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Effects of climate on intra- and interspecific size variation in bumble-bees

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Summary

1. In contrast to other social bees, bumble-bees exhibit considerable size variation within the worker caste. This size variation has not been adequately explained, although it is known that larger workers tend to be foragers and smaller bees spend more time in the nest. We quantify size variation and mean size for foragers of 22 bumble-bee species inhabiting climates ranging from arctic and montane to the lowland tropics.

2. Mean size was larger in bee species from cold climates compared with temperate bumble-bees. Within species, individuals from Scotland tended to be larger than those from southern England. However, tropical bumble-bees (mostly belonging to the sub-genus *Fervidobombus*) were largest of all. We suggest that although a lower limit to size may be imposed by inhabiting cold climates, overheating does not constrain large size in bumble-bees from hot climates, perhaps because they have efficient mechanisms for heat loss through shunting heat to their extremities.

3. Tropical bees had shorter thoracic setae than species from cooler climates, while *B. terrestris* from Greece had shorter setae than those from southern UK. Presumably shorter setae enhance heat loss in warm climates.

4. Larger workers of *B. terrestris* were found to have smaller extremities, in proportion to their size, than small workers. We suggest that heat retention is more important in large bees that spend more of their time foraging, than in small bees which spend much of their time in the nest where incubation of the brood requires them to lose heat.

5. In the temperate climate of southern UK, we found no evidence for ambient temperature having a differential effect on activity of workers of *B. terrestris* according to their size. We suggest that, at least in temperate climates, size variation in bumble-bee foragers is probably not an adaptation to temperature variation. Instead it may improve colony foraging efficiency since foragers of different sizes are suited to, and tend to visit, different flower species.

Key-words: *Bombus*, Hymenoptera, insulation, temperature, thermoregulation

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Introduction

Bumble-bees (*Bombus* spp.) include approximately 250 species found predominantly in temperature, subarctic and montane regions of the northern hemisphere, with a small number of lowland tropical species (Williams 1998). Bumble-bee workers exhibit up to a tenfold variation in mass within species and even within single nests (Alford 1975; Goulson *et al*. 2002). In contrast, other eusocial bee species such as honey-bees and stingless bees generally exhibit less than a twofold variation in worker mass within nests (Waddington, Herbst & Roubik 1986; Ramalho, Imperatriz-Fonseca & Giannini 1998; Roulston & Cane 2000). This prominent difference has yet to be adequately explained.

What causes size variation in bumble-bee workers? In species such as *Bombus terrestris*, larvae spend most of their development in individual cells, and are fed directly by the adults (Alford 1975). Therefore the size attained by each larva is probably determined by the adults (Ribeiro 1994). Why do the adults rear workers of greatly varying size? In part the explanation may relate to division of labour according to size, known as alloethism. In a range of bumble-bee species, foragers have been found to be larger, on average, than bees that remain in the nest (Colville 1890; Sladen 1912; Meidell 1934; Richards 1946; Cumber 1949; Brian 1952; Free

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1955; Goulson *et al.* 2002). In honey-bees (*Apis mellifera*) all workers are approximately the same size. They begin life by working within the nest, and then all switch to foraging. It would thus not be possible for foragers to be larger than nest bees. By contrast, in bumble-bees large workers tend to switch from within-nest tasks to foraging at an earlier age than small workers, and the smallest workers may remain within the nest for their entire lives (Pouvreau 1989). Thus on average foragers are larger than nest bees.

A number of adaptive explanations have been proposed as to why foragers should be larger than nest bees, which relate to the greater foraging efficiency of large *vs* small bees (Goulson *et al.* 2002; Spaethe & Weidenmuller 2002; Spaethe & Chittka 2003), or to the improved ability of large bees to thermoregulate in inclement conditions (Free & Butler 1959; Heinrich 1979). Whatever the explanation as to why nest bees are smaller than foragers, it is notable that even among the larger forager class, there is still considerable size variation. In *B. terrestris*, thorax widths of all workers vary from 2·3 to 6·8 mm, with foragers varying from 3·3 to 6·8 mm (Goulson *et al.* 2002).

It seems likely that the optimal size of bumble-bee foragers is influenced by temperature. The thoracic temperature of a flying bumble-bee varies between upper and lower limits. If the muscle is too cold the wing beat frequency becomes too slow to fly, if too hot the bee is liable to die of heat prostration. *Bombus vosnesenskii* workers cannot fly if their thoracic temperature drops below 30 °C or exceeds 45 °C (Heinrich 1975). Given that the thermodynamic properties of objects are largely dependent upon size, workers of different sizes must experience different thermoregulatory constraints. A large bee will have a relatively small surface area to volume ratio and should therefore lose heat from convective cooling relatively slowly. This should enable a large worker to maintain its thoracic temperature in cold ambient temperatures with relative ease. Conversely, a small worker will experience a reduced risk of over-heating in hot ambient temperatures. This may make it advantageous for colonies to have foragers of a range of sizes, so that they have larger foragers suited to activity on cool days and smaller foragers for hot days (Goulson 2003).

In addition to notable size variation within species, there are marked differences in mean size between species (Sladen 1912; Alford 1975). Bergmann (1847) stated that for two similar endothermic species differing in size, we would expect the larger species to inhabit cooler climates. This rule has since been widely applied to intraspecific variation, but this was not Bergmann's intention (see James 1970; Blackburn, Gaston & Loder 1999). There is still controversy as to whether this role holds true, and there are certainly many exceptions (reviewed in Blackburn *et al.* 1999). Nonetheless, we may reasonably predict that, owing to thermoregulatory constraints, bumble-bee species living in cool climates will be larger than those inhabiting warmer climates, and also that geographical races of the same species will be larger in cooler climates.

Allen's rule (after Mayr 1942) states that 'protruding body parts, such as tail, ears, bill, extremities, and so forth, are relatively shorter in the cooler parts of the range of a species than in the warmer parts.' Both Allen's rule and Bergmann's rule are traditionally applied to endotherms such as mammals and birds, but some large insects such as bumble-bees are also endothermic when active. If large workers are adapted for foraging in cool conditions then we predict that they should have reduced extremities.

Another important determinant of heat loss/retention is external insulation, i.e. fur (or setae). Various insects insulate themselves with scales, air sacs and/or setae (Heinrich 1996). Compared with most other insects, bumble-bees have a thick coat of hair all over the body, especially around the thorax. We might expect bees from a relatively hot climate to have shorter setae than bees from a relatively cold one.

In this study we test whether variation in size and depth of thoracic insulation between species can be explained by the climate in which they live by examining both inter- and intraspecific size variation. Within *B. terrestris*, we test whether the proportions of worker extremities vary with size. We also examine the prediction that, within a species, small workers should be active in warmer conditions than large workers.

Materials and methods

Foraging workers of a range of bumble-bee species were obtained from the following sources:

1. Three commercial colonies of Greek *Bombus terrestris* obtained from Koppert UK Ltd (Haverhill, UK). Foragers were distinguished from nest bees through exhaustive monitoring (described in Goulson *et al.* 2002), and only foragers included in subsequent analyses.
2. Bumble-bee samples caught in southern England from 22 May to 27 August and in Scotland from 15 June to 10 August 2003 (13 species in total). All of the species are univoltine with the exception of *B. pratorum*, which sometimes has a partial second brood in late summer. For this species, specimens caught correspond to the first (main) generation.
3. Museum specimens of non-UK species examined in the Department of Entomology, Natural History Museum, London. Five species were selected that inhabit cool climates, and five from hot (Mediterranean or tropical) climates.

Species and sample sizes are given in Table 1. The size of all specimens was estimated as the maximum width of the thorax, measured using Vernier callipers, following Goulson *et al.* (2002).

Coefficients of size variation were calculated for each species, and separately for each population where

Table 1. Mean thorax widths and coefficients of variation in foraging workers from 23 *Bombus* species.

Subgenus	Species (location)	*N*	Mean thorax width (mm ± SE)	Range (mm)	Coefficient of variation (*a*)
Bombus	*B. lucorum* (England)	134	4·87 ± 0·027	3·9–5·6	0·076
	B. lucorum (Scotland)	85	4·70 ± 0·041	3·8–5·8	0·065
	B. magnus (Scotland)	122	4·95 ± 0·041	3·3–6·0	0·091
	B. terrestris (England)	278	4·99 ± 0·024	3·6–6·3	0·081
	B. terrestris (Greece)	216	4·86 ± 0·028	3·6–6·3	0·085
Kallobombus	*B. soroeensis* (England)	22	4·22 ± 0·060	3·4–4·6	0·067
Megabombus	*B. hortorum* (Scotland)	158	4·74 ± 0·034	3·6–5·7	0·091
Melanobombus	*B. lapidaries* (England)	280	4·35 ± 0·017	3·5–5·1	0·064
	B. lapidarius (Scotland)	105	4·46 ± 0·041	3·1–5·9	0·094
Thoracobombus	*B. humilis* (England)	96	4·43 ± 0·060	3·2–6·5	0·133
	B. muscorum (England)	56	4·35 ± 0·074	3·1–6·5	0·127
	B. muscorum (Scotland)	451	4·94 ± 0·022	3·5–6·5	0·094
	B. pascuorum (England)	62	4·17 ± 0·051	3·4–5·5	0·087
	B. pascuorum (Scotland)	193	4·50 ± 0·031	3·2–6·2	0·095
	B. ruderarius (Scotland)	189	4·70 ± 0·036	3·3–6·2	0·106
	B. sylvarum (England)	55	4·11 ± 0·050	3·2–5·0	0·091
Alpinobombus	*B. alpinus* (Scandinavia)	32	5·28 ± 0·089	4·3–6·6	0·095
	B. balteatus (Scandinavia)	30	4·59 ± 0·093	3·7–5·8	0·112
Pyrobombus	*B. huntii* (southern USA)	23	5·13 ± 0·250	3·9–7·6	0·234
	B. pratorum (England)	189	4·21 ± 0·022	3·5–5·7	0·072
	B. jonellus (Scandinavia)	30	4·18 ± 0·059	3·5–4·9	0·077
	B. jonellus (Scotland)	283	4·29 ± 0·029	3·0–6·2	0·114
	B. lapponicus (Scandinavia)	30	5·31 ± 0·183	3·7–6·8	0·189
Fervidobombus	*B. atratus* (Neotropics)	30	5·23 ± 0·073	3·6–5·8	0·077
	B. dahlbombii (Peru, high Andes)	30	6·01 ± 0·125	4·9–7·5	0·114
	B. medius (Neotropics)	23	5·03 ± 0·146	3·1–7·0	0·139
	B. mexicanus (Neotropics)	21	4·84 ± 0·082	4·0–5·5	0·077
	B. transversalis (Neotropics)	30	6·21 ± 0·087	5·3–7·4	0·076
Honey-bee	*Apis mellifera**	53			0·018

*Taken from Roulston & Cane (2000).

the same species was sampled in southern UK and in Scotland. For museum specimens, it is assumed that bees had been sampled without size bias aside from the fact that they are all likely to have been foraging workers. To examine patterns of variation in size of bumble-bee foragers with climate, each population sampled was categorized as being from a cool climate (Scotland, Scandinavia, high Andes), temperate climate (southern England) or hot climate (Greece, southern USA, neotropics).

The thoracic setae length was measured for the 10 *Bombus* species examined at the Natural History Museum, using vernier callipers (destructive sampling of these specimens was not possible). To examine the relationship between setae length, body size and climate, more detailed studies were carried out on *B. terrestris*. For 34 wild-caught southern English foragers and 51 foragers of Greek origin (from Koppert UK Ltd), the head was removed and the width measured using a microscope and eyepiece graticule. This is more accurate than measuring thorax width with callipers, but only possible when specimens can be destructively sampled. Thoracic setae were removed from the posterior dorsal region of the thorax using a scalpel. Five thoracic setae were then randomly selected and measured under the microscope. The mean length of the five setae was used in analyses. Setae length data were analysed using GLM in SPSS, with head width as a covariate and origin (UK or Greece) as a fixed factor.

To examine whether workers varying in size differ in the proportions of their body parts, the mass of the thorax, abdomen, head and legs of 60 Greek *B. terrestris* from commercial colonies were measured using an Oertling NB33 fine balance (Oertling, Maidstone, Kent, UK). Bees had been previously killed by freezing. To determine the relationship between bee size and relative size of abdomen, head and limbs, the ratio of each, for example abdomen mass/thorax mass, was calculated then related to bee thorax width.

To determine whether, within species, foragers of differing size tend to be active in different weather conditions, we observed six replicate patches of *Rubus fruticosus* agg. at Chilworth, Hampshire, UK, from 14 June until 7 July 2003. The number of large and small *Bombus terrestris* workers that visited each patch during a period of 5 min was recorded. Workers were classified as large/small depending on their size relative to an average sized pinned worker (4·9 mm thorax width). This was repeated for all six patches on 32 separate occasions during the trial period. The ambient temperature was recorded during each visit (and varied from 18·2 to 33·5 °C). Data were analysed in

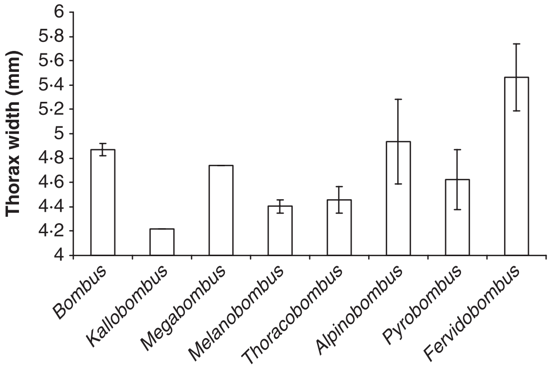

Fig. 1. Mean thorax width of foraging workers of representatives of eight bumble-bee subgenera (±SE). Sample sizes are given in Table 1.

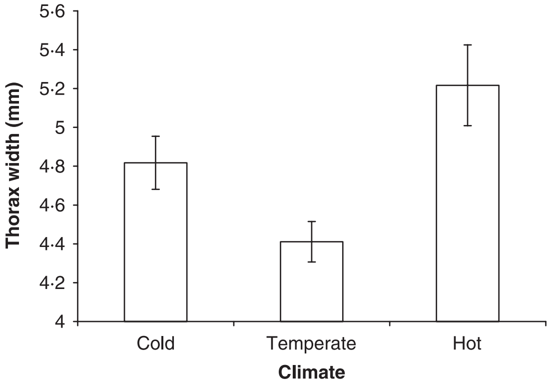

Fig. 2. Mean thorax width of foraging workers of bumble-bee species according to the climate they inhabit.

GLIM with binomial errors, using the proportion of small bees as the dependent variable and ambient temperature and patch as explanatory factors.

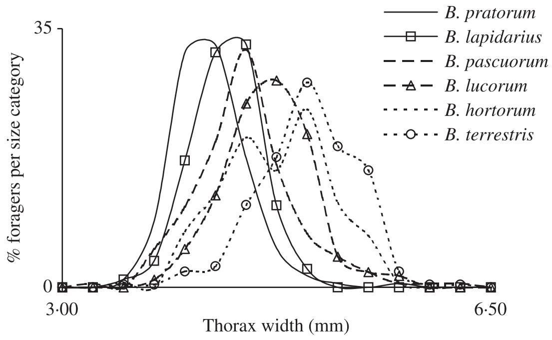

Fig. 3. Size variation among foraging workers in six common and sympatric UK *Bombus* species. Size categories were defined by 0·25 mm divisions.

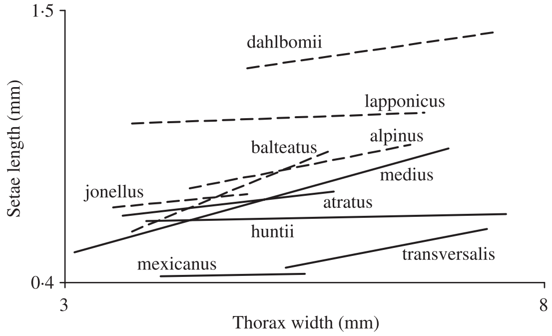

Fig. 4. Size-related thoracic setae length in 10 species of *Bombus* from two climatic extremes. These linear regression lines show a general positive relationship between setae length and thorax width. Cold climate species are represented by dotted lines, hot climate species by solid lines. *B. dahlbombii*, $y = 0{\cdot}056x + 0{\cdot}99$; *B. lapponicus*, $y = 0{\cdot}015x + 1{\cdot}0$; *B. alpinus*, $y = 0{\cdot}087x + 0{\cdot}045$; *B. balteatus*, $y = 0{\cdot}16x + 0{\cdot}018$; *B. medius*, $y = 0{\cdot}11x + 0{\cdot}19$; *B. jonellus*, $y = 0{\cdot}039x + 0{\cdot}57$; *B. atratus*, $y = 0{\cdot}044x + 0{\cdot}51$; *B. huntii*, $y = 0{\cdot}007x + 0{\cdot}62$; *B. transversalis*, $y = 0{\cdot}074x + 0{\cdot}069$; *B. mexicanus*, $y = 0{\cdot}007x + 0{\cdot}40$.

Results

The different bumble-bee species and populations examined differed in mean size ($F_{27,3283} = 77{\cdot}4$, $P < 0{\cdot}001$) (Table 1). This relationship remained when populations of the same species from different geographical regions were pooled ($F_{21,3289} = 90{\cdot}4$, $P < 0{\cdot}001$). Mean size per species differed between subgenera, the largest being the neotropical *Fervidobombus*, and the smallest *Kallobombus* (represented only by *B. soroeensis*) ($F_{7,20} = 3{\cdot}16$, $P = 0{\cdot}020$) (Fig. 1). Species and populations from hot or cold climates tended to be large, while those from temperate climates tended to be small ($F_{2,25} = 5{\cdot}97$, $P = 0{\cdot}008$) (Fig. 2). Thus for example the largest species were *B. transversalis* from the lowland neotropics, and *B. dahlbombii* from the high Andes, while the smallest four species were all from temperate southern UK (*B. sylvarum*, *B. pascuorum*, *B. pratorum* and *B. soroeensis*). Four species were sampled both in Scotland and southern England (Table 1). Overall, populations in Scotland were significantly larger than those from southern UK (two-way analysis of variance on size according to species and locality, $F_{1,1308} = 32{\cdot}4$, $P < 0{\cdot}001$).

Measures of mean size obscure considerable size variation within all bumble-bee species (Fig. 3 and Table 1). For example the six most abundant UK species differ in mean size, but overlap almost entirely in the range of forager sizes (Fig. 3). Size variation as measured by the coefficient of variation of each species did not differ among subgenera ($F_{7,20} = 1{\cdot}05$, NS) or with latitude ($F_{2,25} = 1{\cdot}28$, NS).

On average, setae length of species from cold climates were longer than that of species from hot climates ($F_{1,275} = 17{\cdot}85$; $P < 0{\cdot}0001$) (Table 2), although there was no significant difference in thorax width between the two groups ($F_{1,9} = 0{\cdot}285$, NS) (Fig. 4). An independent comparisons test to take into account phylogenetic non-independence cannot be carried out because the phylogeny of *Bombus* is poorly understood and published phylogenies do not include all of the species studied here. Therefore these results must be treated with caution. Nonetheless, it is worth noting

Table 2. Summary of relative thoracic setae length in bumble-bee species from hot and cold climates

Climate	Subgenus	Species	*N*	Mean setae length (mm)
Cold	*Alpinobombus*	*alpinus*	32	0·86 ± 0·026
Cold	*Alpinobombus*	*balteatus*	30	0·75 ± 0·027
Cold	*Fervidobombus*	*dahlbomii*	30	1·33 ± 0·042
Cold	*Pyrobombus*	*jonellus*	30	0·73 ± 0·024
Cold	*Pyrobombus*	*lapponicus*	30	1·07 ± 0·028
Hot	*Fervidobombus*	*atratus*	30	0·74 ± 0·018
Hot	*Pyrobombus*	*huntii*	23	0·66 ± 0·029
Hot	*Fervidobombus*	*medius*	23	0·73 ± 0·025
Hot	*Fervidobombus*	*mexicanus*	21	0·43 ± 0·018
Hot	*Fervidobombus*	*transversalis*	30	0·53 ± 0·015

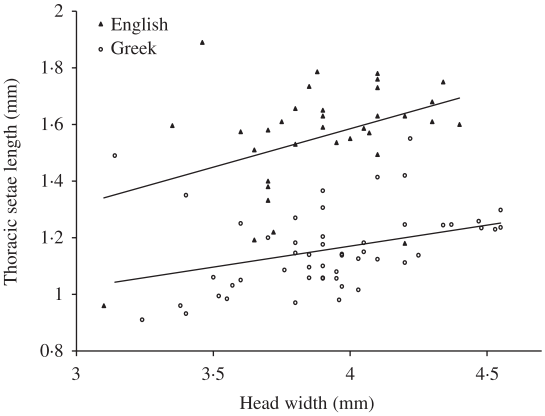

Fig. 5. Size-related thoracic setae length in two races of *Bombus terrestris* (English and Greek). For English bees, $y = 0{\cdot}27x + 0{\cdot}50$. For Greek bees, $y = 0{\cdot}15x + 0{\cdot}58$.

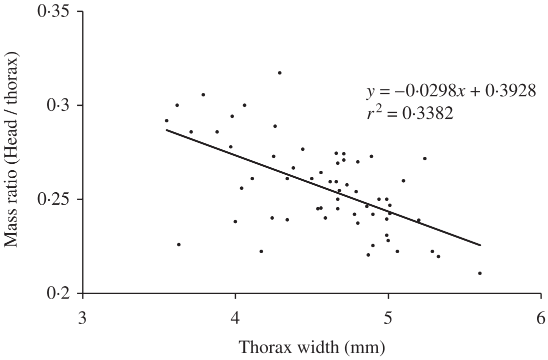

Fig. 6. The relationship between thorax width and the head: thorax mass ratio in *Bombus terrestris* workers.

that where subgenera span different climatic regions, differences in mean setae length are often significant. For example within the subgenus *Fervidobombus*, the cold climate dwelling *B. dahlbomii* has significantly longer setae than the warm climate dwelling *B. atratus* (Fisher's PLSD: $P < 0{\cdot}0001$), *B. medius* (Fisher's PLSD: $P < 0{\cdot}0001$), *B. mexicanus* (Fisher's PLSD: $P < 0{\cdot}0001$) and *B. transversalis* (Fisher's PLSD: $P < 0{\cdot}0001$) and within the subgenus *Pyrobombus,* the hot climate dwelling *B. huntii* has significantly shorter hair than *B. lapponicus* (Fisher's PLSD: $P < 0{\cdot}0001$).

In *B. terrestris*, thoracic setae length was positively correlated with head width ($F_{1,81} = 13{\cdot}58$, $P < 0{\cdot}001$) and differed between Greek and UK races ($F_{1,83} = 117{\cdot}23$, $P < 0{\cdot}001$): for a given body size, English *B. terrestris* workers had significantly longer setae than the Greek subspecies (Fig. 5). There was no difference in mean head width between the samples of the two races ($F_{1,83} = 0{\cdot}13$, NS).

As one would expect, abdomen mass ($T_{1,59} = 16{\cdot}3$, $P < 0{\cdot}0001$), head mass ($T_{1,59} = 21{\cdot}6$, $P < 0{\cdot}001$) and leg mass ($T_{1,59} = 12{\cdot}0$, $P < 0{\cdot}001$) were all positively correlated with thorax mass. The abdomen : thorax mass ratio was negatively correlated with thorax width ($F_{1,49} = 6{\cdot}09$, $P < 0{\cdot}05$, $y = -0{\cdot}084x + 1{\cdot}28$, $r^2 = 0{\cdot}11$) as were the head : thorax mass ratio ($F_{1,59} = 29{\cdot}1$, $P < 0{\cdot}001$, $y = -0{\cdot}030x + 0{\cdot}39$, $r^2 = 0{\cdot}34$) (Fig. 6) and the leg : thorax mass ratio ($F_{1,59} = 9{\cdot}28$, $P < 0{\cdot}01$, $y = -0{\cdot}026x + 0{\cdot}347$, $r^2 = 0{\cdot}14$). These relationships show that, compared with their thorax size, bigger workers have relatively light abdomens, heads and legs.

The total number of *B. terrestris* workers observed foraging on *R. fruticosus* was greater on hot days than on cold days ($F_{1,20} = 4{\cdot}49$; $P < 0{\cdot}05$). The number of large workers *vs* the number of small workers observed was independent of the ambient temperature ($F_{1,106} = 0{\cdot}01$, NS).

Discussion

We confirm that bumble-bee foragers exhibit considerable size variation both within and between species. As predicted, species from cool climates tended to be larger than those from temperate climates, and in three out of four species sampled in both cool and temperature climates, the populations from cool climates were larger. Contrary to expectation, species from hot climates were largest of all. We would expect these bees to be susceptible to overheating. However, bumble-bees have means of increasing heat loss if required, particularly by increasing the flow of warm haemolymph from the thorax to the abdomen (Heinrich 1979). Moreover, the species from hot climates tended to have shorter thoracic setae, and thus less insulation, presumably to aid heat loss. This pattern occurred both among species, and among races of *B. terrestris*. Although there is good evidence to suggest that bumble-bees have a minimum temperature for activity and that this is related to size, there is no evidence that natural temperatures encountered by bumble-bees exceed the maximum with which they can cope (Heinrich 1979). Presumably heat transfer to the abdomen and low insulation of the thorax enable tropical bumble-bees to remain active despite their large size. Of course this does not explain why these bumble-bee species are large. Perhaps the lack of seasonality in the tropics and a greater abundance of floral resources allow production of larger workers, or perhaps other ecological conditions such as predation pressure favour large size. Rather little is known of the ecology of the small number of bumble-bee species found in the tropics, so it is not possible to draw conclusions. It must also be noted that the tropical bumble-bees are overwhelmingly dominated by a single genus (*Fervidobombus*), so that their large size could be a phylogenetic artefact. An independent comparisons test to take into account phylogenetic effects was not possible owing to inadequate knowledge of the phylogeny, and would have little power with the number of species examined here, so these results must be treated with caution. Also, our analysis considers only climatic variation in temperature, but other aspects of climate are likely to be important. For example precipitation is likely to strongly influence nectar availability, so that we might expect larger (and thus more energetically costly) bees in wetter climates such as the lowland tropics.

In *B. terrestris* foragers the mass of the abdomen, head and legs were all positively correlated with thorax width, but more interestingly these relationships were not directly proportional. In all three cases larger bees had smaller heads, legs and abdomens relative to their thorax size. This may indicate an adaptation to temperature, allowing larger workers to conserve heat in cold weather and smaller workers to lose heat in hot weather more effectively by further reducing/increasing their surface area to volume ratio. From the perspective of small workers, there are potential advantages to having a large head, legs and abdomen. Firstly, larger extremities will facilitate cooling in high ambient temperatures more than small extremities by increasing the body's overall surface area relative to volume. Smaller workers forage less and spend more time in the nest (Goulson *et al*. 2002), where one of their tasks is maintenance of a high nest temperature for incubation of the brood; to do this they need to lose heat from their thorax which will be facilitated by large extremities. Losing heat via the head occurs in honey-bees (Cooper, Schaffer & Buchmann 1985), Yellowjacket Wasps (Coelho & Ross 1996) and Carpenter Bees (Heinrich & Buchmann 1986). A larger head can also accommodate larger eyes. Spaethe & Chittka (2003) have shown that in *B. terrestris*, larger eyes are superior at resolving objects allowing efficient sighting of floral resources. Secondly, the amount of pollen a bee can carry is probably dependent on the length of the corbiculum. Thorax width in *Bombus terrestris* workers is positively related to corbicula hair length (Goulson *et al*. 2002) so it is possible that small workers can carry a greater amount of pollen than large workers, relative to their mass. Finally, a larger abdomen can contain more nectar than a smaller one, which may be useful while foraging or when performing nest duties.

From the perspective of large workers, there are also potential advantages to having reduced extremities. Small extremities should minimize heat loss in low ambient temperatures by reducing the overall surface area of the body, and since large foragers do most of the foraging, they are more exposed to low temperatures than smaller bees. Making smaller extremities also reduces the nutritional input.

Despite the evidence that size is an important determinant of thermoregulatory ability in bumble-bee foragers, we found no evidence for workers of different size tending to forage in different weather conditions. It has been suggested that one advantage of the production of a range of worker sizes may be that this ensures that whatever the temperature, at least some workers will be able to forage efficiently (Goulson *et al*. 2002). This does not appear to be the case. During our study of *B. terrestris* forager sizes on patches of flowers, ambient temperature was generally high (18·2–33·5 °C). No differences were observed in the mean size of foragers according to temperature. It seems likely that this temperature range did not fall below the minimum required for activity of small bees, or go above the maximum for activity of large bees.

Why then do bumble-bees produce foragers of such varying size, compared with other social bees? The answer may lie in their evolutionary past, for bumble-bees are thought to have originated in the mountains of central Asia (Williams 1985) where temperatures probably fluctuate more than in southern UK. It would be interesting to examine whether bumble-bee size variation and the magnitude of temperature fluctuations within their flight period are correlated.

Alternatively, having foragers of a range of sizes may be unrelated to climate, but may enable the colony to efficiently exploit a range of floral resources. Workers of different sizes are known to visit different flowers. It has long been known that interspecific differences in tongue length between bumble-bee species explain differences in foraging preferences, with long-tongued bees tending to visit flowers with deep corollae (Inouye 1978, 1980; Pyke 1982; Barrow & Pickard 1984; Harder 1985; Johnson 1986; Graham & Jones 1996). Within species, tongue length correlates with size, so we would expect workers of different size to favour visiting different flowers, and there is some evidence that this is so (Harder 1985; Prys-Jones & Corbet 1991; Peat *et al*., in press). Aside from its influence on tongue length, size has other implications when foraging. Small bees may be better able to crawl into deep flowers, while large bees may have advantages in 'tripping' the flowers of Fabaceae such as *Cytisus scoparius*. If bees of different size from the same colony each specialize in flower types appropriate to their morphology, this will minimize intracolony competition. Differences in size between sympatric species, as found in UK bumble-bees, may reduce interspecific competition in the same way, allowing species that are in other ways very similar to coexist.

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