Pollinator size and its consequences: Predictive allometry for pollinating insects

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**Abstract**

Body size is an integral functional trait for insect pollinator ecology and conservation. As body size is often impractical to measure directly, allometric scaling laws have been used to theoretically overcome this problem. However, most existing models are outdated, rely upon geographically restricted sampling and have limited applicability for non-bee taxa. Therefore, predictive models that consider biogeography, phylogenetic relatedness and intraspecific variation should ensure greater accuracy of body size predictions. Here, we measured dry weight and intertegular distance (ITD) of 391 bee species (4039 specimens) and 103 hoverfly species (399 specimens) across four biogeographic regions: Australia, Europe, South America and North America. We updated existing equations within a Bayesian framework which tested the power of ITD alone and its interaction with different co-variates­—biogeographic region, sex and phylogeny or taxonomy (family or subfamily)—to predict interspecific variation in pollinator body size. We used ordinary least squares (OLS) linear regression to assess intraspecific ITD - body size relationships for 10 bee and five hoverfly species. Including co-variates led to more robust interspecific body size predictions that out-performed pre-existing equations in both bees (*R2*: 0.93 - 0.95) and hoverflies (*R2*: 0.84 - 0.86). However, our results demonstrate that, at the intraspecific level, ITD is an inconsistent predictor of body size for bees (*R2*: 0.02 – 0.66) and hoverflies (*R2*: -0.11 – 0.44). Therefore, predictive allometry is more suitable for interspecific comparative analyses than assessing intraspecific variation. Collectively, these models form the basis of the dynamic R package, '*pollimetry*’, which provides a new resource for allometric research concerning insect pollinators worldwide.

**Keywords**: allometry, Apoidea, biogeography, body size, pollimetry, pollination, R package, Syrphidae

**Introduction**

Body size is an important trait that influences ecological patterns across all levels of biological organisation. In insects, adult body size variation (allometric variation) is the outcome of natural selection affecting physiological and biochemical processes during ontogeny (Chown & Gaston 2010). For example, body size impacts metabolic and growth rates (Angilletta et al. 2004; Ehnes et al. 2011; Harrison et al. 2014)), life history (e.g. life span and reproductive rate) (Speakman 2005; Teder et al. 2008) and ecological attributes such as 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; Velghe & Gregory-Eaves 2013; DeLong et al. 2015). These allometric relationships drive key ecosystem functions and services such as decomposition, carbon cycling, predation, primary productivity and pollination (Woodward & Hildrew 2002; Greenleaf et al. 2007; Rudolf & Rasmussen 2013; Schramski et al. 2015).

Obtaining direct measurements of insect body size as well as allometric traits can be difficult, time consuming and impractical. Direct measurements often require destructive methods, which is unfavourable for museum specimens and threatened species (Rogers et al. 1977; Henschel & Seely 1997). Additionally, a lack of specimens and/or species with poor life-history information, such as cryptic or rare species, may lead to inaccurate measurements of intraspecific variation. Allometric scaling laws can be used to overcome these problems. These 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). When these scaling laws are utilised to estimate body size or a hypothesised allometric characteristic indirectly using a co-varying trait, we define this as ‘predictive allometry’.

Predictive allometry has emerged across many biological disciplines. Most commonly, body length has been used extensively to predict body size (dry body weight), such as in fish (e.g. Karachle & Stergiou 2012), mammals (e.g. Trites & Pauly 1998) and both aquatic (e.g. Burgherr & Meyer 1997; Benke et al. 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), which has led to the proliferation of multiple models for a wide range of taxa, especially insects. However, when compared, these models show considerably different coefficients both within- and between insect orders (Schoener 1980; Sample et al. 1993; Ganihar 1997; Benke et al. 1999; Brady & Noske 2006), often due to biogeography (i.e. latitude, see Martin et al. 2014) and/or methodological influences such as sampling biases (e.g. range of body sizes sampled, Sage 1982). Importantly, they have also notably failed to incorporate sexual size dimorphism which is common in invertebrates (Shreeves & Field 2008).

Insects exhibit a number of key allometric traits that underpin their ability to pollinate plants. For example, in bees, smaller body size can be associated with preferential activity periods related to available light (Streinzer et al. 2016), whereas larger body size is associated with greater pollen load capacity within *Melipona quadrifasciata* colonies (Ramalho et al. 1998) as well as greater interspecific foraging distances (e.g. Greenleaf et al. 2007; van Nieuwstadt & Iraheta 1996). Body size can play a role in plant-pollinator trait matching (Stang et al 2009; Olesen et al., 2010; Bartomeus et al. 2016). Therefore, allometric traits central to pollination-related ecological processes both appear and interact at the intra- and interspecific levels. Despite this ubiquity, few predictive models exist for pollinating insects below the ordinal level with one notable exception. Cane (1987) pioneered a predictive equation 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).Importantly, Cane’s allometric model identified the ITD as an important body size proxy and it has been used in establishing other ecologically important allometric relationships, primarily at the interspecific level (e.g. foraging distances and bee proboscis length; Greenleaf et al. 2007; Cariveau et al. 2016).

With the exception of bumblebees (Hagen & Dupont 2013), the predictive utility of the ITD has not previously been tested beyond North American solitary bee species, despite evidence suggesting allometric coefficients can differ significantly between biogeographical regions (Martin et al. 2014). Neither, has its intraspecific predictive utility been tested. Additionally, sexual size dimorphism is present in 80% of Aculeata (Shreeves & Field 2008), highlighting the need to include sex-specific co-variation. Further, body size variation has been repeatedly linked to phylogeny, compelling allometric studies to incorporate species evolutionary histories (Garland and Ives 2000; Blomberg et al. 2003). Lastly, other key pollinating taxa, such as hoverflies (Diptera: Syrphidae) lack predictive models that could be used to examine allometric patterns. These knowledge gaps are largely due to the lack of: (i) a general repository to house and connect all relevant predictive allometric equations; (ii) high resolution datasets to build more accurate models that can incorporate co-variates and (iii) the lack of an iterative framework (such as is utilised in ecological forecasting (e.g. Dietze et al. 2018; Harris et al. 2018) to continuously update existing models with new datasets, methodologies and technologies. Addressing these key deficiencies will increase model accuracy and applicability of predictive allometry for pollinating insects.

Here, we catalogue pre-existing equations for key pollinating insect taxa and formulate new models that incorporate biogeography, species evolutionary histories and intraspecific variation to develop predictive allometric equations within an iterative framework. These form the basis of a new *R* package, entitled “*pollimetry*”. Specifically, we address the following research questions:

1. Is ITD a robust predictor of inter-specific body size variation for bees and hoverflies?
2. Does incorporating biogeographic region, sexual dimorphism and phylogenetic/taxonomic relatedness improve interspecific predictions of pollinator body size?
3. Is ITD reliable in predicting intraspecific variation in both bees and hoverflies and what sample size is required to accurately estimate intraspecific body size and co-varying trait values?

**Methodology**

*Specimen collection and measurements*

We obtained specimens from recent field research focused on insect pollination and biodiversity. We included studies across four continents. In Australia, collections were made in New South Wales, Victoria, Queensland, South Australia and the Northern Territory. In Europe, we amassed specimens from Belgium, England, Germany, Ireland, Spain and Switzerland. In the Americas, we included collections from USA and Brazil. Cane’s (1987) original data was obtained using Engauge Digitizer version 10.6 (Mitchell et al. 2018).

The majority of specimens were dehydrated and weighed within three to six months of collection, although some, in particular, those from Victoria, Australia, Belgium, Switzerland and Cane’s original samples were of variable ages: ranging from one to five years since collection. We excluded damaged specimens. For every included specimen, we obtained sample location (latitude and longitude) and taxonomic identity.

*Body size and intertegular distance*

Dry weight (mg) was measured on an analytical balance to an accuracy to 0.001g. Both fresh and curated specimens were dehydrated at 70 °C for at least 24hrs 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. Pin weight variance was minimal (range of standard errors: 6.3\*10-4 to 2mg). Intertegular distance (see Cane 1987; Cariveau et al. 2016) was measured in millimetres using a stereo-microscope, either mounted with a calibrated scale or microscope camera. Body length was measured along the lateral side of each specimen with a calibrated scale or microscope camera for Australian, British, German, Irish and Spanish specimens.

*Data analysis: Model structures*

All analyses were undertaken in *R* (version 3.5.1) (R Core Team 2018). For each taxon, we constructed species mean datasets. Every female and male of each species was averaged within their biogeographical region of origin. We first assessed the Pearson’s correlation coefficient between ITD and body length. We then compared both ITD and body length independently in predicting body size using ordinary least squares (OLS) regression. As traditionally performed, we used log-transformed values in the model formulation because allometric relationships are typically described by a power function () which is linearised when log-transformed:

ln(Y) = ln(aj) + bj\*ln(ITD or body length)

where Y = body weight/size, aj = intercept and bj = allometric co-efficient.

We applied the same formula within a Bayesian generalised linear mixed model (GLMM) framework using the *brms* package(version 2.3.1) (Bürkner 2017) to predict body size as a function of the ITD in interaction with sex and taxonomic grouping (family for bees, subfamily for hoverflies). We included a nested random term: species nested within their biogeographical region of origin. Both bee and hoverfly models were run for 11\*105 iterations with a burn-in of 1000 and thinning of 10. We set Δ to 0.99 and set tree depth between 10-20 for individual models to avoid divergent transitions.

*Data analysis: Incorporating phylogeny*

We explored the influence of phylogenetic relatedness in predicting bee body size by first identifying phylogenetic signal in body size. A current phylogeny was unavailable for hoverflies. We obtained a bee genera backbone tree (Hedtke et al. 2013) and removed non-represented genera using the *ape* package (version 5.1) (Paradis et al., 2004). Species tips were added to genera nodes as pure-birth subtrees using the *phytools* package (version 0.6-44) (Revell et al. 2012). As such, we made the explicit assumption that phylogenetic patterns in body size were assessed at and above the genera level. We estimated node ages using the mean path lengths method of Britton et al. (2002). We assessed the significance of phylogenetic signal using Pagel’s λ with the *phytools* package (version 0.6-44) (Pagel 1999: Revell et al. 2012). Phylogenetic signal was highly significant for bee ln body size (λ: 0.818, *p* <0.001) (Figure 1). Therefore, we implemented a nested phylogenetic generalised linear mixed model (PGLMM) which considered ITD in interaction with intraspecific sexual dimorphism whilst accounting for phylogenetic dependencies through a nested random term: species nested within region, with the region:species term constrained by the constructed phylogeny.

*Data analysis: Model selection: Bayesian R2 and K-fold cross-validation*

We first fitted the full model with all predicted explanatory variables for both model types (GLMM and PGLMM). We then performed model selection assessing all subset models. We chose to rank our models based upon their Bayesian *R2* (Gelman et al. 2017) and K-Fold Cross-Validation Information Criterion (K-IC) weighting. Both the Watanabe-Akaike Information Criterion (WAIC) and Leave-One-Out Information Criterion were inappropriate due to pWAIC estimates of >0.4 and problematic observations (Vehtari et al. 2017). Species mean datasets were divided into 10 equal sets containing a random subset of species. Each model was then evaluated iteratively upon each k-1 set (training set consisting of nine sets) by comparing the actual and predicted values within the one left out ‘test’ set. This was done repeatedly so each set was both the test set and contained within the training sets.

*Model comparisons: Root mean square error (RMSE)*

We then assessed model performance on the basis of the root-mean square error (RMSE) between actual-predicted body size values and compared these point-estimates of error between our models and predicted values from Cane’s (1987) original equation:

where = ITD and = body size. Lastly, we derived RMSE for actual-predicted values from existing body length equations for both taxa and our body length measurements.

*Data analysis: Intraspecific predictions*

First, we assessed the utility of ITD in predicting intraspecific body size variation. For the 10 most abundant species of bees and five most abundant species hoverflies we tested the utility of ITD in predicting intraspecific body size variation using species-level OLS regression. We used females in nine out of ten bee species and all hoverfly species as these were most abundant. Second, for each species, we plotted trait means independently against increasing sample size to estimate the adequate sample size whereby variance stabilised within the 95% confidence intervals of the actual sample size.

*Data availability*

All data including R code and R package are available here: <https://github.com/liamkendall/pollimetry/>. DOI: TBC.

**Results**

*Species and specimen distribution*

In total, we measured 391 bee species (4039 specimens) from Australia, Europe, North America and South America, including Cane’s (1987) original 20 species, and 103 hoverfly species (399 specimens) from Australia and Europe only (Table 1). Six out of seven bee families and both hoverfly subfamilies were represented. The number of individuals per bee species ranged from 1 (103 species a ♀ individual, 76 species a ♂ individual) and 201 (♀ *Homalictus urbanus*) and 68 (♂ Bombus impatiens) with a mean of 9 ♀ and 5 ♂ per species (Additional file: “pollimetry\_dataframe.csv”). In hoverflies, specimen number per species ranged from 1 (49 species a ♀ individual, 34 species a ♂ individual) to 32 (♀ *Austrosyrphus* spp.) and 18 (♂ *Austrosyrphus* spp.) with a mean of 3 per species for both sexes.

*Trait co-variation*

ITD and body length (BL) were highly correlated in both bees: *ρ* = 0.932, and hoverflies: *ρ* = 0.854. ITD was marginally more predictive than BL in estimating body size in bees: ITD *R2*:0.896; BL, *R2*: 0.877 and considerably better than BL for hoverflies: ITD *R2*: 0.854; BL *R2*: 0.796.

*Patterns in body size variation*

There were strong trends in the ITD:Body size relationship due to biogeography, phylogeny/taxonomy and sexual dimorphism in both bees and hoverflies (Figure S1A;S1B). In bees, when body size variation was visualised across the phylogeny, larger body size was most pronounced within the Apidae (Figure 1), the largest bee in our dataset being the South American *Xylocopa frontalis* (♀ mean weight: 760.75mg). In contrast, Halictid (i.e. *Halictus*, *Homalictus* and *Lasioglossum* species)and Colletid bees—in particular, the Australian *Euhesma* sp. (♀ mean weight: 0.71mg, ♂ mean weight: 0.66mg) and the European *Hylaeus communis* (♀ mean weight: 6.15mg, ♂ mean weight: 2.76mg)—were smaller than average.

*Interspecific model selection and performance*

For bees, both GLMM and PGLMM analyses found that those models that considered taxonomic family or phylogeny and sex in interaction or in addition with ITD best predicted body size on the basis of Bayesian *R2* and K-IC (Table 2). Overall variation in model parameter estimates were low between both model types (Figure 2A). Incorporating sex and family increased *R2* from 0.937 to 0.95 (ΔK-IC > 94) for taxonomic models, and from 0.932 to 0.945 (ΔK-IC > 56) in phylogenetic models. In hoverflies, incorporating taxonomy and/or sex increased body size predictions relative to ITD models (*R2*: 0.853 to 0.862, ΔK-IC: 15.12). There were only marginal differences between the best fitting sex-specific and/or taxonomic model (ΔK-IC: 0.989, *R2* difference = 0.001, Figure 2B, Table 2).

Increases in model performance as a result of incorporating co-variates was more pronounced in bees in terms of root mean square error (RMSE) (Table 2). RMSE was higher and more variable in bee models than hoverfly models (bee RMSE range 11.329 – 18.355mg; hoverfly RMSE range: 4.237mg – 4.755mg. The range of prediction error for ITD was also considerably lower than any pre-existing and applicable equation using body length: 36.36mg ± 8.29 for bees, 7.99mg ± 0.69 for hoverflies or Cane’s (1987) original equation: 24.569mg.

*Intra-specific predictions*

Across the 10 most abundant species of bees (nine with female specimens, one with male specimens) and five most abundant hoverflies (females only), the strength of intraspecific predictions of body size using ITD was varied (Table 3; Figure 3). All bee species exhibited a significant relationship between ITD and body size, however the adjusted-*R2*differed considerably from 0.02 in *Homalictus urbanus* to 0.66 for *Bombus lapidarius*. Three of five hoverfly species, *Austrosyrphus* sp., *Helophilus parallelus and Melanostoma scalare* exhibited significant trends.

Sample size exhibited an interesting trend in relation to both ITD and dry weight. In bees, mean ITD and dry weight stabilised within the 95% confidence intervals of the total sample size with >20-30 specimens per species (Figure S2A). For hoverflies, small sample sizes of each species limited inference of sample-size / mean stabilisation (Figure S2B).

*Summary of R package functions*

The accompanying R package, ‘*pollimetry’*, includes a total of six (thinking: one wrapper for bees and hoverflies, foraging distance, tongue length. pre-existing body length, head width and length x width) functions for pollinator body size estimation using pre-existing equations (see Table S1 for description of collation and co-efficients) and our new equations (See Table 2). These also include functions for estimating bee foraging distances using ITD (Greenleaf et al. 2007) or head width respectively (Roubik & Aluja 1983; Nieuwstadt & Iraheta 1996), as well as allometric equations for estimating bee tongue length using the ITD and taxonomic family (Cariveau et al. 2016). Existing equations will be periodically updated, and new equations added in the form of package updates as novel data becomes available.

**Discussion**

We present the most inclusive examination of both bee and hoverfly body size variation to date. We used an iterative framework to develop and test a suite of dynamic allometric models for these two key pollinating taxa that took into account body size variation attributable to biogeography, phylogenetic relatedness and sexual dimorphism.

Terrestrial invertebrates show considerable biogeographic variation in body shape and size. Despite previous studies examining biogeographic trends in predictive allometry (Schoener 1980; Gowing & Recher 1984; Martin et al 2014), we chose to represent biogeographical variation within a random effect structure. Observed biogeographical differences within this study likely arise from differing species diversification patterns as well as from sampling biases, such as variation in commonality among species and the range of body sizes measured (Sage 1982). Therefore, discerning biological hypotheses that explain biogeographic variation in the ITD:body size relationship are fraught with difficulty. To develop and test these biological hypotheses driving observed trends, larger-scale efforts incorporating multiple regions, biomes and ecosystems as well as systematic sampling across a taxon’s phylogeny are required. However, it is clear that the influence of biogeography appears in addition to their evolutionary histories and intraspecific variation (i.e. sexual dimorphism). Thus, we focussed our analyses on these two causes of variation.

Phylogenetic signal in body size variation has been inferred in a number of vertebrate and invertebrate groups (see Ashton 2004). Failing to account for dependent phylogenetic patterns is argued to heighten the risk of inaccurate predictions (Martins 1991; Martins et al. 2002; Garland et al. 2005). In our study, both PGLMM and GLMM models were comparable in terms of predictive power as well as parameter values (See Figure 2A). Interestingly, GLMM models incorporating taxonomy over phylogeny ranked better in terms of K-IC and Bayesian *R2*, although not RMSE, demonstrating that influential allometric variation is present at/or below the familial level. Previous studies have analysed widespread allometric differences at the ordinal level (See Martin et al. 2014). However, our results suggest that predictive inferences of body size above the family level are inaccurate and not generalisable.

For prediction, GLMM models are more practical than phylogenetic structures as they do not require a complete phylogeny (i.e. you can predict a species outside the used phylogeny). Further an advantage of using taxonomic grouping over phylogeny is that they provide easy-to-interpret regression intercepts and/or slopes. Therefore, incorporating taxonomy represents a functional equivalent where phylogenetic information is unavailable. However, in hoverflies, including subfamily was less informative in describing body size variation, potentially due to their lower taxonomic ranking. In essence, our results suggest that where previous studies have used taxonomy as a phylogenetic proxy (i.e. Bee family in Cariveau et al. 2016), their results are predictively comparable to incorporating phylogeny.

Sex was retained as an integral predictor either in addition or in interaction with ITD for both taxa. Sexual size dimorphism (SSD) is common among insects. In both Diptera and Hymenoptera, 80% of studied species exhibit female-biased SSD (larger females) including in Apoidea and Syrphidae (Shreeves and Field 2008; Francuski et al. 2011; Milankov et al. 2013). Female-biased SSD is hypothesised to be a result of the greater fitness and increased fecundity inferred by larger female body size (Teder and Tammaru 2005: Stillwell 2010). In bees, SSD is attributed to the physical requirements of nest provisioning and construction. As such, female-biased SSD is more pronounced in ground nesting and/or provisioning taxa than non-provisioning and/or cavity nesting taxa (Shreeves and Field 2008). Furthermore, female bees’ exhibit specialised morphological structures for resource collection (i.e. scopal hairs and corbiculae) as well as self-preservation (i.e. a stinging ovipositor). In hoverflies, SSD was also notably female-biased, with sex retained as an important body size predictor in conjunction with the ITD. There exist, however, few examples of morphological sexual dimorphism, other than eye shape, in hoverflies. In both cases, including sex only explained an additional 1-2% of the variation, highlighting the predictive accuracy of the ITD. Therefore, failing to incorporate it in predictive models will only introduce subtle error (See Figure S1). Sex is easily identifiable in both bees (number of antennal and abdominal segments) and hoverflies (eye shape and size). Therefore, we recommend its inclusion if predictive allometries are used as many ecologically relevant allometric traits are sex-related (e.g. foraging distance and dispersal).

Few previous studies have assessed the utility of predictive models in describing intrageneric or intraspecific allometric traits (e.g. Hagen & Dupont 2013; Cariveau et al. 2016). Our results suggest intraspecific body variation is difficult to predict accurately using co-varying traits such as the ITD. In particular, the large variation in predictive power suggests that it is sensitive to environmental conditions and/or sample sizes. Adult body size variation in holometabolous insects is a direct result of diet and environment during ontogeny and larval development (Davidowitz et al. 2004). Given this natural variability, predictive allometry is sensitive to phenotypic plasticity in body shape and size, as demonstrated in our examination of trait-sample size relationships. By applying an iterative framework, this sensitivity will lessen in time by incorporating novel data sets. However, we can provide a recommendation of measuring 20-30 specimens per species to accurately estimate intraspecific body size and trait values with the caveat that more detailed investigation of morphological co-variation within species is required to understand the biological constraints in the range and variation in body shape, size and traits.

By incorporating biogeography, phylogeny and/or taxonomy and sexual dimorphism we improved model predictions and overcame some of the limitations of traditional predictive allometry. These three predictors represent fundamentally-related causes of body size variation in pollinating insects. In consideration of the multiple metrics (i.e. K-IC, Bayesian *R2* and RMSE) used in model selection and performance, we provide multiple, near-equally accurate predictive models. This is important as sampling regimes and research questions may not garner investigation of sex-related allometric differences and will occur outside the included biogeographic regions. Therefore, disseminating the most appropriate allometric model becomes a hypothesis-driven formula that, to begin with, should consider and then discount each examined factor. Importantly, given the high resolution across our described models and large sample size of specimens within our study, our models will improve predictions relative to pre-existing models. Failing to incorporate sex or phylogeny/taxonomy will not result in considerable error, although we recommend their use as it will enable more ecologically meaningful analyses. Lastly, we caution the use of ordinal-level predictive equations as allometric variation is ubiquitous at the familial level.

The accompanying R package, “*pollimetry*”, provides a user-friendly interface to estimate pollinator body size and modelled allometric traits. Practical predictive allometric libraries require multiple models that will continue to be updated as novel data becomes available. This will enable the investigation and re-evaluation of other allometric traits at both intra- or inter-specific levels with greater accuracy. The consequence of size is ubiquitous within pollination research, yet few have utilised allometric theory in studying pollinating taxa beyond bees. The iterative framework used herein heralds a dynamic new direction for predictive allometry and should provide greater prediction through hypothesis-led model choice, testing and investigation in allometric research.

Table 1. Distribution of included specimens. Numbers in parenthesis denote total specimens and species per country, family and/or subfamily.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Taxa | Region | Country | Family | Subfamily | |
| Bee | | Australasia | Australia (899, 93) | Apidae (185, 20)  Colletidae (130, 15)  Halictidae (519, 38)  Megachilidae | Apinae (125, 13), Xylocopinae (60, 7)  Colletinae (76, 7), Euryglossinae (49, 3)  Hylaeinae (5, 5)  Halictinae (441, 25)  Nomiinae (78, 13)  Megachilinae (65, 20) |
|  | Europe | Belgium (703, 49) | Andrenidae  Apidae (242)  Halictidae  Megachilidae  Melittidae (14) | Andreninae (253, 15)  Apinae (192, 9), Nomadinae (50, 4)  Halictinae (120, 9)  Megachilinae (74, 9)  Dasypodainae (3, 1), Melittinae (11, 2) | |
|  |  | England (46, 4) | Apidae | Apinae (46, 4) | |
|  |  | Germany (765, 63) | Andrenidae  Apidae (189, 12)  Colletidae  Halictidae  Megachilidae | Andreninae (197, 14)  Apinae (188, 11), Nomadinae (1, 1)  Hylaeinae (13, 6)  Halictinae (337, 18)  Megachilinae (29, 13) | |
|  |  | Ireland (52, 15) | Andrenidae  Apidae  Colletidae  Halictidae | Andreninae (4, 2)  Apinae (29, 6)  Hylaeinae (5, 2)  Halictinae (14, 5) | |
|  |  | Spain (74, 46) | Andrenidae (18, 13)  Apidae (27, 17)  Colletidae  Halictidae (11, 6)  Megachilidae  Melittidae | Andreninae (10, 8), Panurginae (8, 5)  Apinae (16, 10), Nomadinae (6, 4)  Xylocopinae (5, 3)  Colletinae (4, 2)  Halictinae (8, 5), Rophitinae (3, 1)  Megachilinae (7, 6)  Dasypodainae (7, 2) | |
|  |  | Switzerland (210, 63) | Andrenidae  Apidae (60, 20)  Colletidae  Halictidae  Megachilidae  Melittidae | Andreninae (54, 14)  Apinae (54, 16), Nomadinae (4, 3), Xylocopinae (2, 1)  Colletinae (3, 1)  Halictinae (76, 20)  Megachilinae (15, 6)  Melittinae (2, 2) | |
|  | North America | USA (1086, 132) | Andrenidae (157, 35)  Apidae (378, 27)  Colletidae (86, 8)  Halictidae (397, 44)  Megachilidae (17)  Melittidae (1) | Andreninae (152, 30), Oxaeinae (1, 1), Panurginae (4, 4)  Apinae (195, 18), Nomadinae (17, 4), Xylocopinae (166, 4)  Colletinae (3, 2), Hylaeinae (83, 6)  Halictinae (242, 42), Nomiinae (1, 1), Rophitinae (1, 1)  Megachilinae (67, 17)  Dasypodainae (1, 1) | |
|  | South America | Brazil (204, 22) | Andrenidae  Apidae (174, 17)  Halictidae  Megachilidae | Panurginae (8, 1)  Apinae (149, 12), Xylocopinae (25, 5)  Halictinae (11, 2)  Megachilinae (11, 2) | |
| Hoverfly | | Australasia | Australia (120, 19) |  | Eristalinae (25, 7), Syrphinae (95, 12) |
|  | | Europe | Ireland (39, 15) |  | Eristalinae (8, 5), Syrphinae (31, 10) |
|  |  | Spain (8, 8) |  | Eristalinae (6, 6), Syrphinae (2, 2) | |
|  | |  | Switzerland (232, 79) |  | Eristalinae (114, 37), Syrphinae (118, 42) |

Table 2. Model selection tables for bee and hoverfly interspecific models. Models are those selected for inclusion in the *R* package. Model types: i) GLMM: generalised linear mixed models and ii) PGLMM: phylogenetic generalised linear mixed model. Int: Intercept, lnITD: ln intertegular distance, Fam: Family, Subf: Subfamily, df: degrees of freedom, *R2*: Bayesian R2,K-IC: K-fold cross validation information criterion, Δ:ΔK-IC and RMSE: root-mean square error. Rows in bold denote models used in comparisons (Figure 2) and described in Table S3.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Taxa | Model type | Int | lnITD | Fam | Subf | Sex | Fam:lnITD | Subf:lnITD | Sex:lnITD | df | R2 | K-IC | Δ | RMSE |
| Bee | GLMM | **1** | **2.2** | **+** | **NA** | **+** | **+** | **NA** | **NA** | **21** | **0.950** | **362.347** | **0.000** | **15.487** |
|  |  | 0.96 | 2.25 | + | NA | + | + | NA | + | 22 | 0.951 | 367.137 | 4.790 | 14.311 |
|  |  | 0.8 | 2.4 | + | NA | + | NA | NA | + | 19 | 0.951 | 372.954 | 10.607 | 11.337 |
|  |  | 0.84 | 2.35 | + | NA | + | NA | NA | NA | 17 | 0.950 | 391.976 | 29.629 | 12.044 |
|  |  | 0.91 | 2.22 | + | NA | NA | + | NA | NA | 18 | 0.939 | 408.398 | 46.051 | 18.355 |
|  |  | 0.73 | 2.39 | + | NA | NA | NA | NA | NA | 16 | 0.937 | 418.902 | 56.555 | 14.735 |
|  |  | 0.64 | 2.44 | NA | NA | NA | NA | NA | NA | 14 | 0.937 | 457.165 | 94.818 | 13.535 |
|  | PGLMM | **0.65** | **2.4** | **NA** | **NA** | **+** | **NA** | **NA** | **+** | **13** | **0.945** | **381.144** | **0.000** | **12.561** |
|  |  | 0.7 | 2.35 | NA | NA | + | NA | NA | NA | 12 | 0.945 | 402.218 | 21.074 | 13.456 |
|  |  | 0.58 | 2.43 | NA | NA | NA | NA | NA | NA | 11 | 0.932 | 437.860 | 56.716 | 15.407 |
| Hoverfly | GLMM | **-0.13** | **2.52** | **NA** | **NA** | **+** | **NA** | **NA** | **NA** | **6** | **0.862** | **166.497** | **0.000** | **4.237** |
|  |  | **-0.07** | **2.52** | **NA** | **+** | **+** | **NA** | **+** | **NA** | **8** | **0.861** | **167.486** | **0.989** | **4.416** |
|  |  | -0.02 | 2.42 | NA | + | NA | NA | NA | NA | 6 | 0.842 | 171.170 | 4.673 | 4.535 |
|  |  | -0.17 | 2.51 | NA | NA | NA | NA | NA | NA | 5 | 0.843 | 172.585 | 6.088 | 4.607 |
|  |  | -0.12 | 2.57 | NA | + | + | NA | + | + | 9 | 0.856 | 173.911 | 7.414 | 4.741 |
|  |  | -0.11 | 2.51 | NA | + | NA | NA | + | NA | 7 | 0.845 | 173.969 | 7.471 | 4.659 |
|  |  | 0.02 | 2.44 | NA | + | + | NA | NA | NA | 7 | 0.858 | 174.581 | 8.084 | 4.247 |
|  |  | -0.17 | 2.58 | NA | NA | + | NA | NA | + | 7 | 0.856 | 176.634 | 10.137 | 4.656 |
|  |  | -0.06 | 2.51 | NA | + | + | NA | NA | + | 8 | 0.853 | 181.617 | 15.120 | 4.755 |

Table 3. Model parameters of intraspecific ln(body size)~ln(ITD) size relationships. F: F-statistic and degrees of freedom for each model. A: intercept, B: ITD co-efficients ± standard error, *R2*: Adjusted *R2* and P: p-value of full model. Only females were used in both analyses.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Taxa | Species | F(df) | A | B | *R2* | P |
| Bee | *Andrena flavipes* | 17.63 (1,70) | 1.575 ± 0.367 | 1.73 ± 0.412 | 0.189 | <0.001 |
|  | *Andrena nigroaenea* | 30.17 (1,50) | 0.893 ± 0.488 | 2.459 ± 0.448 | 0.364 | <0.001 |
|  | *Bombus impatiens* | 20.14 (1,66) | 2.128 ± 0.365 | 1.275 ± 0.284 | 0.222 | <0.001 |
|  | *Bombus lapidarius* | 110.2 (1,54) | 0.277 ± 0.343 | 2.761 ± 0.263 | 0.665 | <0.001 |
|  | *Bombus terrestris* | 137.8 (1,81) | 1.242 ± 0.274 | 2.136 ± 0.182 | 0.625 | <0.001 |
|  | *Homalictus urbanus* | 6.055 (1,209) | -0.164 ± 0.033 | 1.166 ± 0.474 | 0.024 | 0.014 |
|  | *Lasioglossum glabriusculum* | 6.444 (1,47) | 0.302 ± 0.127 | 2.802 ± 1.104 | 0.102 | 0.014 |
|  | *Lasioglossum lanarium* | 53.87 (1,61) | 0.702 ± 0.198 | 2.13 ± 0.29 | 0.46 | <0.001 |
|  | *Lasioglossum pauxillum* | 37.46 (1,129) | 0.488 ± 0.057 | 2.715 ± 0.444 | 0.219 | <0.001 |
|  | *Trigona spinipes* | 0.285 (1,48) | 2.144 ± 0.243 | 0.287 ± 0.537 | -0.02 | 0.596 |
| Hoverfly | *Austrosyrphus spp.* | 12.7 (1,30) | 0.087 ± 0.458 | 2.032 ± 0.57 | 0.274 | 0.001 |
|  | *Episyrphus balteatus* | 0.08 (1,8) | 1.334 ± 1.885 | 0.885 ± 2.229 | -0.11 | N.S. |
|  | *Helophilus parallelus* | 14.84 (1,17) | 0.286 ± 0.857 | 2.485 ± 0.645 | 0.435 | 0.001 |
|  | *Melanostoma scalare* | 6.38 (1,7) | -2.172 ± 1.324 | 7.619 ± 3.016 | 0.4 | 0.03 |
|  | *Sphaerophoria macrogaster* | 0.04 (1,8) | 0.361 ± 0.274 | 0.195 ± 0.907 | -0.11 | N.S. |

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Figure 1. Bee genera tree (Hedtke et al. 2013) with species subtrees. Colour denotes mean ln body size of each bee species included in analyses

Figure 2A. Bees: Intertegular distance (ITD):Body size (dry weight) relationships Actual **(\*)** and predicted values for each bee family for best-fitting GLMM (**blue**) and PGLMM (**red**) models. **Circles**: Predictions with population-level effects only. **Triangles**: Predictions with population-level effects and random effects.



Figure 2B. Hoverflies: Intertegular distance (ITD):Body size (dry weight) relationships for each hoverfly subfamily. Actual **(\*)** and predicted values for two best-fitting GLMMs (blue: ITD + Sex, red: ITD\*Subfamily + Sex) models. **Circles**: Predictions with population-level effects only. **Triangles**: Predictions with population-level effects and random effects.

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**Figure 3.** Intraspecific predictions of body size with intertegular distance. Lines denote line of best fit from OLS regression. N.B. Only female specimens except for *Bombus impatiens* for which male specimens were used.

**Supplementary Material**

*Description of* *pre-existing equations*

We selected three key pollinating insect orders: Diptera, Hymenoptera and Lepidoptera and collated all known predictive allometric models. From an initial literature search, we obtained the publications analysed by Martin et al. (2014). We then reviewed each publication individually, including their references and citations for additional 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. 12 for the three main suborders Nematocera (6), Brachycera (4) and Cycllorapha (2) and two for specific families; Asilidae and Bombyliidae.

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). Sample et al’s (1993) body length (BL) and body length\*width (BW) 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.

Foraging distance and proboscis length: We collated six bee foraging distance models from van Nieuwstadt and Iraheta (1996) and Greenleaf et al. (2007) and three models for bee proboscis length from Cariveau et al. (2016)

Table S1. Allometric equations for pollinating taxa. BL = Body length, BW = Body width, ITD = intertegular distance. OLS = Ordinary Least Squares regression. MA = Major axis 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 | -2.603 ± 0.0688 | 1.64 ± 0.1224 | NA | 0.795 |
| Schoener (1980) | |  | |  | |  | | Rain forest, CR | | | BL | N.P. | OLS | PF | -2.688 ± 0.051 | 1.59 ± 0.1173 | NA | 0.775 |
| Schoener (1980) | |  | |  | | (#:171) | | Massachusetts | | | BL | N.P. | OLS | PF | -3.816 ± 0.561 | 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 | 0.655 ± 0.105 | 2.526 ± 0.139 | 0.47 | **0.933** |
|  | | NEM | |  | | (10) | | “ | | | HW | NA | OLS | PF | 3.942 ± 0.259 | 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* | *0.006 ± 0.007* | *3.05 ± 0.36* |  | *0.85* |
| *“* | | *NEM* | |  | |  | | *“* | | | *BL* | *N.P.* |  | *PF* | *0.1 ± 0.06* | *1.57 ±0.2* |  | ***0.9*** |
| *“* | |  | | *Asilidae* | | *(1:9)* | | *“* | | | *BL* | *N.P.* |  | *PF* | *0.38 ± 2.625* | *1.5 ± 2.469* |  | *0.74* |
| *“* | |  | | *Bombyliidae* | | *(1:10)* | | *“* | | | *BL* | *N.P.* |  | *PF* | *0.007 ± 0.011* | *3.337 ±0.676* |  | ***0.95*** |
| *Brady and Noske (2006)* | | *NA* | | *NA* | | *(9 sp:78 spe)* | | *NT, AUS* | | | *B:* | *2-28* | *OLS* | *L* | *-0.041 ± 0.004* | *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.**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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 | | ITD | 1-6 | | | NL | | EXP | | 0.6453 | | 2.4691 | |  | | **0.96** | |
| *Schoener (1980)* | | *ALL* | | *\*\** | | *(#:174)* | | *Dry forest, C. Rica* | | *BL* | *N.P* | | | *OLS* | | *PF* | | *0.043 ± 0.05* | | *2.07 ± 0.091* | | *NA* | | *0.87* | |
| *“* | | *“* | | *“* | | *(#:122)* | | *Rain forest, C. Rica* | | *BL* | *N.P.* | | | *OLS* | | *PF* | | *0.022 ± 0.056* | | *2.29 ± 0.137* | | *NA* | | *0.835* | |
| *“* | | *“* | | *“* | | *(#:82)* | | *Massachusetts* | | *BL* | *N.P.* | | | *OLS* | | *PF* | | *0.016 ± 0.072* | | *2.55 ± 0.107* | | *NA* | | *0.937* | |
| *“* | | *“* | | *FOR* | | *(#:25)* | | *Dry forest, C. Rica* | | *BL* | *N.P* | | | *OLS* | | *PF* | | *0.012 ± 0.113* | | *2.72 ± 0.26* | | *NA* | | ***0.907*** | |
| *“* | | *“* | | *“* | | *(#:20)* | | *Rainforest, C. Rica* | | *BL* | *N.P.* | | | *OLS* | | *PF* | | *0.21 ± 0.127* | | *2.31 ± 0.224* | | *NA* | | ***0.934*** | |
| *“* | | *“* | | *“* | | *(#:13)* | | *Massachusetts* | | *BL* | *N.P.* | | | *OLS* | | *PF* | | *0.034 ± 0.155* | | *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 | | 1.999 ± 0.112 | | 2.09 ± 0.132 | | 0.51 | | **0.919** | |
| “ | |  | | FOR – Workers | |  | | “ | | HW |  | | |  | | “ | | 0.552 ± 0.068 | | 2.550 ± 0.116 | | 0.19 | | **0.982** | |
| “ | |  | | FOR –Winged | |  | | “ | | HW |  | | |  | | “ | | 1.607 ± 0.127 | | 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* | | *0.56 ± 0.64* | | *1.56 ± 0.4* | |  | | *0.75* | |
| *“* | |  | | *API* | | *(1:10)* | | *“* | | *BL* | *N.P.* | | | *NLL* | | *PF* | | *0.006 ± 0.041* | | *3.407 ± 2.471* | |  | | *0.81* | |
| *“* | |  | | *VES* | | *(1:19)* | | *“* | | *BL* | *N.P.* | | | *NLL* | | *PF* | | *0.001 ± 0.002* | | *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. \*\* = excluded ants. \*\*\*\*Seven families = ANT, API, CHR, FOR, ICH, SPH, VES

1. **Lepidoptera**.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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** | |
| Hodar (1996) | | HET | |  | | (10) | Gaudix-Baza, Spain | | | HW | |  | |  | | | PF | | 2.053 ± 0.25 | | 2.804 ± 0.236 | | 0.493 | | 0.946 | |
| “ | | ROP | |  | | (10) | “ | | | HW | |  | |  | | | “ | | 1.634 ± 0.46 | | 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* | | *0.026 ± 0.186735* | | *2.55 ± 0.571429* | |  | | ***0.958*** | |
| *“* | |  | | *NA* | | *(#:7)* | *Rainforest, Guipiles, Costa Rica* | | | *BL* | | *N.P.* | |  | | | *“* | | *0.078 ± 0.139796* | | *1.32 ± 0.683673* | |  | | *0.749* | |
| *“* | |  | | *NA* | | *(#:18)* | *Massachusetts* | | | *BL* | | *N.P.* | |  | | | *“* | | *0.014 ± 0.18673* | | *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 | |

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

Table S2. Predictive allometries for bee foraging distance. HW: Head width, IT: Intertegular distance.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | Metric | Taxa | Measure | Equation |
| Roubik and Aluja (1983) (in van Nieuwstadt & Iraheta (1996) | Foraging distance | Apidae: Meliponini | Artificial nectar source |  |
| van Nieuwstadt & Iraheta (1996) |  |  | Artificial nectar source |  |
| Greenleaf et al. (2007) |  | Hymenoptera: Apoidea | Max |  |
|  |  |  | Typical |  |
|  |  |  | Feeder |  |
|  |  |  | Comm |  |

Table S3A. Bees: Model parameters of best-fitting GLMM and PGLMM models. Post.: Posterior mean estimate (95% confidence intervals). ESS: Effective sample size.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | GLMM#1 |  |  | PGLMM#1 |  |
|  | Parameters | Post. | ESS | Post. | ESS |
| Intercept |  | 1 (0.56:1.45) | 3800 | 0.65 (0.14:1.17) | 3938 |
| lnITD |  | 2.2 (2.09:2.32) | 4000 | 2.4 (2.28:2.53) | 3828 |
| Sex | Male | -0.07 (-0.17:0.03) | 4000 | -0.1 (-0.2:0) | 3873 |
|  | Male:lnITD | NA | NA | -0.13 (-0.25:-0.01) | 3969 |
| Family | Andrenidae | -0.11 (-0.24:0.13) | 4000 | NA | NA |
|  | Colletidae | -0.38 (-0.59:-0.16) | 4000 | NA | NA |
|  | Halictidae | -0.51 (-0.68:-0.34) | 3696 | NA | NA |
|  | Megachilidae | -0.23 (-0.48:0.03) | 3970 | NA | NA |
|  | Melittidae | -2.82 (-4.16:-1.43) | 4000 | NA | NA |
|  | Andrenidae:lnITD | 0.17 (-0.1:0.44) | 4000 | NA | NA |
|  | Colletidae:lnITD | 0.11 (-0.23:0.43) | 4000 | NA | NA |
|  | Halictidae:lnITD | 0.64 (0.4:0.88) | 3643 | NA | NA |
|  | Megachilidae:lnITD | 0.11 (-0.16:0.38) | 4000 | NA | NA |
|  | Melittidae:lnITD | 2.38 (0.95:3.79) | 4000 | NA | NA |
|  | Region | 0.36 (0.12:0.95) | 3926 | 0.35 (0.11: 0.95) | 3813 |
|  | Region:Species | 0.22 (0.17:0.26) | 3285 | 0.44 (0.32:0.55) | 2824 |
|  | Sigma | 0.27 (0.24:0.3) | 3402 | 0.28 (0.25:0.31) | 3169 |

Table S3B. Hoverflies: Posterior mean model parameters of two best-fitting GLMMs. Post.: Posterior mean estimate (95% confidence intervals). ESS: Effective sample size.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | GLMM1 |  | GLMM2 |  |
|  | Post. | ESS | Post. | ESS |
| Intercept | -0.13 (-1.32:0.99) | 3766 | -0.07 (-1.19:1.07) | 4000 |
| lnITD | 2.52 (2.31:2.74) | 3877 | **2.52 (2.22:2.84)** | 3959 |
| Male | -0.14 (-0.26:-0.01) | 4000 | **-0.13 (-0.25:0)** | 3792 |
| Syrphinae | NA | NA | 0.04 (-0.39:0.49) | 4000 |
| Syrphinae:lnITD | NA | NA | -0.2 (-0.69:0.28) | 4000 |
| Region | 0.56 (0.06:1.78) | 4000 | 0.54 (0.06:1.75) | 3832 |
| Species | 0.2 (0.02:0.34) | 2776 | 0.19 (0.02:0.33) | 2710 |
| Sigma | 0.37 (0.3:0.45) | 3096 | 0.38 (0.3:0.46) | 2829 |



**Figure S1A.** Bees; ITD-body size (dry weight) interspecific relationships. From left to right: influence of region, sex and taxonomic family.



**Figure S1B.** Hoverflies; ITD-body size (dry weight) interspecific relationships. From left to right: influence of region, sex and taxonomic subfamily.

**Figure S2A.** Intraspecific variation in ITD and body size in relation to sample size in the 10 most abundant bee species. Red line denotes the total trait mean and green lines represent 95% confidence intervals.



**Figure S2B**. Intraspecific variation in ITD and dry weight in relation to sample size in the five most abundant hoverfly species. Red line denotes the total trait mean and green lines represent 95% confidence intervals.

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