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# Estimating body size in the large carpenter bees (*Xylocopa*)

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**Abstract.** Body size is a salient functional trait in bees, with implications for reproductive fitness, pollination ecology, and responses to environmental change. Methods for quantifying bee body size commonly rely on indirect estimates and vary widely across studies, particularly in studies of the large carpenter bees (*Xylocopa* Latreille) (Apidae: Xylocopinini). We evaluate the robustness of three common body size parameters (intertegular distance, head width, and costal vein length) as predictors of dry body mass within and among 11 species of *Xylocopa* (and 5 subspecies). We found that all three size measurements provide robust body size estimates, accounting for 92–93% of intraspecific variation in body mass. Within species, however, these measurements were considerably less predictive of body mass, explaining on average only 36.8% (intertegular distance), 57.4% (head width), and 38.8% (costal vein length) of the variation in body mass. We also highlight a novel application of photogrammetry and 3D modeling to estimate surface area and volume across species, and comment on the utility of these methods for body size estimates in *Xylocopa* and in insects more broadly. These findings provide practical guidelines for body size estimation methods within and among carpenter bee species.

## INTRODUCTION

Body size is a well-known predictor of major ecological patterns, correlating with a variety of life history, behavioral, and physiological traits (Blueweiss *et al*., 1978; Peters, 1983; Blackburn & Gaston, 1994; Angilletta *et al*., 2004; Brown *et al*., 2004). In bees, known effects of body size span levels of biological organization, including impacts on individual physiology and fitness, group-level dynamics, and ecosystem functioning (Benjamin *et al*., 2014; Jauker *et al*., 2016; Chole *et al*., 2019). Efforts to measure bee body size directly as mass or volume are often impeded by practical considerations (*e.g.*,

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due to specimen damage, variation in wet tissue content, etc.). These challenges have prompted the development of indirect methods for body size estimation, especially via allometric equations (Cane, 1987; Kendall *et al*., 2019). However, the effectiveness of these methods should be validated for the taxon in question and with respect to the level of comparison. Here, we examine the robustness of three common body size estimation methods for inter- and intraspecific comparisons in the large carpenter bees (Genus *Xylocopa* Latreille).

Comparative studies of bee body size have proliferated in recent years, offering important insights into size as a mediating factor in bee responses to environmental change and habitat degradation (Carrié *et al*., 2017; Bartomeus *et al*., 2013; Jauker *et al*., 2013). The most widely adopted method for comparative estimation of bee body size is by measurement of the distance between the two tegulae (sclerites covering the base of the forewing), known as intertegular span or intertegular distance (hereafter, ITD) (*e.g*., Bullock, 1999; Ostwald *et al*., 2024). Cane (1987) described an allometric equation relating ITD to dry mass for 20 North American bee species. The small sample size and restricted geographic scope of this original study prompted Kendall *et al*. (2019) to revisit the question of ITD as a predictor of size variation, incorporating coefficients for sexual dimorphism, biogeographic region, and phylogeny. In agreement with the original Cane model, they found that ITD was a robust predictor of inter- but not intraspecific size variation (Kendall *et al*., 2019). Despite known phylogenetic effects on bee body size variation, few studies have assessed the reliability of these size estimation methods within a taxonomic context (*Bombus:* Hagen & Dupont, 2013; *Osmia:* Rust, 1991; Bosch & Vicens, 2002), which could provide valuable methodological guidance.

The large carpenter bees are valuable pollinators of natural and agricultural systems (Keasar, 2010; Gautam & Kumar, 2018; Buchmann & Minckley, 2019), as well as important model systems for questions in physiology (Nicolson & Louw, 1982; Heinrich & Buchmann, 1986; Gonzalez *et al*., 2020), social evolution (Hogendoorn & Velthuis, 1993; Dunn & Richards, 2003; Vickruck & Richards, 2021), and the evolution of mating systems (Gerling & Hermann, 1978; Marshall & Alcock, 1981). In the genus, body size has been implicated in social dynamics, mating strategies, and reproductive traits (Barthell & Baird, 2004; Richards, 2011; Richards & Course, 2015; Vickruck & Richards, 2018). These studies, and others in the genus, vary considerably in their body size estimation methods, most commonly relying on head width (Barthell & Baird, 2004; Peso & Richards, 2010; Vickruck & Richards, 2017; Ostwald *et al*., 2020) and ITD (Richards & Course, 2015; Gonzalez *et al*., 2020; Goffinet *et al*., 2023; Saleh *et al*., 2023) to estimate intraspecific size variation. This diversity of approaches, along with interesting behavioral and ecological co-variates of size and morphology in *Xylocopa* more broadly (Leys & Hogendoorn, 2008; Skandalis *et al*., 2009), calls for a closer examination of body size estimation methods in the genus. Here, we evaluate ITD, head width, and costal vein length as inter- and intraspecific estimates of dry body mass in *Xylocopa*. Beyond mass, surface area and volume are also biologically relevant metrics of bee size, useful for quantifying heat flux and water balance (Kühsel *et al*., 2017; Johnson *et al*., 2022) yet are uncommonly measured due to technical quantification challenges. We overcome these challenges through photogrammetry, which allows us to accurately quantify body surface area and volume from 3D models. Together, these findings serve as a guide for robust size estimation methods in service of a range of questions in carpenter bee behavior, ecology, and physiology.

## MATERIAL AND METHODS

### Bee Specimens

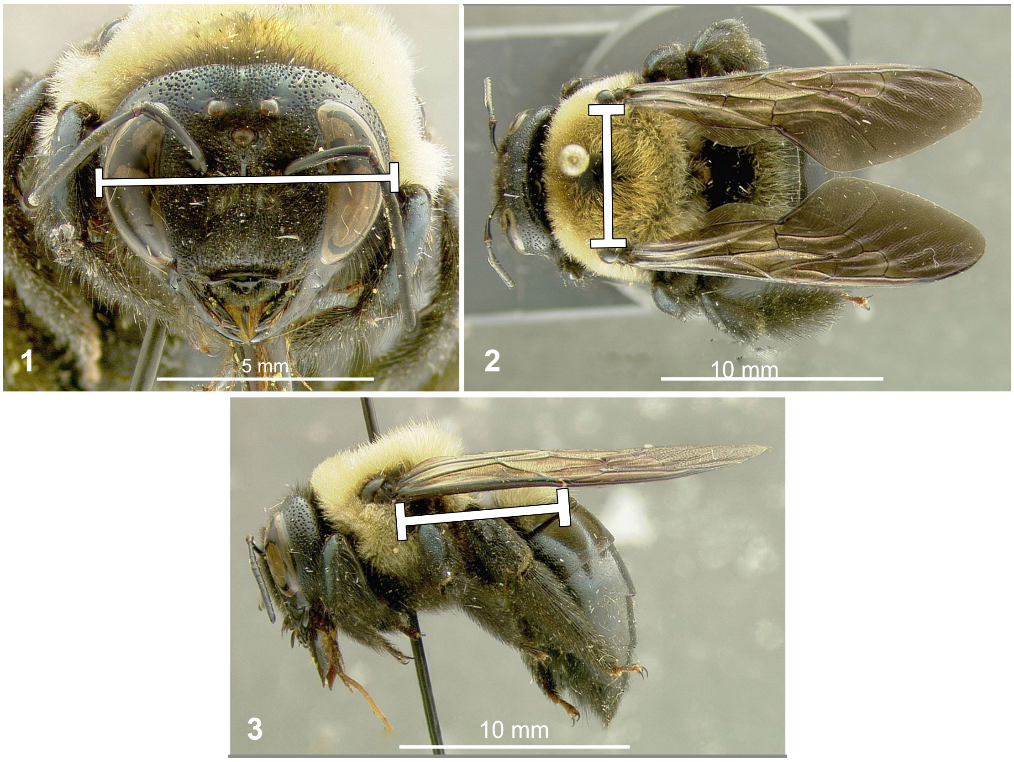
To understand how body mass scales with morphometric measurements, we obtained 308 adult *Xylocopa* specimens from the entomological collections at the University of California, Santa Barbara, and the Natural History Museum of Los Angeles County. These included male (*n* = 128) and female (*n* = 180) specimens from the following 11 species (including 5 subspecies): *X. californica arizonensis* Cresson (*n* = 33), *X. californica californica* Cresson (*n* = 2), *X. californica diamesa* Cresson (*n* = 4), *X. frontalis* Olivier (*n* = 23), *X. inconstans* Smith (*n* = 20), *X. latipes* Drury (*n* = 23), *X. micans* Lepeletier (*n* = 28), *X. ruficornis* Fabricius (*n* = 1), *X. sonorina* Smith (*n* = 50), *X. tabaniformis orpifex* Smith (*n* = 71), *X. tabaniformis tabaniformis* Smith (*n* = 20), *X. tenuiscapa* Westwood (*n* = 10), *X. tranquebarica* Fabricius (*n* = 14), and *X. virginica* Linnaeus (*n* = 28). These species are distributed across temperate, desert, and tropical regions of North and South America, Africa, and southeast Asia. Full specimen sampling data is available at https://doi.org/10.5281/zenodo.11106428.

### Morphometric and Mass Measurements

We weighed all dried, pinned specimens with labels removed (precision = 0.001 g). Only specimens with no or very little pollen present were measured, to avoid biasing mass measurements. To estimate the mass contribution from the specimen pins, we weighed 7 sets of 10 size 2 pins (BioQuip Products Inc.), then divided each set by ten to estimate the average pin mass. We then subtracted the mean pin mass (0.048 ± 0.00 g) from the total mass recorded for each specimen, to obtain our final measure of dry mass. We visually inspected specimen pins to confirm pin type and size was uniform across our sampled specimens. There may still be variation in pin mass across our sample, due to variation in pin age and manufacturer, though we expect that this variation is minimal and does not meaningfully skew our mass measurements. Because *Xylocopa* are large-bodied bees, pins represent a small proportion of total specimen mass (approx. 0.01% on average). We measured the head width of all specimens as the maximum distance between the lateral sides of the head, using digital calipers (precision = 0.01 mm) (Fig. 1). We measured intertegular distance (ITD) and costal vein length using a digital microscope camera (Amscope FMA050, Amscope, Irvine, CA, USA) mounted on a steromicroscope. ITD was measured as the shortest distance between the tegulae (Cane, 1987), and costal vein length was measured from the wing nodus to the distal end of the costal vein (Skandalis *et al*., 2009) (Figs. 2, 3). To reduce measurement bias, a single observer conducted all morphometric and mass measurements.

### Photogrammetry, 3D Modeling, and Volumetric/Surface Area Measurements

We used 3D photogrammetry and 3D modelling to estimate bee surface area and volume across species. We created 12 photogrammetry suites of 2D focal-stacked



**Figures 1–3.** Example measurements taken from a female specimen of *Xylocopa virginica* Linnaeus (MCZ:Ent:610038). **1.** Head width. **2.** Intertegular distance. **3.** Length of the costal vein.

images. Each suite represents a single specimen from one of the following species: *X. californica arizonensis*, *X. frontalis*, *X. inconstans*, *X. latipes*, *X. micans*, *X. ruficornis*, *X. sonorina*, *X. tabaniformis orpifex*, *X. tabaniformis tabaniformis*, *X. tenuiscapa*, *X. tranquebarica*, *X. virginica*. Bees were photographed using a Macropod Pro 3D imaging system (Macroscopic Solutions, LLC, East Hartford, CT, USA) comprised of a Canon EOS 6D Mark II camera with a Canon RF 100 Macro USM AF/MF Lens mounted on a tripod and attached to a stage for automated specimen rotation. Specimens were pinned to a stage and tilted at a 15° angle so that both the ventral and dorsal surfaces of the specimen are captured in the images. We rotated bees 360°, every 2.6° taking a set of photos with a 0.85 mm step size across the entire focal plane of the bee, using Stackshot macro rails. We assembled photos at each angle using Zerene Stacker Software and then modified photos in Adobe Photoshop to improve image contrast. All images were then 3D modeled in Agisoft Metashape Pro Software (see Smith *et al.*, 2024 for full imaging and modeling protocol) (Fig. 4). We used the 3D models to calculate body surface area and volume for each specimen, excluding wings, in Agisoft Metashape Pro, using a photographed scalebar to calibrate our measurements.

**Figure 4.** Example 3D model (left figure) and 2D image (right figure) of *Xylocopa virginica* Linnaeus. Models are compiled from photogrammetric suites of 2D images, taken every 2.6° around the specimen. 3D models can be used for empirical measurements of surface area and volume of entire specimens or of particular body segments.

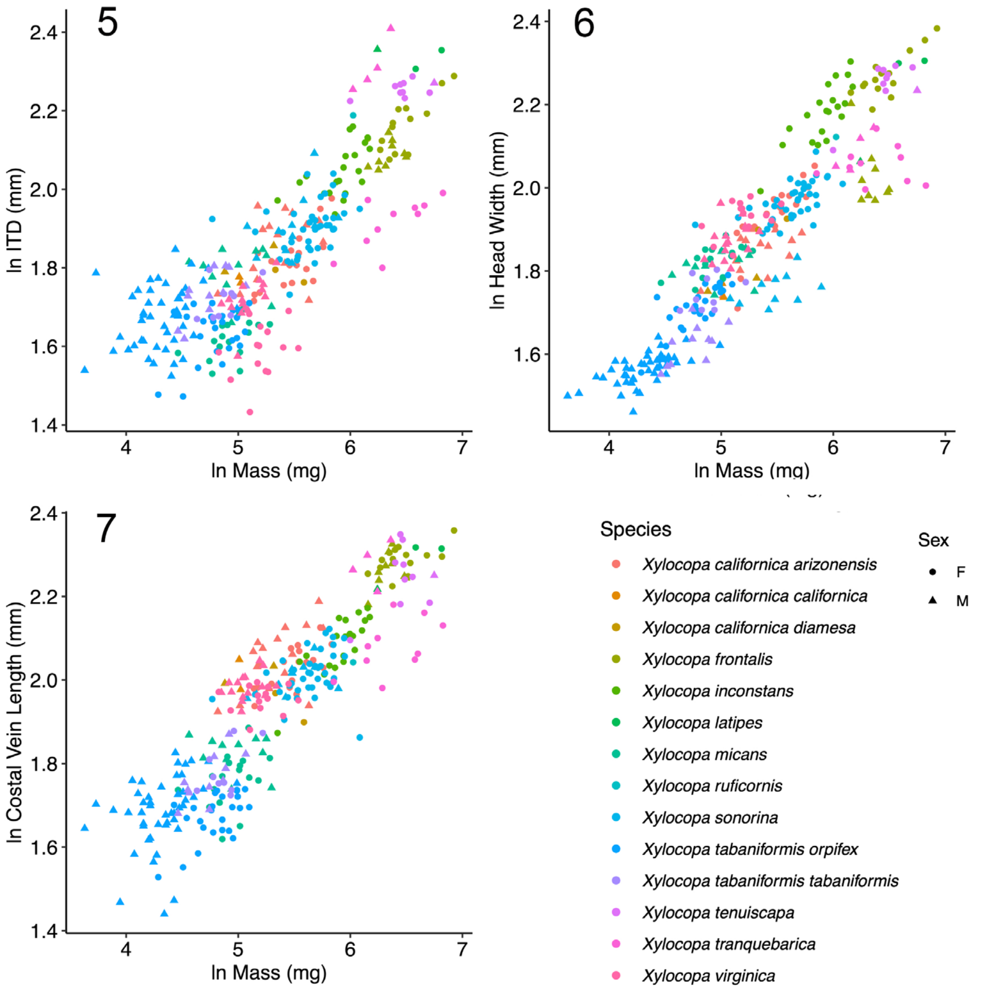
### Statistical Analyses

To understand the relationships between mass and morphological size estimates, we fit inter- and intraspecific linear models of natural log-transformed data, as is standard in analysis of allometric size relationships (Huxley, 1932; Cariveau *et al.*, 2016; Kendall *et al.*, 2019). For our interspecific comparison, we fit three linear models as follows: ln(dry mass) ~ ln(measurement)*Sex*Species, where "measurement" refers to either ITD, head width, or costal vein length. We used stepwise model selection and chose the best fitting model for each size measurement based on the Akaike information criterion (AIC). For our intraspecific comparisons, due to relative rarity of males in our dataset, we evaluated only female bees and only those species for which we had 14 or more female specimens per species or subspecies. We then fit linear models for each species or subspecies as follows: ln(dry mass) ~ ln(measurement). To characterize the relationships between mass and volume and surface area, we similarly fit two linear models, as ln(dry mass) ~ ln(volume) and ln(dry mass) ~ ln(surface area). For all analyses, we considered subspecies as separate groups. For all models, we confirmed that data met assumptions of normality and homoscedasticity with QQ-plots and by plotting fitted values versus residuals. All analyses were conducted in R version 4.2.1 (R Core Team, 2022).

## RESULTS

### Interspecific Body Size Variation

All three size parameters significantly predicted interspecific variation in dry mass (Figs. 5–7, Table 1) The best fitting model predicting the relationship between ln(mass) and ln(ITD) included sex, species, the interaction between species and sex, and the interaction between sex and ITD as variables. For head width, the best fitting model included ln(head width), species, sex, and the interaction between species and sex as variables. Finally, for costal vein length, the best fitting model included ln(costal



**Figures 5–7.** Interspecific relationship between dry mass (mg) and various body size estimates (mm) for males and females of 11 species of *Xylocopa*, including 5 subspecies. **5.** Intertegular distance (ITD). **6.** Head width. **7.** Costal vein length. Axes are natural log-transformed.

**Table 1.** Model parameters from stepwise selection for interspecific models relating body size to intertegular distance (ITD), head width (HW), and costal vein length (CVL).

| Size Parameter | Chosen Model | $R^2$ | AIC | *P*-value | Residual Standard Error |
|---|---|---|---|---|---|
| **Intertegular Distance** | ln(mass) ~ ln(ITD) + Species + Sex + Species:Sex + Sex:ln(ITD) | 0.925 | -965.12 | <0.001 | 0.200 on 281 df |
| **Head Width** | ln(mass) ~ ln(HW) + Species + Sex + Species:Sex | 0.934 | -1028.16 | <0.001 | 0.181 on 282 df |
| **Costal Vein Length** | ln(mass) ~ ln(CVL) + Species + Sex + Species:Sex + Sex:ln(CVL) | 0.926 | -969.06 | <0.001 | 0.199 on 281 df |

vein length), species, sex, the interaction between species and sex, and the interaction between sex and ln(costal vein length) (Table 1).

Head width was (marginally) the best proxy for dry mass when comparing the three selected models, with the highest $R^2$ value and the lowest AIC. This model predicted 93.4% of the variation in dry mass ($P < 0.001$). However, the head width model only minorly outperformed the models for ITD and costal vein length, which predicted 92.5% and 92.6% of the variation in dry mass, respectively ($P < 0.001$ for both comparisons).

Volume and surface area were both significantly predictive of dry mass variation across species ($n = 12$) (surface area: $R^2 = 0.760$, $P < 0.001$; volume: $R^2 = 0.669$, $P < 0.001$) (Fig. 8).

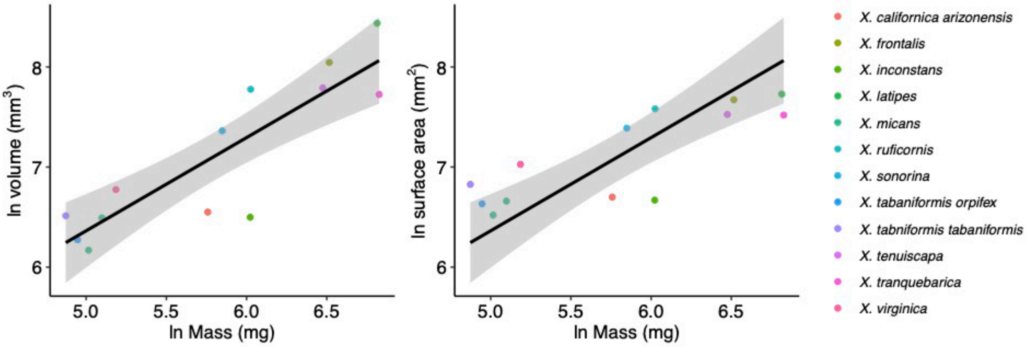


**Figure 8.** Log-body volume (left figure) and log-surface area (right figure) of 12 3D-modelled specimens of *Xylocopa* linearly related with specimen dry mass. Each point represents a single specimen.

## Intraspecific Body Size Variation

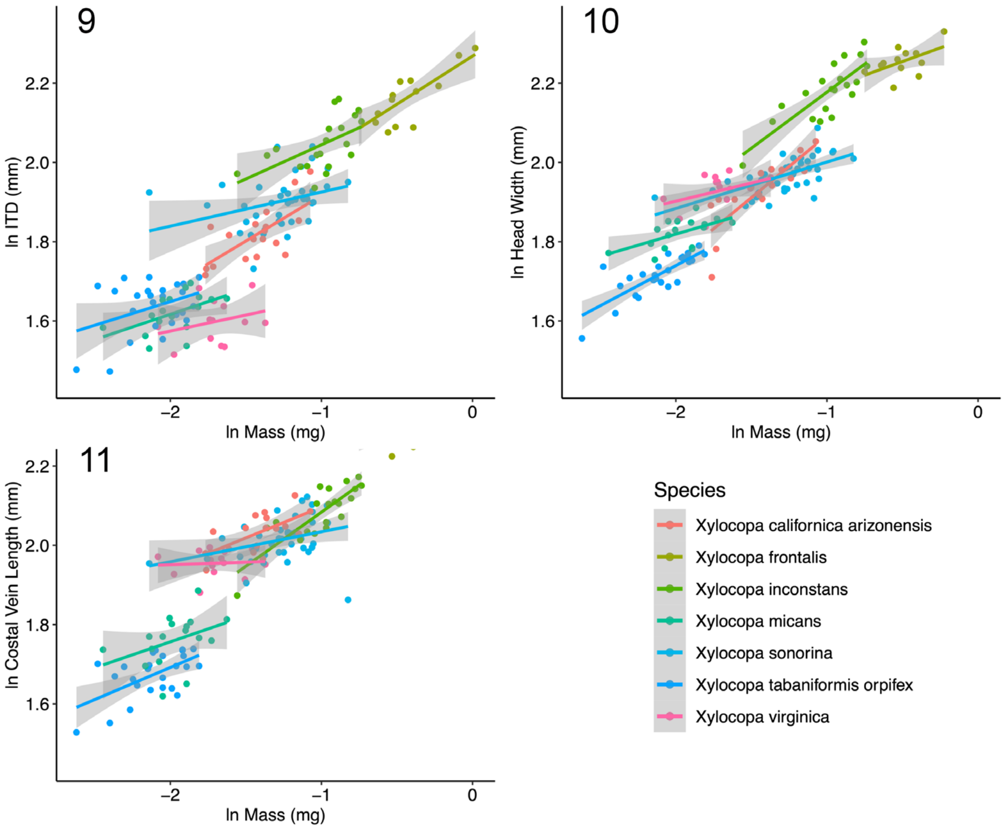
Within species, we observed significant linear relationships between female dry mass and each size parameter for some, but not all of the 7 species groups tested. $R^2$ values for these intraspecific models were lower than those of the interspecific models, explaining on average 36.8 ± 9.4% (ITD), 57.4 ± 7.5% (head width), and 38.8 ± 9.7% (costal vein length) of the variation in ln(dry mass) for a given species (values represent mean ± standard errors) (Table 2, Figs. 9–11).

## DISCUSSION

Comparative estimation of body size in the large carpenter bees can provide important insights into stress tolerance, mating systems, pollination services, social dynamics, and more. We found that three linear measurements of body size, ITD, head width, and costal vein length, were all strong predictors of adult dry mass across 11 *Xylocopa* species, but were inconsistent predictors within species. Sex, species, and their interaction were important covariates of size variation that should be considered when estimating size from these measurements. We also demonstrated the utility of photogrammetry and 3D modeling of specimens for precise estimates of body surface area and volume.

**Table 2.** Model parameters from intraspecific ln(dry mass) ~ ln(measurement) regressions, where the measurement is either intertegular distance, head width, or costal vein length. The regression data includes only female bees. Bold values indicate groups for which a given measurement significantly predicts variation in mass ($P < 0.05$).

| **Species** | *n* | Intertegular distance | | Head width | | Costal vein length | |
|---|---|---|---|---|---|---|---|
| | | $R^2$ | *P*-value | $R^2$ | *P*-value | $R^2$ | *P*-value |
| *X. californica arizonensis* | 18 | **0.549** | **0.002** | **0.746** | **<0.001** | **0.490** | **0.004** |
| *X. frontalis* | 14 | **0.613** | **0.001** | **0.676** | **<0.001** | **0.300** | **0.042** |
| *X. inconstans* | 20 | **0.320** | **0.009** | **0.662** | **<0.001** | **0.689** | **<0.001** |
| *X. micans* | 17 | **0.256** | **0.038** | **0.343** | **0.014** | 0.151 | 0.124 |
| *X. sonorina* | 39 | **0.104** | **0.045** | **0.389** | **<0.001** | **0.111** | **0.039** |
| *X. tabaniformis orpifex* | 25 | 0.137 | 0.068 | **0.629** | **<0.001** | **0.348** | **0.112** |
| *X. virginica* | 14 | 0.098 | 0.277 | 0.177 | 0.134 | 0.006 | 0.798 |



**Figures 9–11.** Intraspecific relationships between dry mass (mg) and various body size proxies for female specimens of *Xylocopa*. **9.** Intertegular distance (ITD). **10.** Head width. **11.** Costal vein length. Lines represent ln(dry mass) ~ ln(size parameter) regressions for each species. Grey areas represent 95% confidence intervals for each regression.

Our results align with previous studies demonstrating that ITD strongly predicts intraspecific size (mass) variation in bees (Cane, 1987; Bullock, 1999; Kendall *et al.*, 2019). ITD emerged as a useful proxy for bee size estimation based on the rationale that thoracic volume should correspond to flight musculature volume, which should correspond to the amount of lift necessary for flight by a bee of a given size (Cane, 1987). Importantly, thorax size can also be influenced by non-muscle tissue. Male *Xylocopa*, in particular show enormous variation in the morphology of their thoracic sex pheromone glands (dorsal mesosomal glands), which range from absent or reduced in some species (*e.g.*, *X. tabaniformis*), to greatly hypertrophied in other species (*e.g.*, *X. sonorina*), where it can occupy as much as 20% of thoracic volume (Minckley, 1994; Ostwald *et al.*, 2022). Similarly, Cane reasoned that head width would be an unreliable proxy for body size due to head allometry related to gland development and variation in mandibular musculature (Cane, 1987). Interestingly, we found that ITD, head width, and costal vein length all performed similarly well as predictors of interspecific body size variation, explaining more than 90% of the variation in dry mass when accounting for sex and its interaction with these measurements. Together, these findings suggest that these estimates are robust to important sources of morphological variation related to physiological and life history factors.

Importantly, these measurements do not reliably predict body size variation within *Xylocopa* species, as previous studies have shown in other bees (Cane, 1987; Kendall *et al.*, 2019). These estimates ranged from reasonably predictive for some combinations of species and measurements (*e.g.*, *X. californica*, head width $R^2 = 0.75$), to not at all significantly predictive of body mass variation. Within species, body size can be affected by local ecological factors; body size in the eastern carpenter bee (*X. virginica*) is influenced by geographic, seasonal, and inter-annual variation. Where possible, body size should be measured directly as dry mass when making comparisons within a species. Where dry mass measurements are not possible (*e.g.*, for live bees or for specimens that have been partially dissected), indirect measurements could be sufficiently effective, depending on such factors as sample size, effect size, and taxon of interest. Our samples do not capture the full geographic and seasonal breadth of intraspecific body size variation in our focal species, nor do they capture other potential sources of size variation (*e.g.*, voltinism). Preliminary measures of the relationship between dry mass and the size measurement for the focal species (and population) should be taken to clarify the expected error in intraspecific comparisons.

While mass is the most studied property of body size, surface area and volume are important and understudied size properties with major implications for physiological responses to environmental conditions. For example, these measures are used to estimate heat and water exchange between organisms and their environments (Porter & Gates, 1969), serving as a basis for biophysical modeling of species responses to climate change (Buckley *et al.*, 2010; Briscoe *et al.*, 2023). Standard practices for quantifying insect surface area and volume involve geometric calculations based on linear measurements (*e.g.*, thorax width = diameter), and assume that body segments represent geometric volumes (*e.g.*, assume the thorax is a sphere) (Chappell, 1982; Roberts & Harrison, 1999). Empirical measurements are more challenging to obtain but may be instrumental for questions requiring more precise size estimates or estimates across species with diverse body morphologies (Kühsel *et al.*, 2017). Advances in photogrammetry and 3D modeling provide tractable pathways for complex morphometric measurements (Kouraiss *et al.*, 2019; Tsuboi *et al.*, 2020) but have not yet been widely adopted for insects. While the time-demanding nature of this method precludes its practicality for estimating dry mass, 3D modeling offers important insights into other questions related to body surface area and volume. To demonstrate the potential of this method, we generated 3D models of 12 species of *Xylocopa* (available at https://zenodo.org/doi/10.5281/zenodo.11106427), with accompanying surface area and volume measurements. Due to their large body size, carpenter bees are particularly appropriate test cases for this methodology, which can be resolution-limited for smaller bees. Further, carpenter bees have served as fascinating model systems for physiological questions due to their longevity, their thermoregulatory behaviors, and their impressive nest boring behaviors (Chappell, 1982; Nicolson & Louw, 1982; Heinrich & Buchmann, 1986; Roberts *et al*., 2004; Ostwald *et al*., 2021); empirical size measurements of carpenter bees from 3D models could advance diverse questions in physiological ecology.

Robust and validated size metrics are essential for standardizing comparisons across a range of applications in bee ecology. In general, the choice of size measurement will depend on the focal taxa and the biological question of interest. Head width, for example, is implicated in reproductive strategies in *Xylocopa* and may be useful for understanding within-group social interactions (Vickruck & Richards, 2018). Alternatively, for example, measuring the ratio between ITD and costal vein length could illuminate patterns of selection for particular morphologies under climate change (Peters *et al*., 2016; Maebe *et al*., 2021). Importantly, however, when using these linear measurements as a proxy for overall body size, adherence to prevailing measurement standards (ITD) can promote re-usability of data for future meta-analyses (Ostwald *et al*., 2024). Consideration of appropriate size metrics based on the taxon of interest, research question, and the estimation precision required will advance our understanding of size effects on ecological, physiological, and behavioral questions in this important pollinator group.

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