

## Body Size and Shape of the Large Carpenter Bee, *Xylocopa virginica* (L.) (Hymenoptera: Apidae)

DIMITRI A. SKANDALIS, GLENN J. TATTERSALL, SEAN PRAGER,  
AND MIRIAM H. RICHARDS\*

Dept. Biological Sciences, Brock University, St. Catharines, Ontario,  
Canada, L2S 3A1

**ABSTRACT:** In bees, both body size and shape may show considerable variation associated with differences between females and males, among populations, and due to local environmental variation. We studied multiple parameters of body size and shape of the large carpenter bee *Xylocopa virginica*, to understand how body size and shape are influenced by sex, and by seasonal and annual variation. In addition, we compared bees from a population near the northern edge of the range (southern Ontario, ON) which experience relatively severe winters, to bees from the central portion of the range (Maryland, MD), which experience milder winters. Overall, males and females differed in linear dimensions but were more or less the same mass. Seasonal variability was investigated using ON bees. In winter, females and males had the same overall mass, but male thoracic volume and linear dimensions such as head capsule width, intertegular width, and costal vein length, were all larger for a given mass. In summer, males weighed less than females, due to loss of mass from the abdomen. Year-to-year differences in size and shape were indicated in MD bees, which exhibited significant differences in linear dimensions and dry mass, but not wet mass. In addition, northern bees were smaller than southern bees in terms of linear dimensions, but it is not entirely clear if overwintering mass differs. We suggest that seasonal and sex differences in size are related to the different flight activity patterns of males and females in summer, and that geographic differences between the two populations are related to the length and duration of winters.

**KEY WORDS:** sexual dimorphism, morphometry, geographic variation

*Xylocopa virginica* is the most common large carpenter bee in eastern North America, with a range extending through the entire eastern United States and into Canada (Hurd, 1955). Across its range, *X. virginica* encounters a huge variety of local environmental conditions which together may induce epigenetic effects that result in modification to their body proportions (Emlen and Allen, 2003). As a result, bee body size and shape is likely to reflect the influence of geographic, seasonal, and interannual variability in local environments (Richards and Packer, 1996). In addition, differences in the ecology and behavior of males and females are expected to generate further variation in body size and shape.

*Xylocopa virginica* is univoltine throughout its range (Gerling and Hermann, 1978). Both sexes overwinter together, but males generally emerge from overwintering hibernation before females. Males are highly territorial, and body size influences their behaviour: large males are more likely to be territorial around female nest sites, whereas small males disperse to other sites, such as foraging sites, and other landmarks where females may be encountered (Baird, 1986; Barthell and Baird, 2004). Most female flight activity consists of flights to flowers in search of food, whereas most male flight activity involves long periods of hovering flight,

---

\* Corresponding author: Miriam H. Richards, Dept. Biological Sciences, Brock University, St. Catharines, ON L2S 3A1, Canada; Phone 905 688 5550, x4166; Fax 905 688 1855; E-mail: mrichards@brocku.ca

interspersed with fast chases of intruders (Barrows, 1983; Barthell and Baird, 2004; Barthell *et al.*, 2006). Differences in linear body dimensions, especially of the thorax, might influence the efficiency of costly flight behaviors such as hovering (e.g., Roberts *et al.*, 2004).

The activity patterns of female *Xylocopa* in summer are quite different than those of males, and mostly comprise commuting between their nests and patches of flowers as they gather nectar and pollen to provision brood. Large body size is probably an advantage to females, both in aggressive encounters with other females (Richards and Packer, 1996) and in foraging, as large females likely can carry larger pollen or nectar loads, and can probably fly longer distances to flower patches (Cartar, 1992; Stone, 1993; Gathmann *et al.*, 1994; Kim, 1997; Strohm and Linsenmair, 1997; Tomkins *et al.*, 2001; Pereboom and Biesmeijer, 2003). Proximately, in mass provisioning bees like *X. virginica*, adult body size is directly determined by the amount of pollen and nectar provided to larvae (Danforth, 1990), and so is indirectly linked to maternal foraging efficiency. Within a breeding season, female foraging is influenced both by physical wear (Cartar, 1992; Alcock *et al.*, 2006), and by local weather conditions which influence foraging time and resource availability (Minckley *et al.*, 1994; Richards, 2004). Therefore, as resource availability varies within and between seasons, as well as among habitats, bee body size should also vary from year to year and among populations in different geographic areas.

In this paper, we investigate variation in body size in *X. virginica* from two different populations, one in the middle of the species' geographic range (Maryland) and one near the northern edge of its range (southern Ontario). We focus on linear dimensions of the head, thorax, and forewing, and on different components of body mass, to investigate sexual dimorphism, interseasonal and interannual variation within populations, and latitudinal variation between populations. We also use these data to comment on the practicality and usefulness of estimating body size from single linear dimensions, in this bee.

## Methods

### *Specimen Collection and Storage*

In the winters of 2005 and 2006, wooden boards containing nests were collected from the campus of the USDA Beltsville Agricultural Research Station, Beltsville, Maryland (39°N, 76°W), and from residential sites in St. Catharines, Ontario (43°N, 79°W). All specimens were collected at external temperatures of <10°C, and housed in the laboratory at Brock University between -1 and 0°C. In Maryland, 43 carpenter bees (22 females, 21 males) were collected from 12 nests on 15 March 2005 (MD 2005 population), and 42 bees (20 females, 22 males) were collected from 7 nests on 26 January 2006 (MD 2006 population). In Ontario, 54 wintering adults (40 females, 14 males) were collected from 12 nests (ON 2006 population), on 10 January 2006. A smaller sample of flying summer bees (eight females and seven males) was collected on 2 June 2007 near a nesting site on the Brock University campus, St. Catharines.

We compared our values to carpenter bee masses in the literature, from Athens, Georgia (GA: ca. 34°N, collected during winter hibernation; Gerling and Hermann, 1978) and New Jersey (NJ: ca. 39–41°N, collected during spring foraging; Baird, 1986). Barthell and Baird (2004) have also published head capsule width

measurements for males from Wellston, Oklahoma (OK: ca. 36°N). Literature values are not included in any statistical analyses which we report.

### *Masses and Morphometry*

Bees were weighed immediately upon returning to the laboratory (the wet mass) and then killed by freezing. The specimens were desiccated at 60°C until two successive weight measurements yielded a difference of <1.0 mg (<0.5% of dry mass). Water mass was calculated as the difference between wet mass and dry mass. The costal vein length (CVL) to the nodus (a measure of wing length that can be used even for individuals with heavily damaged wings whose total wing length cannot be measured accurately) was measured with a handheld ocular (1/10 mm resolution), intertegular width (ITW) was measured on a microscope (1/10 mm resolution), and head capsule width (HW) and the length, width, and depth of the thorax (mesosoma) were measured with digital calipers (1/100 mm resolution). From the thoracic linear measurements, we estimated the total volume of the thorax according to the equation for an ellipsoid volume,  $4/3\pi abc$ , where  $a, b, c$  are the radii of length, width, and depth (Bishop and Armbruster, 1999).

In spring of 2007, the heads, thoraces, abdomens, and legs of Ontario bees were weighed separately, to determine the contributions of each body part to the wet and dry weights. Linear measurements were also obtained from these bees. After estimating the thoracic volume for this sample of bees, we applied the density value for mammalian striated muscle, 1.06 g/mL (Dudley, 2000), to estimate the mass of the thorax that we would expect for a given set of thoracic linear dimensions, provided that the thorax is composed primarily of muscle.

Statistical analyses were carried out using SAS 9.1.3. Principal components analysis (PCA) was used to group similar measurement variables and thus reduce the number of comparisons among different groups of bees. To minimize pseudoreplication caused by treating nestmates as independent data points, we averaged over the males and females separately in each nest. Using nest means did not produce qualitatively different results than considering all individuals independently. Relationships among different components of body size were modeled using general linear modeling and ANOVA. Patterns suggested with PCA were confirmed with two-way ANOVA on each measurement variable separately (by sex and location); partial effects were based on Type III SS. For these analyses, 2005 and 2006 data from MD were pooled, but inclusion of a term for differences between these two years gave qualitatively the same results for all variables except ITW. All results are reported as model or partial F scores, as appropriate.

## Results

The body size measurements of male and female *X. virginica* from Maryland and Ontario are reported in Table 1. The results of the PCA considering all wintering bees (MD and ON together) are reported in Table 2. The eight measurement variables were reduced to three principal components, with the first principal component (PC1) broadly describing the size of the thorax, PC2 describing body mass (both wet and dry), and PC3 describing HW. The strong differentiation of body measurements onto different PCs demonstrates independence in the variation of different body parts.

### *Sex and Population Differences*

To avoid complications due to seasonal variation, body size differences between the sexes and between MD and ON were analyzed with respect to bees collected in winter only (Fig. 1). Overall, males were larger than females in terms of their linear dimensions (PC1: Type III SS,  $F = 8.07$ , d.f. = 1,  $P = 0.007$ ), although females had wider heads (PC3:  $F = 110.34$ , d.f. = 1,  $P < 0.0001$ ). The masses of the two sexes were more or less similar (PC2) regardless of source population. When considering both sexes together, bees from MD were larger than bees from ON, based on linear dimensions (PC1:  $F = 57.68$ , PC3:  $F = 23.9$ , d.f. = 1,  $P < 0.0001$ ), but ON bees were significantly heavier (PC2:  $F = 9.15$ , d.f. = 1,  $P < 0.0001$ ). This latter effect was due primarily to the heavier weights of the sample of ON males (collected in winter 2006), which were much heavier than any other group of bees (Table 1).

The above patterns were examined in greater detail using each of the eight measurement variables separately, and using the same two-way ANOVA model. All variables, analyzed separately, followed the same patterns as noted above. Moreover, when an additional term was added to the ANOVA to account for differences between 2005 and 2006 in the MD bees, qualitatively the same sex and population results were obtained.

Although there were no significant overall differences in mass between females and males (above), differences in their linear dimensions (Table 1) suggested differences in the anatomical distributions of mass. To determine sources of variation in mass between the sexes, we sectioned the summer 2007 bees and weighed their heads, thoraces, abdomens, and legs separately (Fig. 3a). A new PCA was performed considering all linear dimensions, and also the wet and dry masses of the body parts. Measurements unrelated to the thorax formed PC1 (HW, wet and dry masses of the head, legs, and abdomen), and thoracic components formed PC2 (length, width, depth, and wet mass of the thorax, ITW, CVL). Overwintering males had the largest thoracic dimensions, while spring males and females differed only in components unrelated to the thorax (PC1:  $F = 109.58$ , d.f. = 1,  $P < 0.0001$ , PC2:  $F = 0.85$ , d.f. = 1,  $P = 0.3743$ ), primarily HW and abdominal wet mass (Fig. 3b).

Thoracic mass was virtually indistinguishable between females and males collected in the summer (Fig. 3a), although females had slightly more water for a given dry mass (data not shown). This contrasts with our observation that in wintering bees, males had significantly larger thorax volume (Table 1). To examine differences in the thorax more closely, we calculated a theoretical muscle mass based on bees' estimated thoracic dimensions (see Methods). We found that males had a lower thoracic mass than predicted, while females had a greater thoracic mass than predicted (Fig. 3c).

Finally, since mass can vary temporally (see below) and so may not always be a good measurement of overall size, we used estimated thoracic volume as an indicator of overall body size in all the wintering bees, to find how well it predicted other components of body size. HW showed the tightest correlation with thoracic volume (Fig. 4a), ITW and CVL showed weaker relationships (Fig. 4b, c), and wet mass was unrelated (Fig. 4d). Thoracic volume increased proportionately with ITW and CVL in both sexes, and males had a larger thoracic volume for a given wet mass (Fig. 4d). This suggests that while males of a given body size have proportionately smaller HW than females, and may contain less water, the overall body plan of *X. virginica* is consistent between the sexes.

Table 1. Parameters of body size used in this study of Maryland (MD) and southern Ontario (ON) bees. Head capsule width (HW), intertegular width (ITW), and costal vein length (CVL) are commonly reported proximate measures of body size. Thorax length, width, and depth can be measured to provide an estimate of thoracic volume, which we have used as an indicator of the true "size" of an individual. Wet mass and dry mass were measured to contrast with the size estimated from the linear dimensions.

	Females			
	MD 2005 (winter)	MD 2006 (winter)	ON 2006 (winter)	ON 2007 (summer)
HW (mm)	7.33 ± 0.18 (42)	7.20 ± 0.23 (15)	6.68 ± 0.30 (38)	6.78 ± 0.17 (8)
ITW (mm)	6.1 ± 0.3 (42)	5.8 ± 0.3 (14)	5.6 ± 0.4 (38)	6.0 ± 0.43 (8)
CVL (mm)	6.6 ± 0.3 (33)	6.4 ± 0.2 (20)	6.1 ± 0.4 (39)	6.5 ± 0.3 (8)
Thoracic length (mm)	7.43 ± 0.31 (39)	7.17 ± 0.27 (14)	6.72 ± 0.45 (36)	6.98 ± 0.26 (8)
Thoracic width (mm)	8.02 ± 0.27 (39)	7.86 ± 0.30 (14)	7.40 ± 0.38 (36)	7.48 ± 0.25 (8)
Thoracic depth (mm)	7.00 ± 0.26 (39)	6.90 ± 0.27 (14)	6.44 ± 0.32 (36)	6.29 ± 0.23 (8)
Thoracic volume (mm <sup>3</sup> )	219 ± 22 (39)	204 ± 22 (14)	169 ± 27 (36)	172 ± 17 (8)
Wet mass (mg)	57.28 ± 9.70 (21)	59.81 ± 9.54 (19)	58.22 ± 8.95 (39)	55.93 ± 8.74 (8)
Dry mass (mg)	22.20 ± 4.09 (19)	24.59 ± 4.53 (18)	26.41 ± 6.56 (39)	22.63 ± 5.15 (8)

### *Temporal Variation within Populations*

Bees from Maryland were collected during the same season (winter) and so are appropriate for investigating annual variation in body size (Figure 1). We used the PC scores obtained by considering all wintering bees simultaneously. Bees in 2005 were larger than in 2006 on PC1 ( $F = 6.11$ , d.f. = 1,  $P = 0.02$ ), but not PC2 ( $F = 1.26$ , d.f. = 1, ns) or PC3 ( $F = 0.09$ , d.f. = 1, ns). The significance of PC1 reflects significant differences between years in each linear dimension (minimum  $F > 4.08$ , d.f. = 1,  $P < 0.05$ ). The lack of difference in PC2 obscures the fact that wet mass was not significantly different between years ( $F = 2.34$ , d.f. = 1, ns), whereas dry mass was greater in 2005 ( $F = 7.91$ , d.f. = 1,  $P = 0.009$ ).

Differences between bees collected in winter 2006 and in summer 2007 were investigated using specimens collected in Ontario. Fig. 2 indicates that males collected in summer 2007, were significantly smaller than all other ON bees (including females), either a seasonal effect or some special circumstances for males in 2007. Therefore we analyzed males and females separately. As in the larger data set, PC1 described variability in external measurements, PC2 described body mass, and PC3 described HW (data not shown). Summer 2007 males were significantly smaller than winter 2006 males, especially in terms of mass (PC2:  $F = 102.45$ , d.f. = 1, 11,  $P < 0.0001$ ) but also in terms of HW (PC3:  $F = 13.77$ , d.f. = 1, 11,  $P = 0.0015$ ; no difference in PC1:  $F = 0.06$ , d.f. = 1, 19, ns). Summer 2007 females were somewhat lighter than winter 2006 females (PC2:  $F = 10.97$ , d.f. = 1, 41,  $P = 0.0019$ ), although there was no difference in their linear dimensions (PC1:  $F = 1.07$ , PC3:  $F = 1.11$ , both d.f. = 1, 41, ns).

## Discussion

### *The Carpenter Bee Body Plan*

We used PCA on wintering individuals to examine how multiple, commonly reported measurements of bee size vary within and between populations of *X. virginica*. The relationships among these variables are indicated by their factor loading

Table 1. Extended.

Males			
MD 2005 (winter)	MD 2006 (winter)	ON 2006 (winter)	ON 2007 (summer)
6.69 ± 0.19 (41)	6.56 ± 0.26 (12)	6.05 ± 0.16 (14)	6.23 ± 0.15 (7)
6.4 ± 0.4 (38)	6.0 ± 0.2 (11)	5.8 ± 0.2 (14)	6.5 ± 0.4 (7)
6.9 ± 0.3 (40)	6.7 ± 0.3 (22)	6.3 ± 0.3 (14)	6.8 ± 0.4 (7)
7.90 ± 0.36 (40)	7.52 ± 0.26 (11)	7.18 ± 0.25 (14)	7.41 ± 0.33 (7)
8.27 ± 0.39 (40)	8.06 ± 0.37 (11)	7.73 ± 0.26 (14)	7.67 ± 0.21 (7)
7.30 ± 0.36 (40)	7.04 ± 0.26 (11)	6.67 ± 0.17 (14)	6.44 ± 0.29 (7)
251 ± 32 (40)	224 ± 24 (11)	194 ± 15 (14)	192 ± 22 (7)
54.83 ± 14.32 (19)	59.86 ± 9.87 (22)	65.75 ± 9.74 (14)	36.77 ± 2.98 (7)
20.44 ± 4.72 (17)	25.27 ± 5.67 (21)	31.96 ± 6.45 (14)	13.59 ± 1.26 (7)

scores on each PC (Table 2). All size variables except masses loaded positively on PC1, suggesting that PC1 be interpreted as a “growth axis” of overall size: large individuals grow larger in all linear dimensions (Jolicoeur and Mosimann, 1960). Thoracic size components increase proportionately to each other, as revealed by their similar loading scores on PC1. In contrast, head width increased more slowly with total body size than expected, with the largest males having proportionately the smallest heads (Fig. 4a). The negative loading of dry mass on PC1 suggests that larger individuals are proportionately slightly lighter than smaller individuals.

Mass was the primary source of the variation on PC2, with some contribution from variation in thoracic dimensions; this is expected because the thorax comprises 30–50% of carpenter bees’ total mass (Roberts *et al.*, 2004; Skandalis, unpubl. data). PC2 can therefore be interpreted as an axis which represents the growth of weight, in contrast to PC1, which represents the growth of size. Individuals that weigh more (PC2) are also larger (PC1). The variable loading most strongly on PC3 was HW. In some subsets of the data, HW in fact loaded strongly on PC2 (data not shown). Both these patterns suggest that HW is not well correlated with other linear dimensions of body size in *X. virginica*. The weak and inconsistent loading of the remaining variables on PC3, represents no obvious pattern in the shape of these bees.

#### *Differences Between Males and Females*

Male and female *X. virginica* exhibited some important differences in body shape. As in most bees, females had wider heads than males. HW showed the strongest correlation to thoracic volume (Fig. 4a), with a higher intercept in the females than in males. ITW and CVL showed the same relationship to thoracic volume in both sexes, although males were larger in these dimensions (Fig. 1b, c). On the other hand, males had greater thoracic dimensions for a given mass. A second distinction between the sexes emerged when we compared the thoracic mass predicted from the dimensions of the thorax to that obtained empirically, in summer bees. Curiously, male thoraces were slightly lighter than predicted, while female thoraces were heavier for their thorax size (Fig. 3c). If this is due to a difference in thoracic tissue content, one explanation could be that males have increased tracheal volume, allowing

Table 2. Principal components (PC) analysis factor loading scores of eight measurement variables used in this study. PC1 broadly describes the size of the thorax, PC2 primarily describes mass, while PC3 is dominated by head capsule width.

	PC1	PC2	PC3
HW	0.38461	-0.20999	0.89415
ITW	0.88847	0.04494	-0.14944
CVL	0.87184	-0.02899	-0.15113
Wet mass	-0.09514	0.95761	0.20426
Dry mass	-0.37867	0.91032	0.00517
Thoracic length	0.92024	0.17426	-0.21414
Thoracic width	0.94457	0.21915	0.08375
Thoracic depth	0.96065	0.14008	0.06243
Eigenvalue	4.5117	1.8907	0.9432
Proportion of total variance explained	56.4	23.6	11.8

greater delivery of oxygen during high-cost behaviors. Although honeybee females (workers) are not oxygen-limited during flight (Joos *et al.*, 1997; Harrison *et al.*, 2001), *X. virginica* are much larger, and male flight appears to be more costly than female flight (see below). Another possibility could be that the morphology of the circulatory systems differs between the sexes, but Heinrich and Buchmann (1986) noted no major differences between the sexes of *X. californica* and *X. varipuncta*.

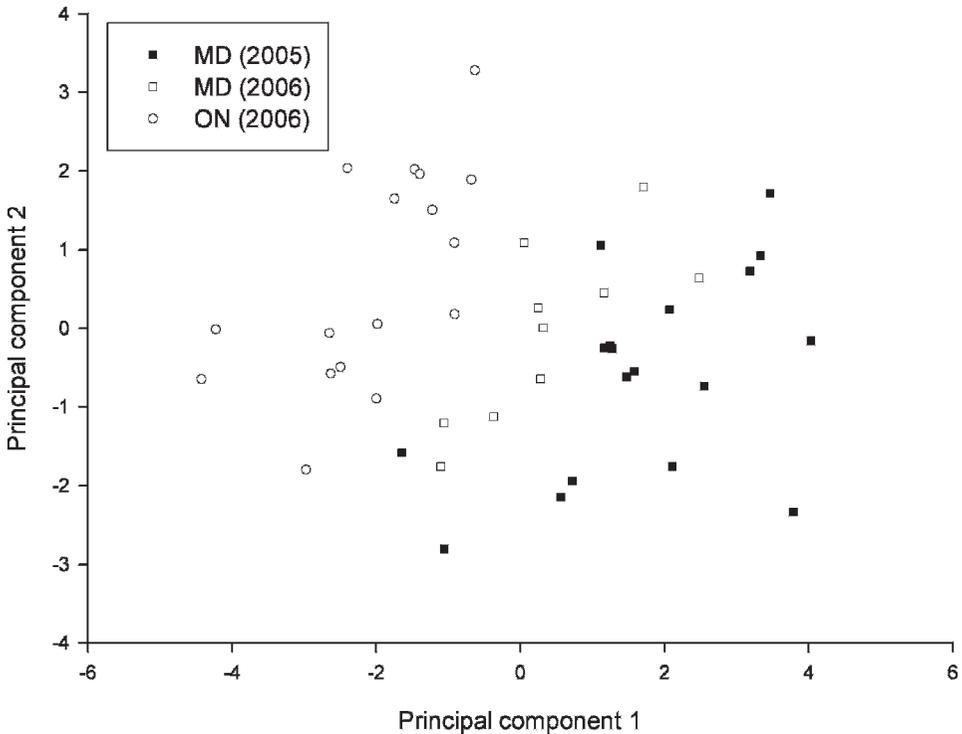


Fig. 1. Principal components comparison of winter bees collected in Ontario (ON) and Maryland (MD). ON bees were smaller than MD bees on principal component 1. MD bees from 2006 were smaller than those from 2005 on principal component 1.

Alternatively, the dichotomy in predicted and actual masses could be a simple consequence of geometry, if the female thorax is less spherical than the male thorax; in that case, the relationship would only indicate that we underestimated volume in one case, and overestimated it in the other.

A third distinction between the sexes was observed when comparing winter and summer bees in Ontario. Summer 2007 males weighed about half as much as winter 2006 males; summer females were also lighter than winter females, but the difference was much smaller (Table 1). Some of the decrease between winter 2006 and summer 2007 may reflect inter-year variation, with 2007 bees being smaller than 2006 bees. However, the differences between the sexes suggest that in males, there is a major seasonal decrease in mass from winter to summer. This decrease appeared to be due almost entirely to a loss of weight in the abdomen, a pattern also noted by Baird (1986), but not by Gerling and Hermann (1978). Louw and Nicolson (1983) also found that crop volume of summer male *X. capitata* was drastically lower than in females. The lack of seasonal change in female mass is somewhat surprising, as summer ovarian development in females might be expected to result in summer weight gain. This probably indicates that the gain in mass by ovarian development is offset by a loss of wintering fat bodies, as occurs in males.

The radically different behavioral patterns of males and females in summer suggest different priorities in morphological design. In *X. virginica*, males guarding nesting sites are more aggressive and have larger heads than males away from the nesting sites (Barthell and Baird, 2004; Barthell *et al.*, 2006). Territorial *X. virginica* males spend a large portion of their time engaged in aggressive interactions with other males (Barrows, 1983; Barthell and Baird, 2004). Larger HW, reflecting larger overall body size, may confer greater resource holding power on males, especially during direct confrontations with other males, and larger males may also be better able to catch and copulate with females. In the Australian carpenter bee, *X. aeratus*, territory holding males are also larger, in both HW and ITW (Leys, 2000). In that species, both the first males and the repeatedly observed males in a new territory are larger. The advantage of large size to males is not universal in *Xylocopa*, as *X. varipuncta* males loyal to a specific territory are no larger than less site-faithful males. However, unlike *X. virginica* and *X. aeratus*, *X. varipuncta* males use pheromonal attractants and the majority of males exhibit very low fidelity for a single territory (Alcock, 1993).

Males spend more time than females in energetically costly behaviors, such as hovering. Males of *X. capitata* spend at least 34% of their time hovering (Louw and Nicolson, 1983). Continuous hovering has been observed in *X. virginica* for periods between 35 mins and one hour (Baird, 1986; Gerling and Hermann, 1978), and during full day observations of males at a Brock University nesting site, hovering comprised approximately 75% of total flight time (Prager, unpubl. data). Conversely, females spend little or no time hovering. It could be that males shed excess mass in the summer (Fig. 3a, 5a; Louw and Nicolson, 1983; Baird, 1986) to minimize the expense of flight. Males consequently incur significantly lower wing loading than females (Nicolson and Louw, 1982), likely resulting in reduced wing beat frequency (Roberts *et al.*, 2004). The trade off to this may be that male carpenter bees carry nearly no abdominal fuel reserves, so flight would need to be fueled by frequent foraging trips (Louw and Nicolson, 1983; Gäde and Auerswald, 1998).

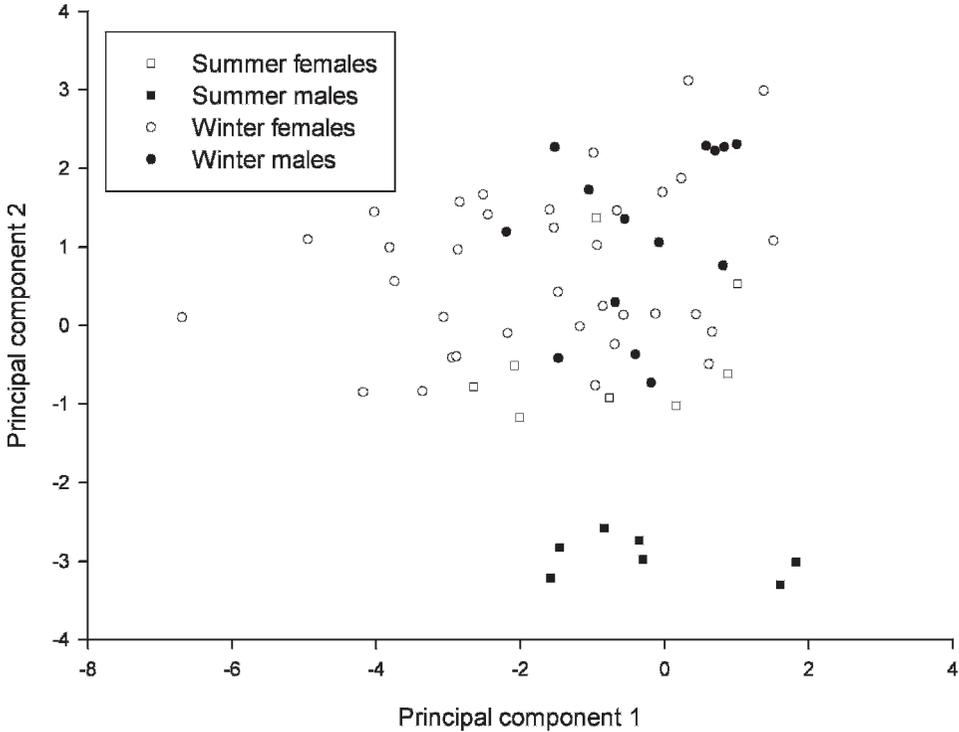


Fig. 2. Principal components comparison among winter and summer bees collected in Ontario (ON). As indicated by differences in the second principal component, males from 2007 had considerably lower mass than all other bees.

*Geographic Variation*

We have not found any consistent latitudinal pattern in body size of *X. virginica* across its range. We compared our size measurements with published values of mass for populations from Athens, GA (Gerling and Hermann, 1978) and NJ (Baird, 1986), and of HW for males from Wellston, OK (Barthell and Baird (2004)). Comparison of masses across the range of *X. virginica* (Fig. 5a) suggests that there is little evidence that wet mass varies with latitude, in either overwintering or summer

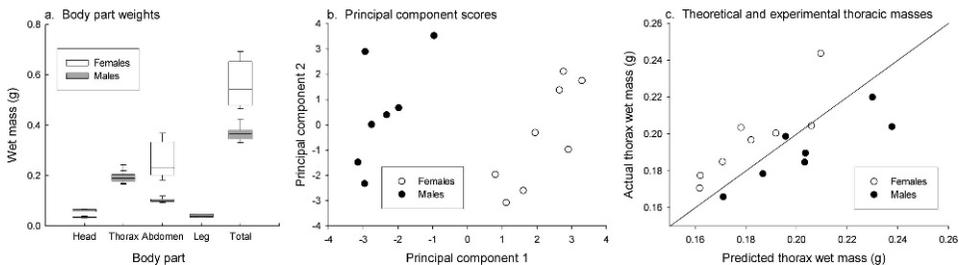


Fig. 3. Sex differences in anatomical distribution of mass. a. Comparison of head, thorax, abdomen and leg masses. b. Differentiation between males and females based on head and abdomen size (PC1), but not thorax size (PC2). c. When predicting thoracic wet mass from the volume of the thorax, females are heavier than predicted, while males are lighter, suggesting that female thoraces hold more water.

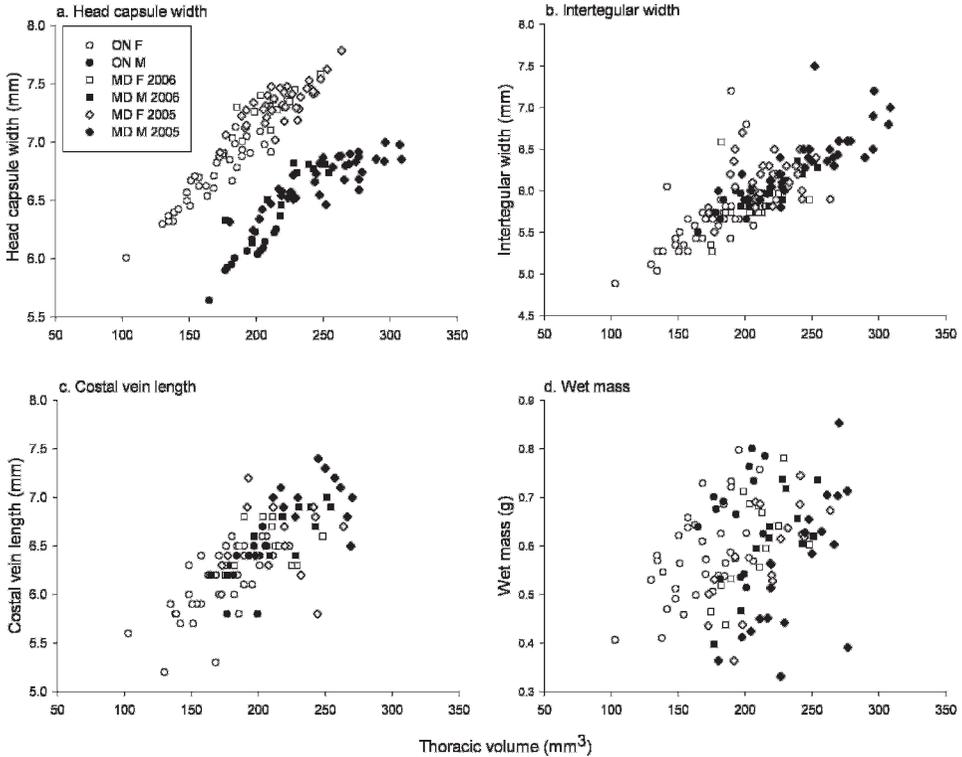


Fig. 4. Correlation of body size parameters to an estimate of overall size, thoracic volume. Head capsule width (a), commonly used as marker of bee body size, is very strongly correlated to overall body size, although differently by sex. Intertegular width (b) and costal vein length (c) are also correlated with thoracic volume. Conversely, thoracic volume was not a predictor of overall body wet mass (d).

bees. Overwintering bees from Ontario appear somewhat exceptional, in that the males were significantly heavier than all other bees. Although linear body dimensions were significantly greater in MD than ON (Table 1), ON bees do not appear to have larger HW than MD bees (Fig. 5b). ON bees have the same mass as MD bees, for a smaller thoracic volume, so more mass must reside in the abdomen of ON bees. We hypothesize that ON bees, which must survive a longer, colder winter, must allow for more stores (abdominal mass), at the cost of larger size (especially thoracic dimensions). Since *X. virginica* is a mass-provisioning species, the final size of the adult at eclosion is dictated mostly by the amount of food provided by the mother. Adults eclose in late summer, then remain in the nest and overwinter until the following spring, and their overwintering fat bodies are already present at emergence (Gerling and Hermann, 1978; Louw and Nicolson, 1983).

#### *On the Measurement of Size in Bees*

In many studies of bees, a single measurement of size, usually HW, is used. Our data suggest that HW may not always adequately describe intraspecific variation in body size. The major advantage of using HW is that it can be measured with very high precision (the average coefficient of variation between three replicates in this study was 0.5%,  $n = 108$ ). However, the loading of HW on its own PC indicates that

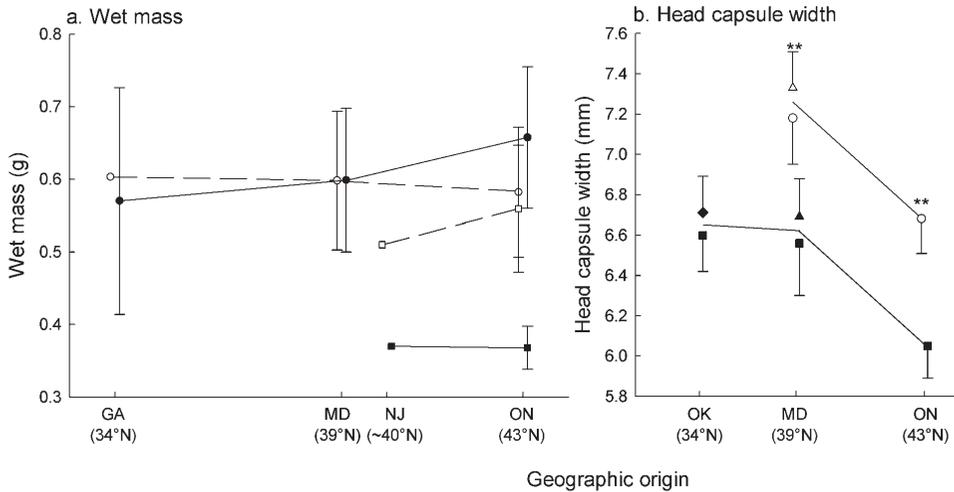


Fig. 5. Lack of evidence for a consistent latitudinal pattern in body size based on body size comparisons with literature values for *X. virginica* from Georgia (GA), New jersey (NJ), and Oklahoma (OK). See text for references.

much of the variation in this body part can be explained independently of other body parts. Although the correlation between HW and thoracic size is strong (Fig. 4a), the remaining variation is considerable and may mask important biological consequences of body size differences in certain contexts. For instance in Fig. 4a, for a thoracic volume of  $\sim 250 \text{ mm}^3$ , the range of male HW is larger than the rather small difference in mean HW Barthell and Baird (2004) reported for territorial versus non-territorial males (6.7 vs. 6.6 mm respectively). Conversely, ITW and CVL are more closely related to the size of the thorax, but are less precise measurements. They lack the absolute measurement frame of reference of HW, due to the necessity of estimating the exact position of the tegulae (ITW) or the base of the wing (CVL) (which likely also explains why they do not correlate as homogeneously with thoracic volume as does HW; Fig. 4). Cane (1987) and Bullock (1999) concluded that ITW is strongly correlated with dry mass in bees, but Cane (1987) also found that *X. virginica* was too variable in both ITW and dry mass to be properly fit with the same relationship as other species. In *Euglossa hyacinthina*, another relatively large bee, larger female thoraces were reflected only by larger ITW, not HW or wing length (Capaldi *et al.*, 2007). A multivariate approach is likely to be advantageous and present a better picture of bee size.

#### Acknowledgements

The authors gratefully acknowledge the assistance of Joshua C. Shaw during data collection, Sam Droege for help collecting the nests, Jean M.L. Richardson for the use of equipment, and conversations with Marianne Peso, Sandra Rehan, and Brent J. Sinclair during the research. We are indebted to Charles D. Michener and two anonymous reviewers, and Viviana Cadena-Ruiz and Charles-A. Darveau for comments which very substantially improved the quality of this manuscript. DAS was supported by a Brock Undergraduate Student Research Award (BUSRA), and

GJT and MHR were supported by grants from the National Sciences and Engineering Research Council (NSERC) of Canada.

### Literature Cited

- Alcock, J. 1993. Differences in site fidelity among territorial males of the carpenter bee *Xylocopa varipuncta* (Hymenoptera, Anthophoridae). *Behaviour* 125:199–217.
- Alcock, J., L. W. Simmons, and M. Beveridge. 2006. Does variation in female body size affect nesting success in Dawson's burrowing bee, *Amegilla dawsoni* (Apidae : Anthophorini)? *Ecological Entomology* 31:352–357.
- Baird, J. M. 1986. A field-study of thermoregulation in the carpenter bee *Xylocopa virginica virginica* (Hymenoptera, Anthophoridae). *Physiological Zoology* 59:157–168.
- Barthell, J. F., and T. A. Baird. 2004. Size variation and aggression among male *Xylocopa virginica* (L.) (Hymenoptera: Apidae) at a nesting site in central Oklahoma. *Journal of the Kansas Entomological Society* 77:10–20.
- Barthell, J. F., R. T. Reidenbaugh, and J. L. Griffith. 2006. Persistent size and behavioral variation among males of the large carpenter bee, *Xylocopa virginica* (Hymenoptera : Apidae). *Southwestern Entomologist* 31:223–232.
- Barrows, E. M. 1983. Male territoriality in the carpenter bee *Xylocopa virginica virginica*. *Animal Behaviour* 31:806–813.
- Bishop, J. A., and W. S. Armbruster. 1999. Thermoregulatory abilities of Alaskan bees: Effects of size, phylogeny and ecology. *Functional Ecology* 13:711–724.
- Bullock, S. H. 1999. Relationships among body size, wing size and mass in bees from a tropical dry forest in Mexico. *Journal of the Kansas Entomological Society* 72:426–439.
- Cane, J. H. 1987. Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society* 60(1):145–147.
- Capaldi, E. A., C. J. Flynn, and W. T. Wcislo. 2007. Sex ratio and nest observations of *Euglossa hyacinthina* (Hymenoptera: Apidae: Euglossini). *Journal of the Kansas Entomological Society* 80:395–399.
- Cartar, R. 1992. Morphological senescence and longevity: an experiment relating wing wear and life span in foraging wild bumble bees. *Journal of Animal Ecology* 61:225–231.
- Danforth, B. N. 1990. Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behavioral Ecology and Sociobiology* 27:159–168.
- Dudley, R. 2000. *The biomechanics of insect flight: Form, function, evolution*. Princeton University Press, Princeton, New Jersey. xii + 476 pp.
- Emlen, D. J., and C. E. Allen. 2003. Genotype to phenotype: Physiological control of trait size and scaling in insects. *Integrative and Comparative Biology* 43:617–634.
- Gäde, G., and L. Auerswald. 1998. Flight metabolism in carpenter bees and primary structure of their hypertrehalosaemic peptide. *Experimental Biology Online* 3:6.
- Gathmann, A., H. J. Greiler, and T. Tschardt. 1994. Trap nesting bees and wasps colonizing set-aside fields: Succession and body size, management by cutting and sowing. *Oecologia* 98:8–14.
- Gerling, D., and H. R. Hermann. 1978. Biology and mating-behavior of *Xylocopa virginica* L. (Hymenoptera, Anthophoridae). *Behavioral Ecology and Sociobiology* 3:99–111.
- Harrison, J. F., S. Camazine, J. H. Marden, S. D. Kirkton, A. Rozo, and X. Yang. 2001. Mite not make it home: Tracheal mites reduce the safety margin for oxygen delivery of flying honeybees. *Journal of Experimental Biology* 204:805–814.
- Heinrich, B., and S. L. Buchmann. 1986. Thermoregulatory physiology of the carpenter bee, *Xylocopa varipuncta*. *Journal of Comparative Physiology* 156:B557–562.
- Hurd, P. D., Jr. 1955. The carpenter bees of California. *Bulletin of the California Insect Survey* 4:35–72.
- Jolicoeur, P., and J. E. Mosimann. 1960. Size and shape variation in the painted turtle. A principal component analysis. *Growth* 24:339–354.
- Joos, B., J. R. B. Lighton, J. F. Harrison, R. K. Suarez, and S. P. Roberts. 1997. Effects of ambient oxygen tension on flight performance, metabolism, and water loss of the honeybee. *Physiological Zoology* 70:167–174.
- Kim, J. Y. 1997. Female size and fitness in the leaf-cutter bee *Megachile apicalis*. *Ecological Entomology* 22:275–282.

- Leys, R. 2000. Mate locating strategies of the green carpenter bees *Xylocopa (Lestis) aeratus* and *X. (L.) bombylans*. *Journal of Zoology* 252:453–462.
- Louw, G. N., and S. W. Nicolson. 1983. Thermal, energetic, and nutritional considerations in the foraging and reproduction of the carpenter bee *Xylocopa capitata*. *Journal of the Entomological Society of Southern Africa* 46:227–240.
- Minckley, R. L., W. T. Weislo, D. Yanega, and S. L. Buchmann. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. *Ecology* 75:1406–1419.
- Nicolson, S. W., and G. N. Louw. 1982. Simultaneous measurement of evaporative water loss, oxygen consumption, and thoracic temperature during flight in a carpenter bee. *Journal of Experimental Zoology* 222:287–296.
- Pereboom, J. J. M., and J. C. Biesmeijer. 2003. Thermal constraints for stingless bee foragers: the importance of body size and coloration. *Oecologia* 137:42–50.
- Richards, M. H., and L. Packer. 1996. The socioecology of body size variation in the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae). *Oikos* 77:68–76.
- Richards, M. H. 2004. Annual and social variation in foraging effort of the obligately eusocial sweat bee, *Halictus ligatus* (Hymenoptera : Halictidae). *Journal of the Kansas Entomological Society* 77:484–502.
- Roberts, S. P., J. F. Harrison, and R. Dudley. 2004. Allometry of kinematics and energetics in carpenter bees (*Xylocopa varipuncta*) hovering in variable-density gases. *Journal of Experimental Biology* 207:993–1004.
- Stone, G. N. 1993. Endothermy in the solitary bee *Anthophora plumipes*: independent measures of thermoregulatory ability, costs of warm-up and the role of body size. *Journal of Experimental Biology* 174:299–320.
- Strohm, E., and K. E. Linsenmair. 1997. Low resource availability causes extremely male-biased investment ratios in the European beewolf, *Philanthus triangulum* F. (Hymenoptera, Sphecidae). *Proceedings of the Royal Society of London B* 264:423–429.
- Tomkins, J. L., L. W. Simmons, and J. Alcock. 2001. Brood-provisioning strategies in Dawson's burrowing bee, *Amegilla dawsoni* (Hymenoptera: Anthophorini). *Behavioral Ecology and Sociobiology* 50:81–89.