigidus*, *B. flavifrons* and *B. occidentalis*). However, the difference in thermoregulatory capability in these three species varied between castes in a manner largely consistent with the overall relationship between thermoregulatory capability and mass. This observation was confirmed by the ANCOVA, which showed no significant differences in the thermal biology of queens and workers after correcting for body mass. This finding contrasts with Heinrich & Heinrich (1983a), who found that queens and workers fly with the same T_{th} despite the disparity in size. They suggested that worker bumble-bees are genetically constrained to fly at the same T_{th} 'set points' as queens, and thus workers fly with the thermal attributes of much larger bees. Our observation that queens have a higher T_{th} for flight initiation (consistent with their size) suggests the absence of a genetically constrained set point common across both castes. However, failure to find a size-corrected difference in thermoregulation of queens and workers does not alone demonstrate its absence.

The relationship between cooling constant and dry mass appears to be a negative exponential function (Fig. 2). Below ≈ 0.015 g dry mass (-4.2 g \ln mass) the cooling constant rises quickly, and bees show no appreciable ability to regulate T_{th} independently of T_e . Thus small bees may be poorer thermoregulators because they are unable to retain metabolically generated heat. Studies by Church (1960), Chappell (1982) and May & Casey (1983) also suggest that this phenomenon is the result of small size rather than less extensive pubescence in small bees.

This study is in agreement with others showing that large bees can generally regulate and elevate T_{th} better than small bees (e.g. Stone & Willmer 1989b; Stone 1993a,b). It is also consistent with the observation that large queen bumble-bees forage in much cooler conditions than smaller workers (Heinrich & Heinrich 1983a), and bumble-bees can forage in cooler habitats than smaller solitary bees (Armbruster & Guinn 1989). There would thus be a clear thermoregulatory advantage for solitary bees at high latitudes (and elevations) to be relatively large. However, solitary bees in the Arctic and subarctic are generally smaller than their relatives in the tropics (Armbruster & Guinn 1989; Roubik 1989; O'Toole & Raw 1991). Indeed the largest bees (e.g. *Chalicodoma*, *Xylocopa*, *Eulaema*), which dwarf bumble-bees, are tropical or subtropical (Roubik 1989). This observation suggests that there are other constraints on body size at high latitudes, such as resource availability, the rate of development and time available for growth. At high

latitudes bees must develop in one short growing season (or complementary parts of two growing seasons), and this limits the size they can attain (see Adolph & Porter 1996). Thus the length of growing season at high latitudes probably constrains body size of solitary bees, and this in turn constrains thermoregulatory ability and amount of time to forage. Sociality and temporal variability in body size may be one way to overcome the thermal constraints on foraging in cool climates, e.g. in *Bombus*, larger individuals (queens) forage during colder parts of the season.

RELATIONSHIP BETWEEN SIZE AND MINIMUM T_{th} NECESSARY FOR TAKEOFF

A positive relationship was found between the minimum T_{th} necessary for initiation of flight and size and wing loading in bees. *Andrena frigida* and *Evyllaesus comagenensis* may deviate from this relationship in that they can fly with a T_{th} lower than would be predicted from size and wing loading (Fig. 8, lower ● and ■). Both species forage very early in the season when T_e rarely reaches 20 °C. These two species may have evolved some attribute (e.g. enzyme activities adapted to lower temperatures) that allows them to fly with unusually low T_{th} , and this deserves more study. In general, the reduction of minimum T_{th} for flight with size allows small bees more foraging time in cool climates, and may be a second way to partially overcome the constraints of size, thermal ecology and life history discussed above.

MEASURING THERMOREGULATORY CAPABILITY AND COMPARING SPECIES

Thermoregulatory capability was measured by regressing T_{th} against T_e instead of T_a as has been done in most previous studies on insect thermoregulation (e.g. Heinrich 1971, 1972a,b, 1975, 1984; May & Casey 1983; Chappell 1984; Dyer & Seeley 1987; Armbruster & McCormick 1990; Underwood 1991). The use of T_e has two advantages over using T_a . First, it is a more accurate measure of the thermal environment an insect actually experiences in nature (Bakken 1976, 1980, 1992). Second, it allows accurate comparison of T_{th} of insects under different microclimatic conditions (e.g. sun vs shade) because T_e integrates radiative and convective heat exchanges in a single measurement. While the measurement of T_e is especially useful in studies of microclimatic influences on insect activity in cold climates, it has also been informative in studies of insect activity in warm temperate and tropical regions (Chappell 1982; Bakken 1992; O'Neill & Kemp 1992; Armbruster & Berg 1994; Rutowski, Demlong & Leffingwell 1994; Ward & Seely 1996; Frears, Chown & Webb 1997; Schultz 1998).

The relationship between size and three measures of thermal biology was estimated by treating each size

group (species) as an individual observation. Implicit in this procedure is the assumption that the thermal biology of each species is independent and the relationship is similar at all levels of phylogenetic (taxonomic) organization. If species are not independent with respect to thermal biology, treating each species as a separate point inflates the degrees of freedom and confounds phylogenetic similarity with ecophysiological similarity. The risk is that species may show an apparent association between thermoregulatory capability and size because of common ancestry rather than a functional relationship between the variables (Felsenstein 1985; Pagel & Harvey 1991).

To test the likelihood that the apparent relationships were created by phylogenetic effects, the among-species comparisons were compared with among-family comparisons and analysis of phylogenetically based independent contrasts (Felsenstein 1985; Pagel 1992). The correlation and regression coefficients were statistically indistinguishable across the three analyses. This suggests that the relationship between size and thermoregulatory abilities is not strongly influenced by phylogenetic history in these bees, but rather is more strongly influenced by physical parameters of the bee (and the laws of thermal physics). However, it would be unwise to ignore phylogenetic effects in comparative physiological studies (Huey 1987). Indeed the greater ability of *Bombus* to maintain elevated T_{th} than would be expected from its body mass alone is correlated with phylogeny.

It was found that the differences in thermoregulatory capabilities between conspecific queen and worker bumble-bees and between male and female *Anthophora bomboidea* were adequately explained by their size differences (Figs 4, 6 and 8). However, our power to detect sex- or caste-related differences was not great, because the sample size was small and it was not the main aim of the study. In contrast, Stone (1993a,b) found significant differences in thermoregulatory abilities between sexes of *Anthophora* after controlling for effect of body size.

Our results suggest that thermoregulatory capability is strongly influenced by the biophysical constraints of body size, and in the subarctic, at least, adaptive divergence among solitary bees has not greatly altered this pattern. *Bombus* shows evidence of having adapted to cooler climates by slightly improved thermoregulation. There may be other groups of bees not conforming to the general size-thermoregulation relationship we have detected, and future studies may identify these. Nevertheless, body size appears to be the primary factor determining the thermoregulatory abilities of bees.

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