Pollinator size and its consequences: Predictive allometry for pollinating insects

Liam K. Kendall1,2\*, Romina Rader1, Vesna Gagic2, Daniel Cariveau3, Matthias Albrecht4, Katherine C.R. Baldock5, Breno Freitus6, Mark Hall1, Andrea Holzschuh7, Janeally Pereira6, Juanita Rodriguez8, Laura Russo9, Louis Suter4, Nicolas J. Vereecken10 and Ignasi Bartomeus11

1. School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2351, Australia

2. CSIRO Agriculture, GPO Box 2583, Brisbane, QLD 4001, Australia

3. Department of Entomology, University of Minnesota, Minneapolis, MN, USA

4. Eidgenössisches Departement für Wirtschaft, Agroscope Agrarökologie und Umwelt, CH-8046 Zürich, Switzerland

5. School of Biological Sciences & Cabot Institute, University of Bristol, Bristol, BS8 1TQ, UK

6. Departamento de Zootecnia – CCA, Universidade Federal do Ceará, 60.356-000, Fortaleza, CE, Brazil

7. Animal Ecology and Tropical Biology Biocenter, University of Würzburg, 97074 Würzburg, Germany

8. Australian National Insect Collection, CSIRO, Canberra, ACT 2601, Australia

9.. Botany Department, Trinity College Dublin, Ireland

10. Interfaculty School of Bioengineers. Université Libre de Bruxelles, 1050 Bruxelles, Belgium

11. Dpto. Ecología Integrativa, Estación Biológica de Doñana (EBD-CSIC), 41092 Sevilla, Spain

\*Corresponding author: L. K. Kendall, Email: [lkendal2@myune.edu.au](mailto:lkendal2@myune.edu.au)

**Abstract**

Pollinator insect body size is a central trait of ecological and conservation importance however it is often impractical to directly measure. Allometric scaling laws can overcome this problem yet available models are outdated, rely upon geographically restricted sampling and have limited applicability for non-bee taxa. More accurate predictions of pollinator body size require dynamic models that consider biogeography, intraspecific variation and phylogenetic relatedness within an iterative framework. We improved upon pre-existing equations for estimating body size in two key pollinating taxa (bees and hoverflies). We measured dry weight and intertegular distance (ITD) of 337 bee species and 103 hoverfly species across four biogeographic regions: Australia, Europe, South America and North America. We tested the power of ITD alone and in interaction with region, sex and phylogeny or taxonomy to predict interspecific pollinator body size using generalised linear mixed models and assessed intraspecific ITD - body size relationships for five species per taxa. Including biogeography, sex and phylogeny or taxonomy improved interspecific body size predictions by X% (*R2:* 0.X – 0.X). However, intraspecific models found ITD an unreliable predictor of body size for bees (*R2*: 0.02 – 0.46) and hoverflies (*R2*: -0.11 – 0.44). These highly applicable models form the basis of the dynamic R package, '*pollimetry*’, and provide an updated resource for allometric research concerning insect pollinators worldwide.

**Keywords**: allometry, Apoidea, biogeography, body size, pollination, Syrphidae

**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; Velghe & Gregory-Eaves 2013; DeLong et al. 2015). 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, predation, primary productivity and pollination (Woodward & Hildrew 2002; 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 inferred allometric relationships can be impractical for a number of reasons. Firstly, direct measurements can be time consuming and require destructive methods, which are unfeasible for museum specimens and threatened species (Rogers et al. 1977; Henschel & Seely 1997). Secondly, in diet/food web studies, body size estimates come from digested prey items (e.g. Hodar 1997). Thirdly, 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 or a hypothesised allometric characteristic using a co-varying trait, has emerged across many biological disciplines.

Most commonly, body length has been used extensively to predict body size, 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), most commonly at the ordinal level. 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).

A number of key pollination traits exhibit allometric scaling. In bees, body size affects insect activity periods (Streinzer et al. 2016), pollen loads (e.g. Ramalho et al. 1998), foraging distances (e.g. Greenleaf et al. 2007; van Nieuwstadt & Iraheta 1996), proboscis length (Cariveau et al. 2016) and plant-pollinator trait matching (Stang et al 2009; Olesen et al., 2010). Despite this ubiquity, few predictive models exist for pollinating insects below the ordinal level, with one notable exception. Cane (1987) established 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). Cane (1987)’s pioneer model was developed with a sample of females from 20 North American solitary bee species that represented six of the seven global bee families. It is now the most commonly used metric for estimating bee body size and has used in ecological (e.g. 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 ITD as an important body size proxy for establishing other ecologically important allometric relationships (e.g. foraging distances and bee proboscis length; Greenleaf et al. 2007; Cariveau et al. 2016).

Iterative ecological forecasting, whereby equations are periodically updated as well as tested against novel data (e.g. Dietze et al. 2018; Harris et al. 2018) represent an as-yet untested avenue and overarching framework for greater accuracy and wider applicability of predictive allometry. Critical to incorporating this iterative framework are considerations of model choice, development and validation. Traditionally, predictive allometry has typically utilised ordinary least squares or major axis regression (Warton et al. 2006; Legendre & Legendre 2012). However, phylogenetic model structures represent an attractive alternative (see Harvey & Pagel 1991; Hadfield and Nakagawa 2010). 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). Model validation techniques, such as cross-validation (Stone 1974), provide the means to assess model performance on untested data. Combining these methods into a dynamic and easy to update *R* package will allow iterative model building through the incorporation of novel data as it becomes available.

The utility of Cane’s equation has not previously been tested beyond North American solitary bee species except in bumblebees (Hagen & Dupont 2013). Further, it hasn’t been tested in conjunction with biogeography, within more complex model structures or in other key pollinating taxa, such as hoverflies (Diptera: Syrphidae). Therefore, we aimed to develop predictive allometric equations within our iterative framework that take into account these factors and place them alongside a catalogue of pre-existing equations for key pollinating insect taxa within the unified resource of an *R* package, entitled “*pollimetry*”.

**Methodology**

*Specimen collection and measurements*

We obtained specimens from recent field research concerning insect pollination and biodiversity. 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-six months of collection, although some, in particular, those from Victoria, Australia, Belgium, Switzerland and Cane’s original samples were of variable ages: from one-five years since collection. We excluded damaged specimens. 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 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 (FIGURE?) was measured in millimetres using a stereo-microscope, either mounted with a calibrated scale or microscope camera. Body length was measured following the same protocol for Australian, English, German, Irish and Spanish specimens. What about body length? Explain briefly.

*Data analysis: Model structures*

All analyses were undertaken in *R* v3.5.0 (R Core Team , 2018). For each taxon, we constructed species mean datasets. Every female and/or male of each species was averaged within biogeographical region of origin. We first assessed the correlation between ITD and body length and compared each variable independently in predicting body size using OLS regression. We used a power function in model formulation which is typical of predictive allometry:

Ln(Y) = ln(aj) + bj\*ln(IT)

where Y = body weight/size, aj = intercept and bj = allometric co-efficient and its interactions. To test whether allometric relationships vary with sex, biogeographic region and taxonomic family, we included an interaction between IT and these factors. We constructed generalised linear mixed models using *MCMCglmm* (Hadfield 2010) to predict body size as a function of these explanatory variables, with species included as a random term to account for differences between sexes along with an observation-level random term. Models were run for 1.1\*106 iterations with a burn-in of 10000 and thinning of 100.

*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 then implemented a phylogenetic generalised linear mixed model (PGLMM) that took into account phylogenetic dependence and intraspecific differences in body size. We obtained a bee genera backbone tree (Hedtke et al. 2013) and removed non-represented genera using *ape* (Paradis et al., 2004). Species tips were added to genera nodes as pure-birth subtrees using *phytools* (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 of body size using Pagel’s λ with *phytools* (Pagel 1999: Revell et al. 2012). We then formulated an PGLMM which considered ITD in interaction with biogeography with sex without taxonomic family.

*Data analysis: Model selection and 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 using ‘dredge’ within *MuMIn* (Barton 2018). The best fitting models were then ranked by their Deviance Information Criterion (DIC) weighting. For wider applicability of evaluated models, we also extracted the highest-ranked models which excluded region, sex and family for both taxa from the model selection tables.

*Data analysis: Cross-validation*

We implemented k-fold cross validation to test overall model performance and compare prediction error (Stone 1974; Kohavi 1995). 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. We then assessed model performance on the basis of average root-mean square error (RMSE) across the 10 sets. Simplified cross validation was used to test the predictive accuracy of Cane’s (1987) original equation:

where = IT and = body size.

We compared the actual and Cane’s (1987) predicted values for each of the ten test sets and derived a mean RMSE. Lastly, we derived RMSE for actual-predicted values from applicable existing body length equations for both taxa and our body length measurements.

*Data analysis: Intraspecific predictions*

We assessed the utility of ITD in predicting intraspecific body size variation. For the five most abundant species of both bees and hoverflies we tested the utility of ITD in predicting intraspecific female body size variation using species-level OLS regression. For each species, we plotted trait means independently against increasing sample size to estimate the adequate sample size whereby variance stabilised within confidence intervals of the actual sample size.

*Data availability*

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

**Results**

*Species and specimen distribution*

In total, we measured 337 bee species from Australia, Europe, North America and South America, including Cane’s (1987) original 20 species and 103 hoverfly species from Australia and Europe (Table 1). Six out of seven bee families and both hoverfly subfamilies were represented. Number of individuals per bee species ranged from one (103 species a ♀ individual, 76 species a ♂ individual) and 201 (♀ *Homalictus urbanus*) and 68 (♂ Bombus impatiens) with a mean of nine ♀ and five ♂ per species. In hoverflies, specimen number per species ranged from one (49 ♀ only hoverfly species, 34 ♂ only hoverfly species) to 32 (♀ *Austrosyrphus* spp.) and 18 (♂ *Austrosyrphus* spp.) with a mean of three per species for both sexes.

*Trait co-variation*

Body length and IT were highly co-linear (bees: F (1, 256): 1845, *R2*: 0.88, log (IT) = -1.623 ± 0.056 + 1.123 ± 0.026 \* log (BL); hoverflies: F (1,51): 156.5, *R2*: 0.75, log (IT) = -1.745 ± 0.213 + 1.186 ± 0.095 \* log (BL). ITD was marginally more predictive than body length in estimating body size in bees: IT F(1,256): 2214, *R2*:0.896, BL F(1,256): 1836, *R2*: 0.877 and considerably better than body length for hoverflies: IT F(1,51): 304.3, *R2*: 0.854, BL F(1,51): 204.2, *R2*: 0.796.

*Interspecific model selection and performance*

For bees, GLMM analyses found that models which considered region, family and sex in interaction with ITD best-predicted body size on the basis of DIC weighting (Table 2; Figure 2A). Regional differences were most pronounced between European and Australasian and North American bees than between European and South American bees (Table 3A). Interestingly, non-European bees amassed body size per unit ITD greater than European bees. Halictidae, Colletidae and Melittidae exhibited significantly different intercepts to Apidae, with Halictidae and Melittidae also displaying different degrees of mass accumulation per unit ITD. The uncommon Melittidae (total specimens: 24) exhibited the most markedly different intercept and slope. The different intercepts and slopes result in the largest differences being in smaller bees, with larger bees appearing similar in ITD – body size accumulation. In hoverflies, region and sex were most predictive (Figure 2B, Table 3B) with no significant interaction with ITD. However, the best model that included subfamily ranked second, suggesting the two subfamilies have different degrees of mass accumulation per unit ITD.

Phylogenetic signal was highly significant for bee ln? body size (λ: 0.71, *p* <0.001) (Figure 1). Larger body size was most pronounced within the Apidae, the largest bee in our dataset being *Xylocopa frontalis* (♀ mean weight: 760.75mg). In contrast, Halictid (i.e. *Halictus*, *Homalictus* and *Lasioglossum* species)and Colletid bees (in particular, *Euhesma* sp. (♀ mean weight: 0.71mg, ♂ mean weight: 0.66mg) and *Hylaeus* (e.g. *Hylaeus communis* (♀ mean weight: 6.15mg, ♂ mean weight: 2.76mg) were smaller than average. PGLMM found similar trends to GLMM analyses: region and sex were both retained as predictors in interaction with IT. Interestingly, GLMM models which incorporated family along with region and sex ranked better on the basis of DIC weighting than the best fitting PGLMM (Table 2).

Cross-validation indicated that high predictive accuracy persisted across all tested models for both bees and hoverflies. Overall model performance (mean milligram error), measured as root mean square error, was higher in hoverfly models than bee models (bee RMSE range 17.212 – 23.457mg; hoverfly RMSE range: 4.888mg – 5.334mg (Table 2, Figure 3). More complex bee models out-performed Cane’s (1987) original equation (Figure 3). Minimal differences in model performance were observed between Cane’s (1987) equation and phylogenetic- and non-phylogenetic models which considered only ITD. RMSE between actual-predicted values of body size using existing body length equations were 7.99mg ± 0.69 for hoverflies and 36.36 ± 8.29 for bees, respectively. This section is ok, but can be presented more didactically. There are many models, so the reader need guidance on which one you are testing. Maybe name them?

*Intra-specific predictions*

Across the five most abundant species of bees and hoverflies (females only), the strength of intraspecific predictions of body size using ITD was varied (Table 4; Figure 4). All bee species exhibited a significant relationship between ITD and dry weight, however *R2*differed considerably from 0.02 in *Homalictus urbanus* to 0.46 for *Lasioglossum lanarium* (Table 3, Figure 3). 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 S1A). For hoverflies, the lower overall sample sizes of each species limited inference of sample-size / mean stabilisation (Figure S1B).

*Summary of R package functions*

The accompanying R package, ‘*pollimetry’*, includes a total of X functions for estimation of pollinator body size using pre-existing equations (see Table S1 for description of collation and co-efficients) and our new equations (Table 1). Also included are Greenleaf et al.’s (2007) and van Nieuwstadt and Iraheta’s (1996) allometric equations for estimating bee foraging distances using ITD or head width respectively, as well as Cariveau et al’s (2016) allometric equations for estimating bee tongue length. New equations will be periodically updated in the form of package updates as novel data becomes available. In the case of novel data from new biogeographical regions or new allometric trait evaluations, updates will be accompanied by a formal publication.

**Discussion**

Herein, we used an iterative framework to develop and test a suite of dynamic allometric models for two key pollinating taxa, bees and hoverflies. The hoverfly models represent the first predictive allometric models for this important pollinating group. Additionally, we present the most inclusive examination of both bee and hoverfly body variation to date, taking into account biogeography, phylogenetic relatedness and sexual dimorphism. As first defined by Cane (1987), we re-iterate the utility of the intertegular distance (ITD) in predicting interspecific body size variation and demonstrate its superiority over body length in predicting body size. However, we do highlight its sensitivity to the before mentioned factors and demonstrate its unpredictability in predicting intraspecific body size variation. Overall, both GLMM and PGLMM model structures exhibited high predictive precision, resulting in a suite of highly applicable models for researchers worldwide. By incorporating biogeographic and phylogeny or taxonomy and sexual dimorphism we improved model performance and overcame the limitations of traditional predictive allometry. These three predictors represent fundamentally-related causes of body size variation in pollinating insects.

Terrestrial invertebrates show considerable geographic variation in body shape and size and biogeographical differences in predictive allometry are well-established (e.g. Martin et al. 2014). We found significant body size variation in interaction with ITD between all four regions. Differences were most pronounced in small bee species whereas differences were constant across size classes for hoverflies. The most pronounced differences in our study were between Europe and Australia and North America: both North American and European bees were heavier per unit ITD and South America and Europe were most similar in co-variation. Interestingly, the differing slopes appears to show overlap in larger body sizes. These suggests there are significant constraints in the body size:ITD relationship in large-bodied bees, potentially due to the energetic requirements (I NEED A REF FOR THIS).

Previous studies have suggested comparable geographic regions should exhibit similar allometric coefficients (Gowing & Recher 1984; Martin et al 2014), however such a claim requires comprehensive sampling within compared regions to discount sampling effects, and only one prior predictive allometric study examined multiple biogeographic regions in concert, albeit as individual models (Schoener 1980). This study demonstrated that the influence of different biogeographic regions appears in conjunction with species evolutionary histories and sexual dimorphism. Observed biogeographical differences likely arise from differing diversification patterns, and as well as from sampling biases, such as variation in commonality among species and the ranges of body size measured (Sage 1982). Yet in both taxa, we sampled systematically across a wide range of body sizes and incorporated more species than most prior allometric studies that formulated predictive models at either the superfamily or family level. Therefore, differing diversification patterns and random variation in species sampled appear central to biogeographic differences in allometric coefficient patterns in this study. As a result, predictive allometric model development requires large-scale efforts incorporating multiple regions, biomes and ecosystems for greater accuracy in order to develop biological hypotheses and reasoning driving observed trends, especially in small-bodied specimens which show the most variation.

Sex was retained as an integral predictor either in addition or in interaction with ITD for both taxa. This suggests that although ITD is a robust predictive trait, other morphological aspects differ between the sexes resulting in sexual size dimorphism (SSD) in absence of ITD differences.SSD is common among insects. In both Diptera and Hymenoptera, SSD is predominantly (>80%) female-biased, 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). SSD is also smaller in eusocial species (Medina et al. 2016). 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 notable, with sex retained as an important body size predictor in conjunction with ITD. There exist, however, few examples of specialised morphological sexual dimorphism, other than eye shape. Our results demonstrate that ITD as a predictive trait is sensitive to sexual dimorphism, in each case as a co-variate and for bees in interaction with ITD, suggesting SSD is larger in bigger species. Therefore, the use of predictive allometries should consider sex, especially as many ecologically relevant allometric traits are gender-related (e.g. foraging distance).

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. Adult body size variation in holometabolous insects is a direct result of diet and environment during ontogeny and larval development (Davidowitz et al. 2004). Sampled specimens in many cases, came from differing environments and likely developed in disjunct conditions, as such they cannot be assumed to exhibit identical larval-adult development. This suggest that predictive allometry is sensitive to phenotypic plasticity in body shape and size however more detailed investigation of morphological co-variation within species is required to understand these range and variation in body shape constraints.

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 heightens the risk of inaccurate predictions (Martins 1991; Martins et al. 2002; Garland et al. 2005). PGLMM and GLMM models were comparable in terms of model performance. Interestingly, GLMM models incorporating taxonomy over phylogeny ranked higher in terms of DIC, demonstrating the differences at the familial level in allometric variation. 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 beneficial compromise 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. Our results suggest that the prior use of taxonomy as a phylogenetic proxy (Cariveau et al. 2016) is predictively equivalent to incorporating phylogeny in examining bee allometry.

By utilising cross-validation techniques and considering multiple metrics (i.e. DIC in model selection and RMSE in model performance), we provide multiple, near-equally accurate predictive models. 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 potentially discount each examined factor. In essence, predictive allometry requires acceptance of multiple models as equal-best or ‘most accurate’, with model choice and usage becoming the decision of the end-user and based on the aims of the proposed study.

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 reduced 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 (555, 73) | Andrenidae (24, 10)  Apidae (193, 22)  Colletidae (62, 7)  Halictidae (244, 26)  Megachilidae  Melittidae | Andreninae (19, 5), Oxaeinae (1, 1), Panurginae (4, 4)  Apinae (177, 17), Nomadinae (1, 1), Xylocopinae (15, 4)  Colletinae (2, 2), Hylaeinae (60, 5)  Halictinae (242,24), Nomiinae (1, 1), Rophitinae (1, 1)  Megachilinae (31, 7)  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. Shown 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. #: Model number in model selection process, Int: Intercept, lnITD: ln intertegular distance, Fam: Family, Subf: Subfamily, df: degrees of freedom, DIC: deviance information criterion, ΔDIC and RMSE: root-mean square error (k = 10).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Taxa | Model | # | Int | lnITD | Fam | Subf | Biog | Sex | lnITD:Fam | lnITD:Subf | lnITD:Biog | lnITD:Sex | df | DIC | ΔDIC | RMSE |
| Bee | GLMM | 1 | 1.149 | 2.066 | + | NA | + | + | + | NA | + | + | 22 | 289.668 | 0 | 17.238 ± 5.304 |
| Bee | GLMM | 2 | 0.839 | 2.271 | NA | NA | + | + | NA | NA | + | + | 12 | 314.349 | 24.681 | 17.213 ± 3.751 |
| Bee | GLMM | 3 | 0.817 | 2.384 | + | NA | NA | + | NA | NA | NA | + | 11 | 328.477 | 38.810 | 18.523 ± 5.745 |
| Bee | GLMM | 4 | 1.118 | 2.006 | + | NA | + | NA | + | NA | + | NA | 20 | 343.864 | 54.197 | 21.728 ± 6.712 |
| Bee | GLMM | 5 | 0.585 | 2.502 | NA | NA | NA | + | NA | NA | NA | + | 6 | 344.652 | 54.984 | 20.421 ± 5.872 |
| Bee | GLMM | 6 | 0.818 | 2.216 | NA | NA | + | NA | NA | NA | + | NA | 10 | 371.572 | 81.905 | 18.207 ± 5.608 |
| Bee | GLMM | 7 | 0.755 | 2.367 | + | NA | NA | NA | NA | NA | NA | NA | 9 | 392.246 | 102.579 | 23.457 ± 7.376 |
| Bee | GLMM | 8 | 0.554 | 2.467 | NA | NA | NA | NA | NA | NA | NA | NA | 4 | 406.059 | 116.391 | 21.804 ± 6.46 |
| Bee | PGLMM | 1 | 0.783 | 2.248 | NA | NA | + | + | NA | NA | + | + | 12 | 319.609 | 0 | 18.377 ± 5.778 |
| Bee | PGLMM | 2 | 0.610 | 2.429 | NA | NA | NA | + | NA | NA | NA | + | 6 | 330.358 | 10.749 | 21.894 ± 6.642 |
| Bee | PGLMM | 3 | 0.750 | 2.222 | NA | NA | + | NA | NA | NA | + | NA | 10 | 372.365 | 52.756 | 19.579 ± 6.305 |
| Bee | PGLMM | 4 | 0.534 | 2.435 | NA | NA | NA | NA | NA | NA | NA | NA | 4 | 382.299 | 62.689 | 22.993 ± 7.014 |
| Hoverfly | GLMM | 1 | 0.008 | 2.519 | NA | NA | + | + | NA | NA | NA | NA | 6 | 161.197 | 0 | 5.077 ± 1.007 |
| Hoverfly | GLMM | 2 | 0.022 | 2.551 | NA | + | + | + | NA | + | + | NA | 9 | 162.377 | 1.179 | 5.24 ± 1.24 |
| Hoverfly | GLMM | 3 | -0.074 | 2.561 | NA | NA | NA | + | NA | NA | NA | NA | 5 | 166.011 | 4.814 | 5.247 ± 0.99 |
| Hoverfly | GLMM | 4 | -0.031 | 2.565 | NA | + | NA | + | NA | + | NA | NA | 7 | 166.223 | 5.026 | 5.334 ± 1.164 |
| Hoverfly | GLMM | 5 | 0.109 | 2.424 | NA | + | + | NA | NA | NA | NA | NA | 6 | 167.761 | 6.564 | 4.888 ± 0.808 |
| Hoverfly | GLMM | 6 | -0.045 | 2.515 | NA | NA | + | NA | NA | NA | NA | NA | 5 | 168.170 | 6.973 | 5.027 ± 0.809 |
| Hoverfly | GLMM | 7 | 0.031 | 2.456 | NA | + | NA | NA | NA | NA | NA | NA | 5 | 173.382 | 12.185 | 5.087 ± 0.782 |
| Hoverfly | GLMM | 8 | -0.128 | 2.546 | NA | NA | NA | NA | NA | NA | NA | NA | 4 | 174.328 | 13.131 | 5.207 ± 0.804 |

Table 3A. Bees: Posterior mean model parameters of best-fitting GLMM and PGLMM models. ESS: Effective sample size of MCMC model fit.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | GLMM#1 |  |  |  | PGLMM#1 |  |  |
|  | Parameter | Mean (95% C.I.) | p-value | ESS | Mean (95% C.I.) | p-value | ESS |
|  | Intercept | **1.144** (0.965 - 1.315) | **0.001** | 1,220.36 | **0.784** (0.472 - 1.038) | **0.001** | 1,182.44 |
|  | lnITD | **2.068** (1.919 - 2.232) | **0.001** | 1,182.12 | **2.252** (2.109 - 2.417) | **0.001** | 1,000 |
| Region | Australasia | **-0.613** (-0.766 - -0.43) | **0.001** | 1,000 | **-0.495** (-0.674 - -0.3) | **0.001** | 1,000 |
|  | North America | **-0.248** (-0.42 - -0.072) | **0.006** | 1,000 | **-0.263** (-0.414 - -0.109) | **0.006** | 1,000 |
|  | South America | -0.034 (-0.34 - 0.275) | 0.836 | 1,000 | 0.153 (-0.252 - 0.487) | 0.384 | 852.235 |
|  | Australasia:lnITD | **0.416** (0.223 - 0.642) | **0.001** | 1,000 | **0.349** (0.154 - 0.566) | **0.001** | 1,000 |
|  | North America:lnITD | **0.263** (0.061 - 0.436) | **0.008** | 1,000 | **0.303** (0.128 - 0.489) | **0.001** | 1,000 |
|  | South America:lnITD | **0.279** (-0.003 - 0.528) | **0.038** | 1,000 | 0.153 (-0.156 - 0.448) | 0.298 | 1,000 |
| Sex | Male | -0.041 (-0.15 - 0.073) | 0.462 | 1,097.79 | -0.074 (-0.191 - 0.06) | 0.248 | 1,000 |
|  | Male:lnITD | **-0.173** (-0.302 - -0.051) | **0.006** | 1,114.63 | -0.139 (-0.27 - 0.02) | 0.066 | 1,000 |
| Family | Andrenidae | -0.151 (-0.444 - 0.124) | 0.32 | 1,000 | NA | NA | NA |
|  | Colletidae | **-0.397** (-0.637 - -0.148) | **0.001** | 1,000 | NA | NA | NA |
|  | Halictidae | **-0.495** (-0.72 - -0.331) | **0.001** | 1,000 | NA | NA | NA |
|  | Megachilidae | -0.277 (-0.57 - 0.047) | 0.084 | 1,000 | NA | NA | NA |
|  | Melittidae | **-3.293** (-4.845 - -1.725) | **0.001** | 1,000 | NA | NA | NA |
|  | Andrenidae:lnITD | 0.146 (-0.211 - 0.474) | 0.392 | 1,000 | NA | NA | NA |
|  | Colletidae:lnITD | 0.087 (-0.289 - 0.425) | 0.646 | 1,111.28 | NA | NA | NA |
|  | Halictidae:lnITD | **0.609** (0.341 - 0.855) | **0.001** | 1,000 | NA | NA | NA |
|  | Megachilidae:lnITD | 0.146 (-0.13 - 0.495) | 0.392 | 1,000 | NA | NA | NA |
|  | Melittidae:lnITD | **2.895** (1.277 - 4.54) | **0.001** | 1,000 | NA | NA | NA |
|  | Species | 0.065 (0.041 - 0.09) | NA | 1,000 | 0.154 (0.06 - 0.27) | NA | 744.261 |
|  | Obs.level | 0.08 (0.062 - 0.099) | NA | 1,000 | 0.095 (0.074 - 0.116) | NA | 1,032.14 |

B). Hoverflies: Posterior mean model parameters of best-fitting GLMM. ESS: Effective sample size of MCMC model fit.

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter | Mean (95% C.I.) | p-value | ESS |
| Intercept | 0.006 (-0.199 - 0.218) | 0.958 | 1,110.29 |
| lnITD | **2.521** (2.33 - 2.737) | **0.001** | 1000 |
| Australasia | **-0.271** (-0.448 - -0.086) | **0.004** | 1000 |
| Male | **-0.136** (-0.265 - -0.017) | **0.036** | 883.173 |
| Species | 0.041 (0.0004 - 0.095) | NA | 662.055 |
| Obs.level | 0.143 (0.088 - 0.201) | NA | 654.266 |

Table 4. Model parameters of intraspecific ln(body size)~ln(IT) size relationships. F: F-statistic and degrees of freedom for each model. A and B: intercept and IT co-efficients ± standard error, *R2*: Adjusted R-squared 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 |
|  | *Bombus lucorum* | 81.15 (1,101) | 1.413 ± 0.297 | 1.966 ± 0.218 | 0.44 | <0.001 |
|  | *Homalictus urbanus* | 6.055 (1,209) | -0.164 ± 0.033 | 1.166 ± 0.474 | 0.024 | 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 |
| Hoverfly | *Austrosyrphus spp.* | 12.7 (1,30) | 0.087 ± 0.458 | 2.032 ± 0.57 | 0.274 | 0.001 |
|  | *Helophilus parallelus* | 14.84 (1,17) | 0.286 ± 0.857 | 2.485 ± 0.645 | 0.435 | 0.001 |
|  | *Sphaerophoria macrogaster* | 0.04 (1,8) | 0.361 ± 0.274 | 0.195 ± 0.907 | -0.11 | N.S. |
|  | *Episyrphus balteatus* | 0.08 (1,8) | 1.334 ± 1.885 | 0.885 ± 2.229 | -0.11 | N.S. |
|  | *Melanostoma scalare* | 6.38 (1,7) | -2.172 ± 1.324 | 7.619 ± 3.016 | 0.4 | 0.03 |

****

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; ITD-body size interspecific relationships. From left to right: influence of region, sex and taxonomic family.



**Figure 2B.** Hoverflies; ITD-body size interspecific relationships. From left to right: influence of region, sex and taxonomic subfamily.



**Figure 3.** Root mean square error (RMSE) across k-fold training and test sets for each model. A) GLMM #1, PGLMM#1 and three ITD only models: Cane (1987), GLMM #8, PGLMM #4. B) All included hoverfly models: model numbers refer to that provided in Table 2.

****

**Figure 4.** Intraspecific predictions of female body size with intertegular distance. Lines denote line of best fit from OLS regression.

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, IT = intertegular distance. 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.**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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 | 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. \*\* = 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** |
| 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 |

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

Table S2. Predictive allometries for bee foraging distance and proboscis length (to be added). HW: Head width, IT: Intertegular distance.

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

**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, see Leuven et al. 1985). 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 preserved and unpreserved specimens in species. We fitted a linear model with y = log(Specimen weight) ~ log(ITD) + sex + preservative time.

**Result**

There was a significant effect of preservative time on specimen weight (t-value -4.23, p <0.001). Applying the formula: y = 1.273+1.852\*ln(ITD) + -0.0013\*Pres.time + Species-coefficient. where y = log(Dry weight), for an *Andrena flavipes* with an ITD of 2.43mm (female species mean) preservative time of 1, 50 and 100 days results in weight loss of 0.019, 0.93 and 1.81mg.



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.



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.

**References**

Angilletta Jr, M. J., T. D. Steury and M. W. Sears (2004). "Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle." Integrative and comparative biology **44**(6): 498-509.

Ashton, K. (2004). "Comparing phylogenetic signal in intraspecific and interspecific body size datasets." Journal of evolutionary biology **17**(5): 1157-1161.

Barton, K. and M. K. Barton (2018). "Package ‘MuMIn’."

Bates, D., M. Maechler, B. Bolker and S. Walker (2014). "lme4: Linear mixed-effects models using Eigen and S4." R package version **1**(7): 1-23.

Benke, A. C., A. D. Huryn, L. A. Smock and J. Bruce Wallace (1999). "Length-mass relationships for freshwater macroinvertebrates in North America with particular refernce to the Southeastern United States." Journal of the North American Benthological Society **18**(3): 308-343.

Blomberg, S. P., T. Garland Jr and A. R. Ives (2003). "Testing for phylogenetic signal in comparative data: behavioral traits are more labile." Evolution **57**(4): 717-745.

Brady, C. J. and R. A. Noske (2006). "Generalised regressions provide good estimates of insect and spider biomass in the monsoonal tropics of Australia." Australian Journal of Entomology **45**(3): 187-191.

Britton, T., B. Oxelman, A. Vinnersten and K. Bremer (2002). "Phylogenetic dating with confidence intervals using mean path lengths." Molecular phylogenetics and evolution **24**(1): 58-65.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage and G. B. West (2004). "Toward a metabolic theory of ecology." Ecology **85**(7): 1771-1789.

Burgherr, P. and E. I. Meyer (1997). "Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates." Archiv für Hydrobiologie **139**(1): 101-112.

Cane, J. H. (1987). "Estimation of bee size using intertegular span (Apoidea)

" Journal of Kansas Entomological Society **60**(1): 145-147.

Cariveau, D. P., G. K. Nayak, I. Bartomeus, J. Zientek, J. S. Ascher, J. Gibbs and R. Winfree (2016). "The Allometry of Bee Proboscis Length and Its Uses in Ecology." Plos One **11**(3).

Chown, S. L. and K. J. Gaston (2010). "Body size variation in insects: a macroecological perspective." Biological Reviews **85**(1): 139-169.

Davidowitz, G., L. J. D’Amico and H. F. Nijhout (2004). "The effects of environmental variation on a mechanism that controls insect body size." Evolutionary Ecology Research **6**(1): 49-62.

DeLong, J. P., B. Gilbert, J. B. Shurin, V. M. Savage, B. T. Barton, C. F. Clements, A. I. Dell, H. S. Greig, C. D. Harley and P. Kratina (2015). "The body size dependence of trophic cascades." The American Naturalist **185**(3): 354-366.

Dietze, M. C., A. Fox, L. M. Beck-Johnson, J. L. Betancourt, M. B. Hooten, C. S. Jarnevich, T. H. Keitt, M. A. Kenney, C. M. Laney, L. G. Larsen, H. W. Loescher, C. K. Lunch, B. C. Pijanowski, J. T. Randerson, E. K. Read, A. T. Tredennick, R. Vargas, K. C. Weathers and E. P. White (2018). "Iterative near-term ecological forecasting: Needs, opportunities, and challenges." Proceedings of the National Academy of Sciences.

Ehnes, R. B., B. C. Rall and U. Brose (2011). "Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates." Ecology Letters **14**(10): 993-1000.

Ganihar, S. R. (1997). "Biomass estimates of terrestrial arthropods based on body length." Journal of Bioscience **22**(2).

Garland, J., Theodore and A. R. Ives (2000). "Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods." The American Naturalist **155**(3): 346-364.

Garland, T., A. F. Bennett and E. L. Rezende (2005). "Phylogenetic approaches in comparative physiology." Journal of experimental Biology **208**(16): 3015-3035.

Gould, S. J. (1966). "Allometry and size in ontogeny and phylogeny." Biological Reviews **41**(4): 587-638.

Gowing, G. and H. F. Recher (1984). "Length-wight relationships for invertebrates from forests in south-eastern New South Wales." Austral Ecology **9**(1): 5-8.

Greenleaf, S. S., N. M. Williams, R. Winfree and C. Kremen (2007). "Bee foraging ranges and their relationship to body size." Oecologia **153**(3): 589-596.

Hadfield, J. D. (2010). "MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package." Journal of Statistical Software **33**(2): 1-22.

Hagen, M. and Y. L. Dupont (2013). "Inter-tegular span and head width as estimators of fresh and dry body mass in bumblebees (Bombus spp.)." Insectes Sociaux **60**(2): 251-257.

Harris, D. J., S. D. Taylor and E. P. White (2018). "Forecasting biodiversity in breeding birds using best practices." PeerJ **6**: e4278.

Harrison, J. F., C. Klok and J. S. Waters (2014). "Critical PO 2 is size-independent in insects: implications for the metabolic theory of ecology." Current opinion in insect science **4**: 54-59.

Harvey, P. H. and M. D. Pagel (1991). The comparative method in evolutionary biology, Oxford university press Oxford.

Hedtke, S. M., S. Patiny and B. N. Danforth (2013). "The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography." BMC Evolutionary Biology **13**(1): 138.

Henschel, J. R. and M. K. Seely (1997). "Mass-length relationships of Namib Tenebrionids." Madoqua **19**(2): 159-160.

Hodar, J. A. (1997). "The use of regression equations for the estimation of prey length and biomass in diet studies of insectivore vertebrates." Miscellania Zoologica **20**(2): 1-10.

Huxley, J. and J. S. Huxley (1993). Problems of relative growth.

Johnson, M. D. and A. M. Strong (2000). "Length-weight relationships of Jamaican arthropods." Entomological News **111**(4): 270-281.

Kapustjanskij, A., M. Streinzer, H. Paulus and J. Spaethe (2007). "Bigger is better: implications of body size for flight ability under different light conditions and the evolution of alloethism in bumblebees." Functional Ecology **21**(6): 1130-1136.

Karachle, P. K. and K. I. Stergiou (2012). Morphometrics and allometry in fishes, INTECH Open Access Publisher.

Kohavi, R. (1995). A study of cross-validation and bootstrap for accuracy estimation and model selection. Ijcai, Montreal, Canada.

Leuven, R. S., T. C. Brock and H. A. van Druten (1985). "Effects of preservation on dry-and ash-free dry weight biomass of some common aquatic macro-invertebrates." Hydrobiologia **127**(2): 151-159.

Martin, C. A., R. Proulx, P. Magnan, C. Dytham and J. M. Lobo (2014). "The biogeography of insects' length-dry mass relationships." Insect Conservation and Diversity **7**(5): 413-419.

Martins, E. P. and T. Garland Jr (1991). "Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study." Evolution: 534-557.

Martins, E. P. and E. A. Housworth (2002). "Phylogeny shape and the phylogenetic comparative method." Systematic biology **51**(6): 873-880.

Mitchell, M., B. Muftakhidinov, T. Winchen, Z. Jędrzejewski-Szmek, T. G. Badger, badshah400 and A. Wilms. (2018). "Engauge Digitizer Version 10.6." from <http://markummitchell.github.io/engauge-digitizer>.

Olesen, J. M., J. Bascompte, Y. L. Dupont, H. Elberling, C. Rasmussen and P. Jordano (2010). "Missing and forbidden links in mutualistic networks." Proceedings of the Royal Society of London B: Biological Sciences: rspb20101371.

Oliveira, R. and C. Schlindwein (2010). "Experimental demonstration of alternative mating tactics of male Ptilothrix fructifera (Hymenoptera, Apidae)." Animal Behaviour **80**(2): 241-247.

Pagel, M. (1999). "Inferring the historical patterns of biological evolution." Nature **401**(6756): 877.

Paradis, E., J. Claude and K. Strimmer (2004). "APE: analyses of phylogenetics and evolution in R language." Bioinformatics **20**(2): 289-290.

Rall, B. C., G. Kalinkat, D. Ott, O. Vucic‐Pestic and U. Brose (2011). "Taxonomic versus allometric constraints on non‐linear interaction strengths." Oikos **120**(4): 483-492.

Ramalho, M., V. Imperatriz-Fonseca and T. Giannini (1998). "Within-colony size variation of foragers and pollen load capacity in the stingless bee Melipona quadrifasciata anthidioides Lepeletier (Apidae, Hymenoptera)." Apidologie **29**: 221-228.

Revell, L. J. (2012). "phytools: an R package for phylogenetic comparative biology (and other things)." Methods in Ecology and Evolution **3**(2): 217-223.

Rogers, L., R. Buschbom and C. Watson (1977). "Length-weight relationships of shrub-steppe invertebrates." Annals of the Entomological Society of America **70**(1): 51-53.

Rudolf, V. H. and N. L. Rasmussen (2013). "Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem." Ecology **94**(5): 1046-1056.

Sabo, J. L., J. L. Bastow and M. E. Power (2002). "Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed." J. N. Am. Bethol. Soc. **21**(2): 336-343.

Sage, R. D. (1982). "Wet and dry-weight estimates of insects and spiders based on length." The American Midland Naturalist **108**(2): 407-411.

Sample, B. E., R. J. Cooper, R. D. Greer and R. C. Whitmore (1993). "Estimation of insect biomass by length and width." The American Midland Naturalist **129**(2): 234-240.

Schoener, T. W. (1980). "Length-weight regressions in tropical and temperate forest-understory insects." Annals of the Entomological Society of America **73**(1): 106-109.

Schramski, J. R., A. I. Dell, J. M. Grady, R. M. Sibly and J. H. Brown (2015). "Metabolic theory predicts whole-ecosystem properties." Proceedings of the National Academy of Sciences **112**(8): 2617-2622.

Spaethe, J. and L. Chittka (2003). "Interindividual variation of eye optics and single object resolution in bumblebees." Journal of Experimental Biology **206**(19): 3447-3453.

Speakman, J. R. (2005). "Body size, energy metabolism and lifespan." Journal of Experimental Biology **208**(9): 1717-1730.

Stang, M., P. G. Klinkhamer, N. M. Waser, I. Stang and E. van der Meijden (2009). "Size-specific interaction patterns and size matching in a plant–pollinator interaction web." Annals of Botany **103**(9): 1459-1469.

Stevens, V. M., A. Trochet, H. Van Dyck, J. Clobert and M. Baguette (2012). "How is dispersal integrated in life histories: a quantitative analysis using butterflies." Ecology letters **15**(1): 74-86.

Stone, M. (1974). "Cross-validatory choice and assessment of statistical predictions." Journal of the royal statistical society. Series B (Methodological): 111-147.

Streinzer, M., W. Huber and J. Spaethe (2016). "Body size limits dim-light foraging activity in stingless bees (Apidae: Meliponini)." Journal of Comparative Physiology A **202**: 643-655.

Team, R. C. (2018). "R: A language and environment for statistical computing."

Teder, T., T. Tammaru and T. Esperk (2008). "Dependence of phenotypic variance in body size on environmental quality." The American Naturalist **172**(2): 223-232.

Trites, A. W. and D. Pauly (1998). "Estimating mean body masses of marine mammals from maximum body lengths." Canadian Journal of Zoology **76**(5): 886-896.

Van Nieuwstadt, M. and C. R. Iraheta (1996). "Relation between size and foraging range in stingless bees (Apidae, Meliponinae)." Apidologie **27**(4): 219-228.

Velghe, K. and I. Gregory-Eaves (2013). "Body size is a significant predictor of congruency in species richness patterns: a meta-analysis of aquatic studies." PloS one **8**(2): e57019.

Wardhaugh, C. W. (2013). "Estimation of biomass from body length and width for tropical rainforest canopy invertebrates." Australian Journal of Entomology **52**(4): 291-298.

White, E. P., S. M. Ernest, A. J. Kerkhoff and B. J. Enquist (2007). "Relationships between body size and abundance in ecology." Trends in ecology & evolution **22**(6): 323-330.

Williams, N. M., E. E. Crone, T. a. H. Roulston, R. L. Minckley, L. Packer and S. G. Potts (2010). "Ecological and life-history traits predict bee species responses to environmental disturbances." Biological Conservation **143**(10): 2280-2291.

Woodward, G. and A. G. Hildrew (2002). "Body‐size determinants of niche overlap and intraguild predation within a complex food web." Journal of Animal Ecology **71**(6): 1063-1074.