Pollimetry: Predictive allometry for pollinating insects

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**Abstract**

Allometric scaling laws have key implications for the conservation and management of pollinating insects in both managed and unmanaged ecosystems.

Body size (BS) can predict influential ecological traits yet available predictive models are outdated, rely upon geographically restricted sampling and have limited applicability for non-bee taxa.

More accurate predictions of pollinator body size require models that consider biogeography, intraspecific variation and phylogenetic relatedness.

We catalogued existing predictive allometries for pollinating insects (Hymenoptera (BS: 38), Diptera (BS: 26) and Lepidoptera (BS: 21) and improved upon pre-existing equations for estimating body size in key pollinating taxa (bees and hoverflies).

We measured dry weight and intertegular distance (ITD) of bees (species total: 278) and hoverflies (species total: 105) across three biogeographic regions: Australia, Europe and USA.

We then used linear mixed effect (LME) and phylogenetic generalised least squares (PGLS) models to construct a suite of state-of-the-art equations for estimating interspecific pollinator body size.

Model valiation was assessed using k-fold cross validation.

Overall differences between these models were minimal and PGLS models performed similarly to LME models. Intraspecific models found ITD a reliable proxy for body size in bees but not hoverflies, potentially due to sample size issues.

These highly applicable models form the R package 'pollimetry’ and provide an updated resource for allometric research concerning wild and managed pollinators globally.

**Introduction**

Body size is an intrinsic trait of all organisms that influences key patterns across all levels of biological organisation. Adult body size variation (both intra- and interspecific) in insects is the outcome of natural selection affecting physiological and biochemical processes during ontogeny (see Chown & Gaston 2010’s review on body size variation). Therefore, body size is central to physiological (e.g. metabolic and growth rates (Angilletta et al. 2004; Ehnes et al. 2011; Harrison et al. 2014)), life history (e.g. life span, reproductive rate and type (i.e. capital or income breeders) (Speakman 2005; Teder et al. 2008)) and ecological attributes (e.g. species abundance and richness, trophic interactions, geographic range size and dispersal ability) (Brown et al. 2004; White et al. 2007; Chown & Gaston 2010, Rall et al. 2011; Stevens et al. 2012; Dell et al. 2011, 2014; Velghe & Gregory-Eaves 2013). These effects lead to differing spatial and temporal size-frequency distributions within populations and communities as well as drive key ecosystem functions and services such as decomposition, carbon cycling, primary productivity and pollination (Greenleaf et al. 2007; Rudolf & Rasmussen 2013; Schramski et al. 2015).

Studies of body size variation utilise allometric theory. Gould (1966) defined allometry as the ‘study of size and its consequences.’ Allometric scaling laws refer to how traits, which can be morphological, physiological or chemical, co-vary with an organism’s body size, often with important ecological and evolutionary implications (Gould 1966; Huxley 1993). However, direct measurements of body size and allometric traits can be impractical for a number of reasons. First, direct measurements can be time consuming and require destructive methods, which are unfeasible for museum specimens and threatened species (Rogers et al. 1976; Henschel & Seely 1997). Second, where research occurs in remote field sites, equipment limits can prevent direct measurements (Brady & Noske 2006). Thirdly, in diet/food web studies, body size estimates come from digested prey items (e.g. Hodar 1997). Lastly, a lack of life-history information, especially for ecologically cryptic and rare species, may not be known. As such, predictive allometry, which attempts to estimate body size using a co-varying trait, as well as allowing body size proxies has emerged across many biological disciplines.

Body length – body size models have been used extensively to predict body size for fish (e.g. Karachle & Stergiou 2012), mammals (e.g. Trites & Pauly 1998) and both aquatic (e.g. Burgherr & Meyer 1997; Benke 1999) and terrestrial invertebrates (e.g. Rogers et al. 1977; Sample et al. 1993; Sabo et al. 2002). These models often show considerable support (*R2* > 0.9) and this has led to the proliferation of multiple models for a wide range of taxa worldwide, especially insects. However, when compared, these models show significantly different coefficients both within- and between insect orders (Schoener 1980; Sample 1993; Ganihar 1997; Benke et al. 1999; Brady & Noske 2006), often due to biogeography (i.e. latitude, see Martins et al. 2014), and/or methodological influences such as sampling biases and model choice.

These differences highlight a need for consolidation and improvement in predictive allometric theory and practice. Predictive models require a robust and iterative framework in model choice, development and validation. Ordinary least squares (OLS) regression has been seen as ideal for prediction (INSREF from Cariveau) leading to a lack of incorporation of mixed effects and/or phylogenetic model structures (eg. phylogenetic generalized least squares (PGLS) (Harvey & Pagel 1991)) despite their importance in explaining key ecological and evolutionary processes. Further, model validation techniques, such as cross-validation, which are common-place in statistics and the fields of medical sciences (eg. TWO REFS), have been overlooked in predictive ecology, with the exception of ecological distribution modelling (eg.Wenger and Olden 2012, Boria et al 2014). It is becoming clear these methods, in model building and testing, are necessary given the increasing burden of proof in biological prediction (Nature paper about p-valies??). Further, ‘iterative model-building’, whereby equations can be periodically updated rather than simply differentiated and replaced, represents an as-yet untested avenue for greater accuracy and wider application.

A number of key pollination traits exhibit allometric scaling. In bees in particular, body size affects insect activity rates/periods (Strienzer et al. 2015), pollen load (e.g. Ramalho et al. 1998), foraging range (e.g. Greenleaf et al. 2007 and van Nieuwstadt & Iraheta 1996) and proboscis length (Cariveau et al. 2016). Despite these influences, few predictive allometric models exist for pollinating insects, with one notable exception. Cane (1987) established a predictive allometric model for bee body size as a function of the intertegular distance (ITD) (the distance between the wing-attachment points on either side of the thorax). Cane (1987)’s model was developed with a sample of 20 single females from solitary bee species in North America that represented six major bee families. It is now the most commonly used metric for estimating bee body size (Web of Science: 89 citations, Google scholar: 108 citations as of ) and has used in ecological (eg. Williams et al. 2010), sensory (e.g. Spaethe & Chittka 2003; Kapustjanskij et al. 2007) and behavioural studies (e.g. Oliveira & Schlindwein 2010). It also firmly developed the ITD as an important proxy for quantifying other ecologically important allometric relationships (e.g. foraging distances and bee proboscis length; Greenleaf et al. 2007; Cariveau et al. 2016).

The utility of Cane’s equation has not previously been tested beyond North American solitary bee species, except for in bumblebees (REF), in conjunction with biogeography or within more complex model structures that consider mixed effects or species’ phylogenies. Neither has ITD been assessed in other key pollinating taxa, such as hoverflies (Diptera: Syrphidae). Therefore, we aimed to develop state-of-the-art predictive allometric equations that take into account these factors within our prescribed iterative framework and place them alongside a catalogue of pre-existing equations for key pollinating insect taxa within a unified resource, an *R* package, entitled “pollimetry”.

**METHODOLOGY**

*Existing equations*

We selected three key pollinating insect orders: Diptera, Hymenoptera and Lepidoptera and collated all known predictive allometric models using a systematic literature search.

*Specimen collection and measurements*

Only recently curated (<5 years)- or fresh- undamaged specimens were included. For every included specimen, we obtained preservative time, sample location (latitude and longitude), collection method (pan trap, sweeping, malaise trap) and taxonomic designation.

*Body size and intertegular distance*

Dry weight (mg) was measured on an analytical balance with an accuracy to 0.001g. Both fresh and curated specimens were dehydrated at 70 °C for 24 - 48hrs prior to weighing to remove residual humidity.

Specimen pins were not removed prior to weighing. Instead, we identified the pin type and weighed a sample of 10-50 pins per type. The mean weight was then subtracted off total weight.

Intertegular distance was measured in millimetres using a stereo-microscope, either mounted with a calibrated scale or microscope camera.

**Data analysis - Model structure**

For each taxon, we constructed species mean datasets stratified for measurer and country of origin. We used a power function in model formulation which is typical of predictive allometry:

Ln(Y) = ln(a) + b\*ln(IT) + c\*IT

We extended this formula to include multiple interactions with IT: sex, biogeographic region and taxonomic family. We constructed linear mixed effect models to predict body size, over linear regression as species overlap between measurers and within biogeographic regions required a more-complex model structure. Both measurer and species were included as random terms.

**Incorporating phylogeny**

We explored the influence of phylogenetic relatedness on predicting pollinator body size (and associated predictions) using a simplified mean dataset, with a single species mean per region.

Overlapping species: in bees; European honeybee (*Apis mellifera*) and the sweat bee (*Halictus rubicundus*) present in multiple regions, were removed from their introduced regions, Australia and North America respectively.

For bees, we used the genera tree by Hedtke et al. (2013) and for hoverflies, we used genera tree from Skevington et al. unpublished. Non-represented genera were removed and species added to genera using the genus.to.species.tree function within phytools (Revell et al)..

As such, we made the explicit assumption that phylogenetic patterns in body size were assessed at and above the genera level.

To assess if incorporating phylogeny improved body size predictions, we then determined the relationship between dry weight and ITD and biogeographic region using phylogenetic generalized least squares (PGLS) regression.

We inferred phylogenetic signal using Pagel’s lambda (Pagel 1999) correlation structure. Lambda was fitted at an initial value of 0.5 and optimized by maximum likelihood.

**Model selection and cross-validation**

We first fitted the full model with all predicted explanatory variables, for LME: family, region, sex in interaction with ITD and for PGLS: IT in interaction with region.

We then performed model selection assessing all subset models using the ‘dredge’ function within the R library MuMIn (REF). The best fitting models were then ranked by lowest Akaike Information Criterion (AIC).

Given our predictive framework, we iteratively removed terms from LME models, specifically region and sex (for wider utility) and considered ITD in isolation.

**Cross-validation**

We implemented k-fold cross validation to test overall model performance and compare prediction error. Species mean datasets were divided into five equal sets containing a random subset of species. Each model was then evaluated iteratively upon each k-1 set (training set), and then compared against the 5-k set (test set). This was done repeatedly so each set was both the test set and contained within the training sets. New levels of random terms were allowed within each predicted set. We then assessed model performance on the basis of the mean/median root-mean square error (RMSE), R2 and AIC across the five sets.

**Intraspecific predictions and variance**

We assessed intraspecific predictions and sample size variation in trait measurements.

For the five most speciose species of both bees and hoverflies (Bees: *Homalictus urbanus* (n = 251), *Lasioglossum pauxillum* (n = 113), *Bombus lucorum* (n = 111), *Andrena flavipes* (n = 75) and *Lasioglossum lanarium* (n = 68); Hoverflies: *Helophilus parallelus* (n = 19), *Sphaerophoria macrogaster* (n = 17), *Episyrphus balteatus* (n = 15), *Melanostoma mellinum* (n = 12) and *Syritta pipiens* (n = 12)), we tested the utility of ITD predicting body size using species-level OLS regression. Furthermore, we plotted species trait means indepedently against increasing sample size to estimate the adequate sample size whereby mean variance stabilised within confidence intervals of actual sample size. ANY IDEAS FOR A TEST FOR THIS OR IF A TEST IS NEEDED?

**Results**

*Existing equations*

Diptera: 26 allometric models for Diptera were collated (Table S1A). 11 models were reported for the entire order, including nine without any taxonomic breakdown of samples used. 11 for the three main suborders Nematocera (6), Brachycera (4) and Cycllorapha (2) and two for specific families; Asilidae and Bombyliidae. Surprisingly, there were no equations for Syrphidae, a key pollinating taxa in many ecosystems (eg. Biesmeijer et al. 2006, Jauker et al. 2012).

Hymenoptera: 38 allometric models for Hymenoptera were collated (Table S1B). These included eight combined, seven excluding ants (Formicidae) as well as ten for Formicidae. There are three equations for Vespidae and two equations for Apidae (Cane 1987 & Sabo et al. (2002). Only Sample et al’s (1993) body length and body length\*width equations are provided for Braconidae, Ichneumonidae, Halictidae and Pompilidae.

Lepidoptera: 21 allometric models for Lepidoptera were collated (Table S1C). This includes 13 with varying taxa and without lower classifications. Hodar (1997) provides specific models for Heterocera (moths) and Ropalocera (butterflies). Sample et al. (1993) provide BL and BL\*BW models for Microlepidoptera and two moth families Geometridae and Arctiidae. ~~A multivariate regression model using specimens from 61 Lepidoptera families is also included (Garcia-Barros 2015).~~

**Species and specimen distribution**

In total, we measured 278 bee species from Australia, North America and Europe and 105 hoverfly species from Australia and Europe. Five out of six bee families and all syrphid subfamilies were represented.

**Interspecific model selection and performance**

For bees, our non-phylogenetic analyses found that models which considered region, family and sex in interaction with ITD best-predicted body size on the basis of AIC (Table 1A). Interestingly, for hoverflies, taxonomy was less important than region and sex across the best fitting models. The ITD only model ranked higher than the best-fitting model that included taxonomy and ITD (Table 1B, Model 5).

Phylogenetic models exhibited similar trends, with region-specific models best-explaining the dry-weight~ ITD relationship in bees, although sex was not considered in these models.

For hoverflies – TBC – waiting on phylogeny from Jeff Skevington

Cross-validation indicated that high accuracy persisted across all tested models (both LME and PGLS) for both bees and hoverflies, in terms of *R2* (TABLE 2A,B) which ranged from between 0.88 -0.89 for bees and 0.79 – 0.82 for hoverflies and RMSE, which ranged from X – X in bees and X – X in hoverflies (Figure 1).

The ITD only model for hoverflies exhibited the highest *R2* and lowest AIC across all tested models, with a marginal increase in error.

Incorporating phylogeny into model-fitting resulted in similar predictive precision for bees when considered in interaction with biogeographic region. Differences in model precision between phylogenetic- and non-phylogenetic models which considered only ITD were marginal.

Table 1A. AIC and delta for interspecific bee models. Model types: i) LME: linear mixed effect models and ii) PGLS: phylogenetic generalised least squared models. As these two model types used different datasets, AIC values are not directly comparable.

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Formula | AIC | Delta |
| LME | 1. IT \* Family + IT \* Region + IT \* Sex | **426.5** | 0 |
|  | 2. IT \* Family + IT \* Region + Sex | 429.1 | 2.6 |
|  | 3. IT \* Family + IT \* Region | 440.9 | 14.4 |
|  | 4. IT \* Family + IT \* Sex | 485.5 | 59 |
|  | 5. IT \* Family | 498.9 | 72.4 |
|  | 6. IT only | 533.6 | 116.5 |
| PGLS | IT \* Region | **195.1** | 0 |
|  | IT + Region | 215.7 | 20.6 |
|  | IT only | 233.2 | 38.1 |

Table 1B. AIC and delta for interspecific hoverfly models.

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Formula | AIC | Delta |
| LME | 1. IT + Region + Sex | **195** | 0 |
|  | 2. IT + Sex | 195.1 | 0.1 |
|  | 3. IT + Region + IT \* Sex | 195.7 | 0.7 |
|  | 4. IT \* Sex | 195.8 | 0.8 |
|  | 5. IT \* Subfamily | 203.6 | 8.6 |
|  | 6. IT only | 200.1 | 5.1 |
| PGLS | NA | **NA** | NA |
|  | NA | NA | NA |
|  | NA | NA | NA |

Table 2A. Full k-fold cross validation results BEES. MSE: Mean standard error, RMSE: Root mean square error, *R2*: R-squared, AIC: Akaike Information Criterion and BIC: Bayesian Information Criterion. Values are the median across five folds.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | | Formula | MSE | RMSE | *R*2 | AIC | BIC |
| LME | 1. IT \* Family + IT \* Region + IT \* Sex | | **0.159636** | **0.399544** | 0.888365 | 387.383 | 469.849 |
|  | 2. IT \* Family + IT \* Region + Sex | | 0.1618771 | 0.402339 | 0.886757 | **385.992** | 464.531 |
|  | 3. IT \* Family + IT \* Region | | 0.1712714 | 0.413849 | **0.888615** | 388.121 | **462.733** |
|  | 4. IT \* Family + IT \* Sex | | 0.1663228 | 0.407827 | 0.881368 | 433.553 | 500.310 |
|  | 5. IT \* Family | | 0.1777686 | 0.421626 | 0.875640 | 435.508 | 494.411 |
|  | 6. IT only | | 0.1759162 | 0.419423 | 0.876936 | 450.388 | 470.022 |
| PGLS | 1. IT \* Region | | **0.1285079** | **0.35848** | **0.899652** | **171.632** | **199.410** |
|  | 2. IT + Region | | 0.1524221 | 0.390412 | 0.880979 | 189.302 | 210.161 |
|  | 3. IT only | | 0.1525182 | 0.390535 | 0.880904 | 187.424 | 208.283 |

Table 2B. Full k-fold cross validation results for hoverfly models.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Model | Formula | MSE | RMSE | *R2* | AIC | BIC |
| LME | 1. IT + Region + Sex | 0.1707961 | 0.4132749 | 0.8105877 | 173.1652 | 193.5538 |
|  | 2. IT + Sex | 0.1696071 | 0.4118338 | 0.8074276 | 171.9106 | 189.3865 |
|  | 3. IT + Region + IT \* Sex | **0.1683655** | **0.4103236** | 0.8161315 | 174.3796 | 197.6218 |
|  | 4. IT \* Sex | 0.1692803 | 0.4114369 | 0.8100356 | 172.6819 | 193.0705 |
|  | 5. IT \* Subfamily | 0.1800766 | 0.4243543 | 0.7917507 | 177.3329 | 203.5468 |
|  | 6. IT only | 0.183296 | 0.4281308 | **0.821589** | **169.2318** | **183.795** |
| PGLS | NA | NA | NA | NA | NA | NA |
|  | NA | NA | NA | NA | NA | NA |
|  | NA | NA | NA | NA | NA | NA |



Fig 1. Root mean square error (RMSE) across k-fold training and test sets for each model. **Left**: Bees; **Right**: Hoverflies. Model numbers refer to these described in Table 2A and B.

**Intra-specific variation**

Across the five most abundant species of bees and hoverflies (females only), intraspecific predictions of body size using ITD were mixed (Figure 2). All bee species exhibited a significant relationships between ITD and dry weight, however adjusted *R2*varied considerably from 0.02 in *Homalictus urbanus* to 0.46 for *Lasioglossum lanarium* (Table 3). In contrast to bees, only one hoverfly species, *Helophilus parallelus,* showed a significant trend (*R2*:0.43).

Table 3. Model parameters of intraspecific ln(body size)~ln(IT) size relationships. F-stat: F-statistic and degrees of freedom for each model. A and B: intercept and IT scaling co-efficient, *R2*: Adjusted R-squared and P: p-value of full model. Only females were used in both analyses.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Taxa |  | F-stat (df) | A | B | *R2* | P |
| Bees | *Andrena flavipes* | 21.07 (1,57) | 1.308 | 2.029 | 0.257 | <0.001 |
|  | *Bombus lucorum* | 81.15 (1,101) | 1.412 | 1.966 | 0.44 | <0.001 |
|  | *Homalictus urbanus* | 6.055 (1,209) | -0.164 | 1.166 | 0.024 | 0.014 |
|  | *Lasioglossum lanarium* | 53.87 (1,61) | 0.702 | 2.13 | 0.46 | <0.001 |
|  | *Lasioglossum pauxillum* | 43.92 (1,110) | 0.402 | 3.112 | 0.279 | <0.001 |
| Hoverflies | *Helophilus parallelus* | 14.84 (1,17) | 0.286 | 2.485 | 0.435 | 0.001 |
|  | *Sphaerophoria macrogaster* | 0.04 (1,8) | 0.361 | 0.195 | -0.11 | N.S. |
|  | *Episyrphus balteatus* | 0.08 (1,8) | 1.334 | 0.885 | -0.11 | N.S. |
|  | *Melanostoma mellinum* | 0.209 (1,3) | 0.815 | 2.182 | -0.24 | N.S. |
|  | *Syritta pipiens* | 5.339 (1,3) | -2.238 | 6.985 | 0.52 | N.S. |

Sample size exhibited an interesting trend in relation to both ITD and dry weight. In bees, mean ITD and dry weight stabilised within the confidence intervals of the total sample size with >20 specimens per species (Figure S1A). For hoverflies, the lower overall sample sizes of each species limited inference of sample-size / mean stabilisation (FIGURE S1B).



**Figure 3.** Intraspecific predictions of body size with intertegular distance. Left: bees; Right: hoverflies. Lines denote line of best fit from linear regressions.

**#SUPP# Preservative time**

**Method**

A key confounding factor which can affect predictive allometric models for insects is the time specimens spend within preservative (i.e. ethanol Leuven et al. 1982??). As a trade-off between including greater species diversity and those that had been preserved, we assessed the impact of preservative time using Australian and German specimens (species n = 20), where there was considerable overlap in species that had and had not been preserved. We fitted a linear-mixed effect model with y = specimen weight ~ preservative time with two crossed random terms, country and species.

**Result**

Across twenty species, preservative time was found to exhibit an effect upon specimen weight, accounting for a loss of 0.006mg per day preserved (t-value: -3.050). This amount of weight-loss was not considered significant enough to correct.

**DISCUSSION**

This study demonstrated clear and unequivocal proof of the utility of ITD for predicting interspecific differences in body size in two key pollinating taxa, bees and hoverflies. Overall resolutions of predictions were high, however in LME and PGLS model structures incorporating biogeography, gender and taxonomy/phylogeny improved accuracy.

Terrestrial invertebrates show considerable geographic variation in shape and biogeographical differences in predictive allometry are well-established. Martins et al. (2014) contributed differences in allometric coefficients between geographic regions to a latitudinal gradient, suggesting comparable geographic regions (i.e. temperate regions) should exhibit similar allometric trends. However, length-mass models can differ considerably both between and within comparable geographical regions. For example, Rogers et al. (1977) constructed length-mass models for shrub-steppe invertebrates in North America. Remarkably, Gowing & Recher (1984) found their allometric models from both eucalypt forests and woodlands in NSW, Australia, did not differ from Rogers et al. (1977), with the exception of Hymenoptera. However, Schoener (1980) found systemic differences between their models (between two forest types in Costa Rica, and temperate forest in Massachusetts, USA) and those of Rogers et al. (1977).

In contrast, these models attempted to predict body size at the order level, therefore these systemic difference may be attributed to higher-order differences, species distributions. Our observed differences between regions are likely due to different species distributions in sampling, as well as patterns of diversification occurring differently within biogeographic regions.

~~As such, consideration for the specific environmental conditions of differing populations/communities, i.e. ecosystem type (forest, shrub-steppe) is important when constructing predictive allometric models, even in comparable climactic zones or geographic regions. The use of specimens from multiple biogeographic areas in model fitting may provide an avenue to overcome this limitation.~~

Sex was retained as an important predictor for both bees and hoverflies. Male and females exhibit distinctly different life histories so have different morphological adaptations.

Importance of sex

High resolution of predictions – great!

Overall differences between bees and hoverflies

Biogeography important – for some, not others

Incorporating region can improve prediction but ITD is resilient across regions

FROM my review

~~#Biogeographic influences~~

~~Terrestrial invertebrates show considerable geographic variation in shape and form. Body length- mass accumulation rates change over a latitudinal gradient; the rate of body mass/length accumulation increasing with absolute latitude. This may reflect a biogeographic gradient of increased predation pressure toward the tropics (Martin et al. 2014). The presence of larger, comparatively lighter insects in the tropics lends support for the ‘index of bizarreness’ hypothesis (Schoener 1980; Johnson & Strong 2000) whereby larger insects are disproportionately slender due to predation pressure. Increased body mass is associated with a greater cost for both running (Garland 1983) and flying (Marden 1994). As such, slenderness may enable greater predator avoidance and/or fleeing. Crucially, this latitudinal gradient may also be the result of other well-known environmental and ecological gradients, such as primary productivity, niche width, metabolic rate and climate (Martin et al. 2014). How these contribute to this variation in mass-accumulation remains unanswered. There has been considerable under-sampling in mid-latitude arid zones, and this hinders further analyses of causes underpinning latitudinal trends in mass accumulation.~~

*Intra-specific variation and sample size*

Previous studies have cast doubt over the utility of predictive models to accurately describe intraspecific body size variation (INSREF). Cariveau et al. (2016) found that ITD was insufficient to estimate intraspecific allometric variation in bee tongue length. Our results provide reasonable proof that such an aim is achievable but highly species-specific and can exhibit considerable error.

If considerations are made at the population level, sample sizes of >20 individuals are adequate to accurately estimate a species-level allometric co-efficient and extrapolate to a population based off ITD.

How does it place with interspecific model?

Intraspecific variation

* Good enough for bees
* Larger sample sizes needed to adequately test in hoverflies

Model structures and the iterative framework

Complex model structures within an iterative framework provide an new avenue for predictive allometries. We observed a considerable decrease in AIC through the incorporation of phylogeny in our bee dataset. More closely related bee species exhibit similarity in their body size. For example, Apinine bees show marked increase in body size across several lineages, whereas Halictine bees show considerable contractions in body size. Failing to account for these phylogenetic patterns in predictive allometry heightens the risk of inaccurate predictions, a key tenet of the PGLS method (Martins 1991; Martins et al. 2002; Garland et al. 2005). One previous suite of predictive allometric models incorporated taxonomy as a proxy for phylogeny (Cariveau et al. 2016). In hoverflies, we found that taxonomy was insufficient in describing interspecific body size variation. Therefore, this represents an adequate compromise where correct or up-to-date phylogenies are unavailable, such is the case in hoverflies, however models that take into account phylogenetic relatedness directly may be more precise.

LME structures allowed us to accurately account for species overlap within regions to assess macro-ecological trends.

Mixed effect model structures can aid in accounting for methodological issues whereas phylogenetic methods, such as phylogenetic generalized least squares (PGLS) (Harvey & Pagel 1991), correct for the dependent data structure between related species (Rezende & Diniz-Filho 2012).

Not acknowledging phylogenetic relatedness risks pseudo-replication,

Phylogeny

Important consideration as improved bees

Hoverflies not sure yet

Cross-validation

Novelty of cross-validation approach in ecology – should be more ubiquitous given its utility

Can yield interesting results relative to other methods i.e. just AIC – more simplified model can be better performing i.e. IT only in hoverflies.

not always lowest AIC – least error in prediction

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**Fig S1A. Intraspecific variation in IT and dry weight in relation to sample size in bees. Red line denotes the total trait mean and green lines represent 95% confidence intervals.**

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**Fig S1B. Intraspecific variation in IT and dry weight in relation to sample size in hoverflies. Red line denotes the total trait mean and green lines represent 95% confidence intervals.**

Table 1. Allometric equations for pollinating taxa. BL = Body length, BW = Body width, IT = intertegular span. OLS = Ordinary Least Squares regression. MA = Major axis regression, MU = Multivariate regression. Equations are present in the form of y = ln(B0) + ln(B1), which is equivalent to y = b0Xb1. \* = Included body width as well as length

1. **Diptera**.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Source** | | **Taxa** | | **Families** | | **Sample size** | | **Biogeographical region** | | | **Measure** | **Range in body length** | **Reg. Type** | **Type** | **Equation** | | | |
|  |  | |  | |  | | **(Families: species)** | |  |  | | **(mm)** |  | | ***B*0 ± S.E.** | ***B*1 ± S.E.** | **Resi. SE** | ***R2*** |
| Rogers et al. (1977) | |  | |  | | (#:84) | | Washington, USA | | | BL | 0.9-34 | OLS | PF | -3.298 ± 0.115 | 2.366 ± 0.078 | 0.57 | **0.96** |
| Schoener (1980) | |  | |  | |  | | Dry forest, CR | | | BL | N.P | OLS | PF | A=-2.603 ± 0.0688 | B = 1.64 ± 0.1224 | NA | 0.795 |
| Schoener (1980) | |  | |  | |  | | Rain forest, CR | | | BL | N.P. | OLS | PF | A = -2.688 ± 0.051 | B = 1.59 ± 0.1173 | NA | 0.775 |
| Schoener (1980) | |  | |  | | (#:171) | | Massachusetts | | | BL | N.P. | OLS | PF | A=-3.816 ± 0.561 | B=2.42 ± 0.0969 | NA | 0.89 |
| Gowing and Recher (1984) | |  | |  | | (100) | | NSW, Australia | | | BL | 2-11 | OLS | PF | 3.653 ± 0.129 | 2.546 ± 0.071 | 0.37 | **0.93** |
| Sample et al. (1993) | |  | | Combined | | (15:257) | | West Virginia, USA | | | BL | 2.9-23.65 | OLS | PF | -3.184 ± 0.184 | 2.213 ± 0.085 | NA | 0.85 |
| “ | |  | |  | |  | | “ | | | BL\*BW | “ | OLS | PF | -2.197 ± 0.089 | 1.309 ± 0.03 | NA | **0.94** |
| “ | | NEM | | BIB,SCI,TIP | | (3:46) | | “ | | | BL | 3.55-23.65 | OLS | PF | -3.675 ± 0.23 | 2.212 ± 0.141 | NA | **0.92** |
| “ | |  | |  | |  | | “ | | | BL\*BW | “ | OLS | PF | -2.217 ± 0.205 | 1.288 ± 0.071 | NA | **0.94** |
| “ | | BRA | | ASI, DOL, EMP, RHA, STR, THE | | (6:80) | | “ | | | BL | 2.9-17.99 | OLS | PF | -3.374 ± 0.230 | 2.158 ± 0.101 | NA | **0.92** |
| “ | |  | |  | |  | | “ | | | BL\*BW | “ | OLS | PF | -2.2 ± 0.147 | 1.259 ± 0.049 | NA | **0.95** |
| “ | | CYC | | CAL, LAU, MUS, OTI, SYR, TAC | | (6:119) | | “ | | | BL | 2.9-15.65 | OLS | PF | -3.619 ± 0.212 | 2.632 ± 0.101 | NA | **0.92** |
| “ | |  | |  | |  | | “ | | | BL\*BW | “ | OLS | PF | -2.02 ± 0.131 | 1.298 ± 0.042 | NA | **0.94** |
| Hodar (1997) | | BRA | |  | | (26) | | Gaudix-Baza, Spain | | | HW | NA | OLS | PF | A=0.655 ± 0.105 | B=2.526 ± 0.139 | 0.47 | **0.933** |
|  | | NEM | |  | | (10) | | “ | | | HW | NA | OLS | PF | A=3.942 ± 0.259 | B=3.106 ± 0.278 | 0.55 | **0.94** |
| Ganihar (1997) | |  | | NA | | (#:20) | | Goa, India | | | BL |  | OLS | PF | -3.4294 ± 0.01994 | 2.5943 ± 0.0334 | 0.03 | **0.99** |
| Johnson and Strong (2000) | | ALL | | NA | | (75) | | Jamaica | | | BL | 1-12.5 |  | PF | -2.462 ± 0.196 | 1.881 ± 0.146 |  | 0.83 |
| “ | | NEM | | NA | | (21) | | “ | | | BL | 1-4.8 |  | PF | -2.562 ± 0.244 | 1.373 ± 0.207 |  | 0.836 |
| “ | | NEM exc. | | NA | | (54 | | “ | | | BL | 1.2-12.5 |  | PF | -2.105 ± 0.178 | 1.805 ± 0.124 |  | 0.895 |
| *Sabo et al. (2002)* | | *BRA* | |  | |  | | *California, USA* | | | *BL* | *N.P.* |  | *PF* | *A = 0.006 ± 0.007* | *B = 3.05 ± 0.36* |  | *0.85* |
| *“* | | *NEM* | |  | |  | | *“* | | | *BL* | *N.P.* |  | *PF* | *A = 0.1 ± 0.06* | *B = 1.57 ±0.2* |  | ***0.9*** |
| *“* | |  | | *Asilidae* | | *(1:9)* | | *“* | | | *BL* | *N.P.* |  | *PF* | *A = 0.38 ± 2.625* | *B = 1.5 ± 2.469* |  | *0.74* |
| *“* | |  | | *Bombyliidae* | | *(1:10)* | | *“* | | | *BL* | *N.P.* |  | *PF* | *A = 0.007 ± 0.011* | *B = 3.337 ±0.676* |  | ***0.95*** |
| *Brady and Noske (2006)* | | *NA* | | *NA* | | *(9 sp:78 spe)* | | *NT, AUS* | | | *B:* | *2-28* | *OLS* | *L* | *A= -0.041 ± 0.004* | *B = 0.010 ± 0.001* | *0.02* | *0.838* |
| Wardhaugh (2013) | |  | |  | | (#:16) | | QLD, AUS | | | BL |  | MA | PF | -3.29 ± 0.45 | 2.65 ± 0.36 | NA | 0.72 |
| Wardhaugh (2013) | |  | |  | | (#:16) | | QLD, AUS | | | BL \* BW |  | MA | PF | -1.91 ± 0.19 | 1.22 ± 0.11 | NA | 0.87 |

BIB =Bibionidae, SCI = Sciaridae, TIP = Tipulidae, ASI= Asilidae, DOL = Dolichopodidae, EMP = Empidae, RHA = Rhagionidae, STR = Stratiomyidae, THE = Therevidae, CAL = Calliphoridae, LAU = Lauxaniidae, MUS = Muscidae, OTI = Otitidae, SYR = Syrphidae, TAC = Tachinidae.NEM = Nematocera, BRA= Brachycera, CYC = Cyclorrapha

1. **Hymenoptera.** \*\* = excluded ants

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Source** | | **Taxa** | | **Families** | | **Sample size** | | | **Biogeographical region** | | **Measure** | **Range in body length** | | **Reg. Type** | **Type** | **Equation** | | | |
|  |  | |  | |  | | **(Families: species)** |  | |  | | | **(mm)** |  | | ***B*0 ± S.E.** | ***B*1 ± S.E.** | **Resi. SE** | ***R2*** |
| Rogers et al. (1977) | |  | | \*\* | | (#:97) | | | Washington, USA | | BL | 0.7-27 | | OLS | PF | -3.871 ± 0.108 | 2.407 ± 0.06 | 0.55 | **0.97** |
| “ | |  | | FOR | | (#:34) | | | “ | | BL | 1.2-13.5 | | OLS | PF | -4.029 ± 0.171 | 2.572 ± 0.097 | 0.40 | **0.98** |
| Cane (1987) | |  | | Apidae | | (6:20) | | | USA | | ITS | 1-6 | | NL | EXP | A=0.77 | B=0.405 |  | **0.96** |
| *Schoener (1980)* | | *ALL* | | *\*\** | | *(#:174)* | | | *Dry forest, C. Rica* | | *BL* | *N.P* | | *OLS* | *PF* | *A = 0.043 ± 0.05* | *B = 2.07 ± 0.091* | *NA* | *0.87* |
| *“* | | *“* | | *“* | | *(#:122)* | | | *Rain forest, C. Rica* | | *BL* | *N.P.* | | *OLS* | *PF* | *A = 0.022 ± 0.056* | *B = 2.29 ± 0.137* | *NA* | *0.835* |
| *“* | | *“* | | *“* | | *(#:82)* | | | *Massachusetts* | | *BL* | *N.P.* | | *OLS* | *PF* | *A = 0.016 ± 0.072* | *B = 2.55 ± 0.107* | *NA* | *0.937* |
| *“* | | *“* | | *FOR* | | *(#:25)* | | | *Dry forest, C. Rica* | | *BL* | *N.P* | | *OLS* | *PF* | *A = 0.012 ± 0.113* | *B = 2.72 ± 0.26* | *NA* | ***0.907*** |
| *“* | | *“* | | *“* | | *(#:20)* | | | *Rainforest, C. Rica* | | *BL* | *N.P.* | | *OLS* | *PF* | *A = 0.21 ± 0.127* | *B = 2.31 ± 0.224* | *NA* | ***0.934*** |
| *“* | | *“* | | *“* | | *(#:13)* | | | *Massachusetts* | | *BL* | *N.P.* | | *OLS* | *PF* | *A = 0.034 ± 0.155* | *B = 2.19 ± 0.342* | *NA* | ***0.908*** |
| Gowing and Recher (1984) | |  | | \*\* | | (86) | | | NSW, Australia | | BL | 1-12 | | OLS | EXP | -2.860 ± 0.099 | 0.478 ± 0.016 | 0.48 | **0.918** |
| “ | |  | | FOR | | (68) | | | “ | | BL | 2-18 | | OLS | PF | -3.306 ± 0.258 | 2.489 ± 0.051 | 0.32 | **0.973** |
| Sample et al. (1993) | | ALL | | - | | (7:274) | | | West Virginia, USA | | BL | 2.81-34.91 | | OLS | PF | -4.284 ± 0.183 | 2.696 ± 0.083 | NA | 0.89 |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -2.375 ± 0.08 | 1.456 ± 0.028 | NA | **0.95** |
| “ | |  | | Ichneumonidae | | (1: 106) | | | “ | | BL | 3.65-34.91 | |  | “ | -4.149 ± 0.262 | 2.464 ± 0.116 | NA | **0.9** |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -2.497 ± 0.147 | 1.445 ± 0.053 | NA | **0.94** |
| “ | |  | | Braconidae | | (1:41) | | | “ | | BL | 2.81-15.42 | |  | “ | -3.854 ± 0.273 | 2.441 ± 0.147 | NA | **0.94** |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -2.19 ± 0.142 | 1.445 ± 0.069 | NA | **0.96** |
| “ | |  | | Vespidae | | (1:19) | | | “ | | BL | 8.14-20.58 | |  | “ | -3.540 ± 0.544 | 2.782 ± 0.195 | NA | **0.96** |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -1.537 ± 0.307 | 1.319 ± 0.07 | NA | **0.98** |
| “ | |  | | Formicidae | | (1:45) | | | “ | | BL | 3.62-17.41 | |  | “ | -4.727 ± 0.350 | 2.919 ± 0.11 | NA | **0.93** |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -2.378 ± 0.265 | 1.473 ± 0.106 | NA | **0.9** |
| “ | |  | | Halictidae | | (1:21) | | | “ | | BL | 6-12.76 | |  | “ | -2.891 ± 0.386 | 2.302 ± 0.182 | NA | **0.95** |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -2.758 ± 0.357 | 1.590 ± 0.119 | NA | **0.95** |
| “ | |  | | Pompilidae | | (1:15) | | | “ | | BL | 5.55-14.32 | |  | “ | -2.341 ± 0.873 | 2.006 ± 0.396 | NA | 0.81 |
| “ | |  | | “ | | “ | | | “ | | BL \* BW | “ | |  | “ | -1.946 ± 0.431 | 1.444 ± 0.154 | NA | **0.93** |
| Hodar (1997) | | ALL | |  | |  | | | Gaudix-Baza, Spain | | HW |  | | OLS | PF | A= 1.999 ± 0.112 | B= 2.09 ± 0.132 | 0.51 | **0.919** |
| “ | |  | | FOR – Workers | |  | | | “ | | HW |  | |  | “ | A= 0.552 ± 0.068 | B= 2.550 ± 0.116 | 0.19 | **0.982** |
| “ | |  | | FOR –Winged | |  | | | “ | | HW |  | |  | “ | A= 1.607 ± 0.127 | B= 2.752 ± 0.25 | 0.31 | **0.938** |
| Ganihar (1997) | |  | | NA \*\* | | (#:26) | | | Goa, India | | BL |  | | OLS | PF | -3.5917 ± 0.1646 | 2.6429 ± 0.1127 | 0.24 | **0.94** |
| Johnson and Strong (2000) | | ALL | |  | |  | | | Jamaica | | BL | 1.4-24.3 | | OLS | PF | -3.556 ± 0.183 | 2.193 ± 0.110 | NA | **0.923** |
|  | | FOR | |  | |  | | | “ | | BL | 1.6-9.9 | | OLS | PF | -3.730 ± 0.298 | 2.103 ± 0.238 | NA | **0.901** |
|  | | \*\* | |  | |  | | | “ | | BL | 1.4-24.3 | | OLS | PF | -3.295 ± 0.241 | 2.102 ± 0.132 | NA | **0.917** |
| *Sabo et al. (2002)* | | *ALL* | | *7\*\*\*\** | | *(7:54)* | | | *California, USA* | | *BL* | *N.P.* | | *NLL* | *PF* | *A= 0.56 ± 0.64* | *B= 1.56 ± 0.4* |  | *0.75* |
| *“* | |  | | *API* | | *(1:10)* | | | *“* | | *BL* | *N.P.* | | *NLL* | *PF* | *A= 0.006 ± 0.041* | *B= 3.407 ± 2.471* |  | *0.81* |
| *“* | |  | | *VES* | | *(1:19)* | | | *“* | | *BL* | *N.P.* | | *NLL* | *PF* | *A= 0.001 ± 0.002* | *B= 3.723 ± 0.798* |  | *0.95* |
| *Brady and Noske (2006)* | |  | | *FOR* | | *(8 sp:100)* | | | *NT, AUS* | | *BL* | *2-10* | | *OLS* | *P* | *0.001* | *2.330 ± 0.0151* | *0.49* | *0.708/0.956* |
| *“* | |  | | *\*\** | | *(9 sp:28)* | | | *NT, AUS* | | *BL* | *4-29* | | *OLS* | *P* | *6.783 ± 0.001* | *2.544 ± 0.26* | *0.57* | *0.786/0.905* |
| Wardhaugh (2013) | |  | |  | | (#:26) | | | Daintree QL AUS | | BL |  | | MA | PF | -4.3 ± 0.38 | 3 ± 0.24 | NA | 0.83 |
| Wardhaugh (2013) | |  | |  | | (#:26) | | | Daintree QL AUS | | BL \* BW |  | | MA | PF | -2.1 ± 0.09 | 1.34 ± 0.05 | NA | **0.97** |

ANT = Anthophoridae, API = Apidae, CHR = Chrysididae, FOR = Formicidae, ICH = Ichneumonidae, SPH = Sphecidae, VES = Vespidae. \*\*\*\*Seven families = ANT, API, CHR, FOR, ICH, SPH, VES

1. **Lepidoptera**. \*\*\* = Multivariate regression using multiple length measures: length, width, wing area and wing length. See Garcia-Barros (2015) for parameters.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Source** | | **Taxa** | | **Families** | | | **Sample size** | **Biogeographical region** | | | **Measure** | **Range in body length** | **Reg. Type** | | **Type** | **Equation** | | | |
|  |  | |  | |  | **(Families: species)** | | |  |  | | **(mm)** | |  | | ***B*0 ± S.E.** | ***B*1 ± S.E.** | **Resi. SE** | ***R2*** |
| Rogers et al. (1977) | |  | |  | | | (#:22) | Washington, USA | | | BL | 1.6-17 | OLS | | PF | -4.037 ± 0.133 | 2.903 ± 0.08 | 0.31 | **0.99** |
| Sample et al. (1993) | | ALL | |  | | | (#:384) | West Virginia, USA | | | BL | 2.76-40.73 |  | | PF | -5.036 ± 0.157 | 3.122 ± 0.064 |  | **0.93** |
| “ | | “ | |  | | | “ | “ | | | BL \* BW | “ |  | | “ | -2.607 ± 0.088 | 1.457 ± 0.024 |  | **0.95** |
| “ | |  | | MIC. | | | (#:46) | “ | | | BL | 2.76-10.6 |  | | “ | -4.913 ± 0.325 | 2.918 ± 0.169 |  | **0.93** |
| “ | |  | |  | | |  | “ | | | BL \* BW |  |  | | “ | -2.715 ± 0.199 | 1.395 ± 0.08 |  | **0.93** |
| “ | |  | | GEO | | | (1:58) | “ | | | BL | 6.45-21.70 |  | | “ | -4.172 ± 0.411 | 2.628 ± 0.167 |  | **0.9** |
| “ | |  | |  | | |  | “ | | | BL \* BW | “ |  | | “ | -2.343 ± 0.283 | 1.387 ± 0.084 |  | **0.91** |
| “ | |  | | ARC | | | (1:60) | “ | | | BL | 5.05-20.06 |  | | “ | -3.755 ± 0.242 | 2.658 ± 0.105 |  | **0.96** |
| “ | |  | |  | | |  | “ | | | BL \* BW | “ |  | | “ | -1.658 ± 0.148 | 1.222 ± 0.044 |  | **0.96** |
| Sage et al. (1982) | |  | |  | | | (#:25) | Texas, USA | | | BL | 4.9-22.9 |  | | PF |  |  |  | **0.92** |
| Hodar (1996) | | HET | |  | | | (10) | Gaudix-Baza, Spain | | | HW |  |  | | PF | A=2.053 ± 0.25 | B=2.804 ± 0.236 | 0.493 | 0.946 |
| “ | | ROP | |  | | | (10) | “ | | | HW |  |  | | “ | A=1.634 ± 0.46 | B=2.793 ± 0.446 | 0.485 | 0.831 |
| Ganihar et al. (1997) | |  | | NA | | | (#:10) | Goa, India | | | BL |  |  | | PF | -4.7915 ± 0.7507 | 2.8585 ± 0.2567 | 0.4568 | **0.93** |
| Johnson and Strong (2000) | |  | | NA | | | (40) | Jamaica | | | BL | 2.2-18.6 | OLS | | PF | -3.268 ± 0.255 | 2.243 ± 0.130 | NA | **0.942** |
| *Schoener (1980)* | |  | | *NA* | | | *(#:29)* | *Dry forest, Canas, Costa Rica* | | | *BL* | *N.P.* |  | | *PF* | *A= 0.026 ± 0.186735* | *B= 2.55 ± 0.571429* |  | ***0.958*** |
| *“* | |  | | *NA* | | | *(#:7)* | *Rainforest, Guipiles, Costa Rica* | | | *BL* | *N.P.* |  | | *“* | *A= 0.078 ± 0.139796* | *B= 1.32 ± 0.683673* |  | *0.749* |
| *“* | |  | | *NA* | | | *(#:18)* | *Massachusetts* | | | *BL* | *N.P.* |  | | *“* | *A= 0.014 ± 0.18673* | *B= 2.55 ± 0.571429* |  | *0.77* |
| *Brady and Noske (2006)* | |  | |  | | | *((6 sp: 28)* | *NT, AUS* | | | *BL* | *7-34* | *OLS* | | *PF* | *0.001* | *2.313 ± 0.223* | *0.396* | *0.805/0.938* |
| Wardhaugh (2013) | |  | | NA | | | (#:11) | Daintree QL AUS | | | BL |  | MA | | PF | -3.83 ± 0.41 | 2.77 ± 0.27 | NA | 0.83 |
| Wardhaugh (2013) | |  | | NA | | | (#:11) | Daintree QL AUS | | | BL \* BW |  | MA | | “ | -2.1 ± 0.21 | 1.37 ± 0.11 | NA | 0.88 |
| Garcia-Barros (2015) | |  | |  | | |  | Worldwide | | | \*\*\* |  | MU | | - | - | - | - | **0.96** |

HET = Heterocera, ROP = Ropalocera, MIC = Microlepidoptera, GEO = Geometridae, ARC = Arctiidae

Table 2. Predictive allometries for foraging range in pollinating bees.

|  |  |  |  |
| --- | --- | --- | --- |
| **Source** | **Taxa** | **Measure** | **Equation** |
| van Nieuwstadt & Iraheta (1996) | Stingless bees (Apidae:Meliponini) | Artificial nectar source |  |
|  |  | “ |  |
| Greenleaf et al. (2007) | Apidae | Max |  |
|  |  | Typical |  |
|  |  | Feeder |  |
|  |  | Comm |  |