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ORIGINAL PAPER

How to estimate carabid biomass?—an evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement

Fabio Weiss[1,2,3] · **Andreas Linde**[1,2]

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Abstract

Biomass is an important metric for monitoring carabid populations and serves as an ecological indicator. Models that predict carabid weight based on body size represent a simple and straightforward method to estimate biomass and are therefore commonly used. However, such models are rarely evaluated against independent validation data. In this study, we evaluated the two widely used size-weight models by Szyszko (1983) and Booij et al. (1994) drawing on previously published independent data. Additionally, we developed and tested four new models to also evaluate the potential effect of taxonomic parameters; and compared model predictions with actual measurements of biomass using relative deviation graphs and observed versus predicted from regression. We show that the two models by Szyszko (1983) and Booij et al. (1994) contain systematic bias towards larger and smaller carabids, respectively, suggesting restricted applicability of such models. Additional taxonomic parameters improved weight predictions, indicating one possible solution to the issue of restricted applicability. We discuss further relevant limitations of size-weight models and their application and recommend a combined use of the models of Szyszko (1983) and Booij et al. (1994) for carabids ≥ 11.8 mm and < 11.8 mm, respectively.

Implications for insect conservation: Size-weight models are a suitable and simple method to estimate the biomass of carabids and have great potential to be used in monitoring schemes, the investigation of long-term trends and ecological studies. It is, however, essential that researchers pay special attention to potential restrictions in their applicability and methodological limitations.

Keywords Insect monitoring · Size weight equation · Insect biomass · Insect decline · Ecological modelling · Model validation

Introduction

Since the first reports on a global decline in the insect population started to emerge, insect biomass has become an increasingly studied and discussed subject. At first glance, abundance or diversity seem to be the more obvious ways of describing an insect population or community. However, insect biomass might be of similar or even greater importance when it comes to reflecting insects as components of the ecosystem. It reflects the role of insects as trophic component in food webs (Yang and Gratton, 2014; Shaftel et al., 2021), while a study by Barnes et al. (2016) observed that invertebrate biomass can predict ecosystem functioning on larger spatial scales. Insect biomass has been also proposed as an indicator of insect diversity (Hallmann et al., 2021a, b), yet evidence exists highlighting the contrasting patterns in this regard (Homburg et al., 2019; Uhler et al., 2021; Vereecken et al., 2021). When studying insect populations,

✉ Fabio Weiss
fabio.weiss@hnee.de

[1] Biosphere Reserves Institute, Eberswalde University for Sustainable Development, Schicklerstr. 5, 16225 Eberswalde, Germany

[2] Department of Applied Ecology and Zoology, Eberswalde University for Sustainable Development, Schicklerstr. 5, 16225 Eberswalde, Germany

[3] Institute of Ecology, Faculty of Sustainability & Centre of Methods, Leuphana University, Universitätsallee 1, 21335 Lüneburg, Germany

investigating biomass can consequently yield additional insights and lead to very different results and interpretations (Saint-Germain et al., 2007). In the context of the reported global decline of insects, measuring the biomass of insects becomes increasingly relevant. Numerous studies have already reported declines in this regard (e.g. Hallmann et al., 2017; Harris et al., 2019; Seibold et al., 2019), Researchers use a variety of methods: Some studies use fixed protocols to weigh their insect catches manually (Sorg et al., 2013; Hallmann et al., 2017), while others employed size-weight models for the estimation of biomass (Seibold et al., 2019; Hallmann et al., 2020). Predictive models, which are based on the correlation of the body length of an insect and its weight, were developed as early as 1976 (Rogers et al., 1976), but since then there have been various additions, improvements and taxon-specific approaches (e.g. Sample et al., 1993; Sabo et al., 2002; García-Barros, 2015).

Studying biomass has a longer tradition in carabid research (Grüm, 1975; Thiele, 1977; Szyszko, 1983), but recently it has been used increasingly as a tool to monitor long-term population trends. It therefore plays a key role in the investigation of population declines, which have also been reported for ground beetles (Brooks et al., 2012; Hallmann et al., 2020; Liu et al., 2022). Hence, measuring carabid biomass has been included in the recently developed framework for nationwide insect monitoring by the German Federal Agency for Nature Conservation (Federal Agency for Nature Conservation Germany, 2021). Furthermore, carabid biomass has proven to be a valuable indicator of forest naturalness (Winter, 2005; Schreiner, 2011) or habitat succession (Schwerk, 2014), often used in connection with the concept of mean individual biomass (MIB; Schwerk and Szyszko, 2007, 2011).

Table 1 Overview of existing carabid-specific size-weight models (in the order of their publication), their region of origin, the type of modelled weight and examples of use in carabid research

Model/Author(s)	Region	Type of weight	Examples of use
Szyszko (1983)	Poland	fresh	Cárdenas and Hidalgo (2007) Šerić Jelaska et al. (2011) Gobbi (2014) Schreiner (2015) Jambrošić Vladić and Šerić Jelaska (2020)
Jarosik (1989)	Czech Republic	fresh	Saint-Germain et al. (2007)
Booij et al. (1994)	Netherlands	fresh	Homburg et al. (2019) Hülsmann et al. (2019)
Sabo et al. (2002)	California	dry	Hallmann et al. (2020) Skarbek et al. (2021)
Gruner (2003)	Hawaii	dry	

As with insects in general, there exists a variety of methods to determine carabid biomass. Most commonly, ground beetles are sampled with pitfall traps (Barber, 1931), into which individuals fall and are then killed and preserved by a trapping fluid until the trap is collected. Some studies weigh the whole catch or single beetles after letting them drain on a sieve or filtering paper (e.g. Cvetkovska-Gjorgjievska et al., 2017), or they determine dry weights (e.g. de los Santos Gómez, 2013). However, methodological research shows that these methods tend to introduce a certain bias. A study by Knapp (2012), for example, found that different trapping fluids, such as ethylene glycol or propylene glycol or Bryne (saturated sodium chloride solution), and storage fluids, such as ethyl acetate, propylene glycol or ethanol, can change the drained weights and/or dry weights of carabids to a varying extent. Only formaldehyde, which is unfortunately highly toxic, not only to carabids, but also to other animals and humans (Teichmann, 1994), seemed to produce reliable results for both drained and dry weights (but see Wetzel et al., 2005). Moreover, research by Braun et al. (2009) showed that the retention time of carabids in trapping and storage fluids can alter the measured drained and dry weights and even differences in the chemical grades of trapping fluids can affect weights (Braun et al., 2012). Thoroughly cleaning the carabids of adherent dirt or other particles before weighing represents an additional challenge. Few studies use additional non-fatal pitfall traps or hand-collecting to sample live beetles for the determination of actual fresh weight (Knapp, 2012; Heitmann et al., 2021; Yarwood et al., 2021). However, this procedure is very labour-intensive and therefore is often not feasible. Another problem in this regard relates to historic or archived data, in that original beetles often no longer exist and therefore cannot be weighed if biomass needs to be compared with this of more recent data.

The application of size-weight models is one solution to this problem. The abovementioned model by Rogers (1976) has also been used for carabids (Woodcock et al., 2010), but several carabid-specific size-weight models are also regularly used in carabid research (Table 1). There has been some discussion on whether they are restricted in their applicability to certain regions, habitats or taxa (Sabo et al., 2002; Gruner, 2003; de los Santos Gómez, 2013). Despite this they are often used outside their region or habitat of origin (e.g. Cárdenas and Hidalgo, 2007; Hülsmann et al., 2019; Hallmann et al., 2020). Sabo et al. (2002) observed that the accuracy of size-weight models improves with increasing taxonomic specificity. Nevertheless, to date, no taxonomically informed size-weight model for carabids has been proposed. Moreover, none of these models has ever been validated using either original data (e.g. with cross-validation) or independent data. An evaluation of size-weight

models for carabids with independent data would provide important insights in how accurate these models predict carabid weights and shed light on possible restrictions in applicability.

In this study, we evaluate the two commonly used models devised by Szyszko (1983) and Booij et al. (1994) (in the following referred to as $m_{Szyszko}$ and m_{Booij}), as well as four newly developed models, three of which feature taxonomic parameters. This is achieved by using two previously published datasets of measured carabid fresh weights, one of which was used to train our own model candidates and the other one to validate $m_{Szyszko}$, m_{Booij} and our own models. To our knowledge, this is the first time size-weight models for carabids have been validated against independent data.

Materials and methods

Data

We compiled the data for this study from material published by two other studies. Booij et al. (1994) caught ground beetles in May and June of 1987 at "various locations" in the Netherlands. Schultz's (1996) data originated from different habitats (pastures, carrs, red beds, salt marshes, open soil) near the German coast (Baltic Sea) and were collected over a non-specified period in 1995. Both studies caught live ground beetles by hand. Booij et al. (1994) additionally used dry pitfall traps, which were emptied daily. In both cases, the weights represent the mean fresh weights of a varying number of measured carabids of respective species. While Booij et al. (1994) also provided mean size measures for all collected species, Schultz (1996) only stated size classes. Therefore, we supplemented size values for the Schultz (1996) data, according to Müller-Motzfeld (2004), by taking the mid-point of the stated size range for each species. If this information was not available in Müller-Motzfeld (2004), we obtained it from Homburg et al. (2014). In all cases, body length represents the distance of the most forward tip of the mandibles and the rear tip of the elytra (hereinafter simply referred to as "size"). It is important to note that because these weight-size data pairs consist of mean values of a varying number of measurements, they do not represent true data pairs. This adds some level of imprecision to the data, as one may expect a non-linear relationship between size and weight - not only between species (Fig. 1a), but also among differently sized individuals of the same species (but see *Poecilus cupreus*, Booij et al., 1994). Where we complemented sizes from Müller-Motzfeld (2004), this imprecision is likely to be even greater, since midpoints do not necessarily resemble the mean size of the populations actually sampled by Schultz (1996). On the other hand, this aggregation of the data omits the issue of the unequal representation of different species potentially introducing bias into the fitted models. After all, this choice of data is a trade-off. Collecting live ground beetles and recording their fresh weight is extremely work-intensive, which would not have been feasible in our case. Despite the described imprecision, we believe that the data used herein illustrate the general size-weight relationship in carabids and contain valuable information that can be used to develop and evaluate size-weight models.

We used the dataset of Booij et al. (1994), which was originally also used to fit their model, to also fit our own model candidates. The dataset of Schultz (1996) represents truly independent data for all of the six tested models and therefore served as a validation dataset. In order that both datasets featured the same subfamilies with at least two

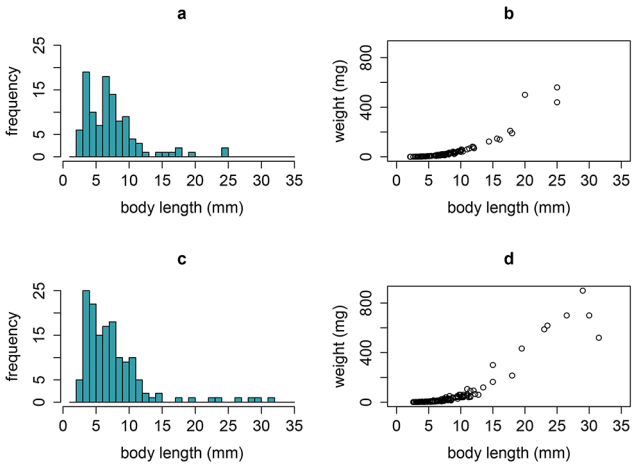

Fig. 2 Size histograms and fresh weights plotted against size for the dataset of Booij et al. (1994) (a, b) andthe dataset of Schultz (1996) (c, d)

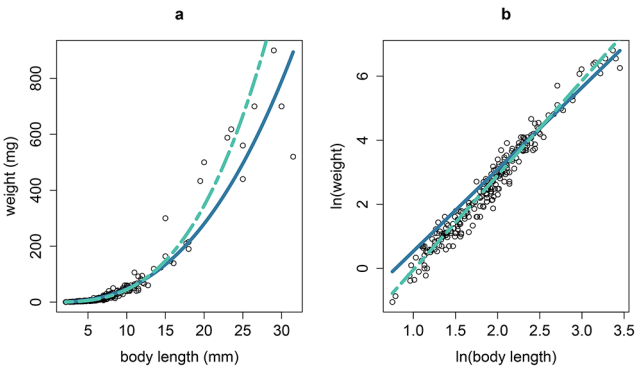

Fig. 1 Fresh weights (y-axis) of different carabid species from both datasets (training and validation) plotted against the respective size (body length)(x-axis) on the original scale (a) and log-transformed (b); added lines display predicted weights calculated with the models of Booij et al. (1994) (dashed) and Szyszko (1983) (solid) on both scales

representing species, we removed three species from the training dataset and five from the validation dataset (Table S1, Supplementary Material). This was done in order to fit and validate model terms with taxonomic predictors. Finally, training and validation data consisted of 107 and 149 species, respectively, belonging to six different subfamilies: Carabinae (n = 4/8), Elaphrinae (n = 2/4), Harpalinae (n = 57/90), Nebriinae (n = 8/8), Scaritinae (n = 6/10) and Trechinae (n = 30/29). In both datasets, smaller carabid species were considerably overrepresented. Histograms and graphs illustrating both datasets can be found in Fig. 2.

Development of taxonomical models

We used the R-statistical language and environment version 4.1.2 (R Core Development Team, 2021) for the development of statistical models and the analyses.

Following the approach of other size-weight models (e.g. Rogers et al., 1976; Sample et al., 1993; Gruner, 2003), we developed power functions by transforming size and weight values, using the natural logarithm and fitting a linear regression model. Overall, we fitted four different models, three of which were fitted using linear models ('lm' function from the 'stats' package, R Core Development Team 2021): the base model without any taxonomic parameters (in the following referred to as m_{base}), a model with an added effect for the subfamily (in the following referred to as m_{fixed}) and a model with an interaction term for the subfamily (in the following referred to as m_{inter}) (Eq. 1).

$$\ln(weight\,[mg]) = a + x + b * z * \ln(bodylength\,[mm]) \quad (1)$$

where a represents the intercept with the y-axis and b the effect of size (slope), x represents the added effect of the subfamily and z represents the interaction coefficient of the subfamily. The simple added effect (m_{fixed}) allows the y-intercept of the size-weight relationship to shift upwards or downwards for the respective subfamily, without changing the slope of the general relationship. The interaction term (m_{inter}) also allows for changed regression slopes for the subfamilies. We assume that the different taxonomic groups in carabids (here subfamilies) have certain shape characteristics, that result in modifications to the general size-weight relationship. Accounting for these characteristics by including taxonomic effects and interactions in the model could therefore increase the accuracy of weight estimates. Our base model m_{base} is very similar to the approach taken by Booij et al. (1994) and is fitted with almost the same dataset. However, validation results can be expected to differ slightly, as we removed three species from the original dataset (see previous section) and use m_{Booij} with the rounded coefficients as provided by its original source (Booij et al. 1994). M_{base} therefore serves as a reference model for the other model candidates. As a fourth model, we fitted a linear mixed-effect model ('lmer' function from the 'lme4' package, Bates et al., 2021) with a random effect for the subfamily (in the following referred to as m_{mixed}). This model accounts for taxonomic effects in the data but allows for estimating the size-weight relationship on the population level. It also considers the unequal representation of the different subfamilies in the data and makes it possible to predict at a later stage the weights of carabids belonging to subfamilies that were not represented in our training data. We checked model assumptions for all models performing post-hoc model diagnostics using the 'DHARMa' package (Hartig, 2021). Diagnostic qq-plots are provided in the Supplementary Material (Fig. S5-S8, Supplementary Material).

Model evaluation

To evaluate the two size-weight models m_{Booij} and $m_{Szyszko}$, as well as our model candidates (m_{base}, m_{fixed}, m_{mixed}, m_{inter}), we calculated fresh weights for all species in the validation dataset, using the equations as originally stated by the authors (Eqs. 2 and 3) or by predicting with the estimated model coefficients from the models previously fitted to the training dataset. Predictions with m_{mixed} were made based on the population level, not applying the random effect.

$$\boldsymbol{m_{Szyszko}}: \ln(weight[g]) = -8.92804283 + 2.5554921 * \ln(size[mm]) \text{ (Szyszko, 1983) (2)}$$

$$\boldsymbol{m_{Booij}}: \log(weight\,[mg]) = -1.3 + 2.95 * \log(size\,[mm]) \text{ (Booijetal., 1994) (3)}$$

We could have refitted m_{Booij} with its original dataset to acquire the unrounded coefficients (Booij et al. (1994) present their model with rounded coefficients, see Eq. 3). However, we decided to use the rounded coefficients as this is how potential users will most likely apply the model.

To evaluate each model's predictions we visualised predicted weights in deviation graphs similar to those proposed by Mitchell (1997). Here, we calculated the deviation of each predicted weight from the respective observed weight. To remove the scale effect of size, we then converted absolute deviation to relative deviation by expressing it as a percentage of the observed weight. The relative deviation of each size-weight model was then plotted against size. Although these relative deviation graphs do not provide any statistic validation, they allow detailed examination of the models' predictions.

In a next step, we regressed observed vs. predicted weights (OP-regression), following the approach presented by Piñeiro et al. (2008). We fitted a linear model ('lm' function from the 'stats' package, R Core Development Team 2021) in which predicted weights were used to predict the

respective observed weights. We added an interaction term for the predicting size-weight model, also adding a reference category in which the "predicted" equalled the observed weights. This was done to check which of the six tested models showed significant differences in intercept and slope in relation to the reference. A significantly altered intercept without a significant change in slope identifies a general over- or under-prediction of the respective size-weight model, while a significantly changed slope (potentially accompanied by a significantly changed intercept) indicates a varying over- or under-prediction along the gradient of weight. Additionally, we calculated the coefficient of determination (R^2) of observed vs. predicted weights, which indicates how much of the linear variation in the observed weights is explained by the variation in the predicted weights (Piñeiro et al., 2008). In this case, R^2 was calculated (sensu Nagelkerke, 1991) by fitting separate linear models with observed vs. predicted weights for each size-weight model. When the OP-regression is fitted with untransformed data (actual weights in milligram), the predicted weights of the few large carabid species will introduce most of the variance and have increased leverage. Model estimates and R^2 values will therefore be mainly driven by these larger species. On the other hand, when the OP-regression is fitted with log-transformed data (as it is used to fit the size-weight equations), the weight and size scales are distorted in favour of the smaller species. In this case, they have an over-proportionate effect on model estimates and R^2 values. To solve this issue, we fitted two OP-regression models with both log-transformed and untransformed data, and used both to draw conclusions about the six models' predictions.

Results

Ln(size) had a significant positive effect on ln(weight) in all four models fitted to the training data. In m_{fixed}, three subfamilies (Nebriinae, Scaritinae and Trechinae) had a significantly changed intercept compared to the reference subfamily (Harpalinae). M_{inter} featured no significant effects except that of ln(size). We provide the full model summaries in Table 2 and plotted prediction curves in the Supplementary Material (Figures S1 – S4).

The deviation graphs for the six evaluated models are shown in Fig. 3. $M_{Szyszko}$ tended to overestimate the majority of smaller carabid species, while all other models over- and underestimated smaller species to a similar extent. Towards the middle of the size range, all models slightly underestimated weights, and especially m_{Booij} and m_{base} had a tendency to overestimate the larger species. For m_{fixed} and m_{mixed} this tendency was less pronounced, and $m_{Szyszko}$ and m_{inter} were most the balanced in their predictions for larger species.

During the OP-regression with log-transformed weights, only $m_{Szyszko}$ showed significant changes in intercept and slope from the reference. Changes in R^2 values between the six models were not detectable or only marginal, with m_{fixed} and m_{inter} having a slightly larger R^2 than the other models (0.9516 and 0.9520 vs. 0.9515). As mentioned in the previous section, these results are primarily of concern for predictions of smaller species. The results of the OP-regression with untransformed weights, which emphasises predictions for larger species, conveyed a different image. Here, m_{base} was the worst-performing model with both significantly altered intercept and slope, and it yielded the lowest R^2 value (0.8516). M_{Booij}, m_{fixed} as well as m_{mixed} displayed a significant change in slope. The R^2 values were 0.8539, 0.8584 and 0.8558, respectively. $M_{Szyszko}$ and m_{inter} were the only two models showing no significant changes in slope or intercept compared to the reference, and they also had the two highest R^2 values of 0.8823 and 0.9052. The main results of the two observed vs. predicted regression approaches are highlighted in Fig. 4. Full model summaries are provided in Table 3. Both regression models display non-normality for residuals (Figure S9, Supplementary Material) and should therefore be interpreted with caution. This is especially the case for the OP-regression of untransformed weights, which is most likely caused by the abovementioned introduced variance and increased leverage of certain data points. Nevertheless, we are convinced that, when considered carefully, both OP-regression models are appropriate for our evaluation of size-weight models. We assume that the results presented above are reliable, as they correspond with the patterns highlighted in the relative deviation graphs.

Discussion

Using an independent dataset, this study set out to evaluate two widely used size-weight models for carabids and to investigate whether the inclusion of taxonomic parameters can help to improve such models.

Based on our validation dataset (Schultz, 1996), our findings reveal general differences in the weight predictions of the two models provided by Szyszko (1983) and Booij et al. (1994). $M_{Szyszko}$ generally overpredicted carabid weights of smaller species. It correspondingly displayed significant changes in prediction compared to the reference during the OP-regression with log-transformed weights (Fig. 4), but it was more accurate for larger carabids and therefore showed no significant changes in intercept and slope and yielded a relatively high R^2 value of 0.882 during OP-regression with

Table 2 Estimated model coefficients of the four developed models. Harpalinae served as reference level for the effect of subfamily. R^2 values are adjusted pseudo-R^2 values (Nagelkerke, 1991) for models m_{base}, m_{fixed} and m_{inter} and marginal / conditional R^2 (sensu Nakagawa et al., 2017) for model m_{mixed}

	m_{base}			m_{fixed}			m_{mixed}			m_{inter}		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
(Intercept)	-3.0848	-3.2290 – -2.9406	**< 0.001**	-2.8707	-3.0966 – -2.6448	**< 0.001**	-3.0309	-3.2354 – -2.8264	**< 0.001**	-2.8287	-3.1108 – -2.5465	**< 0.001**
ln size	2.9783	2.9036–3.0530	**< 0.001**	2.8983	2.7907–3.0059	**< 0.001**	2.9250	2.8322–3.0177	**< 0.001**	2.8778	2.7424–3.0133	**< 0.001**
[Carabinae]				-0.0898	-0.3047–0.1251	0.409				1.9128	-1.9753–5.8010	0.331
[Elaphrinae]				0.1094	-0.1469–0.3656	0.399				1.2201	-2.5670–5.0071	0.524
[Nebriinae]				-0.1377	-0.2723 – -0.0030	**0.045**				-0.4022	-1.2543–0.4499	0.351
[Scaritinae]				-0.3676	-0.5364 – -0.1988	**< 0.001**				-0.0369	-0.8849–0.8111	0.931
[Trechinae]				-0.1175	-0.2246 – -0.0104	**0.032**				-0.2870	-0.7123–0.1383	0.184
ln size * [Carabinae]										-0.6432	-1.9078–0.6214	0.315
ln size * [Elaphrinae]										-0.5538	-2.4360–1.3283	0.560
ln size * [Nebriinae]										0.1324	-0.2894–0.5542	0.535
ln size * [Scaritinae]										-0.2482	-0.8307–0.3343	0.400
ln size * [Trechinae]										0.1118	-0.1493–0.3730	0.397
Random effect							$6_{subfamily}$					
Observations	107			107			107			107		
Degrees of freedom	105			100			103			95		
R^2	0.983			0.986			0.981 / 0.986			0.986		
F statistic (p)	6249 (< 0.001)			1244 (< 0.001)			3910.4 (< 0.001)			668.2 (< 0.001)		

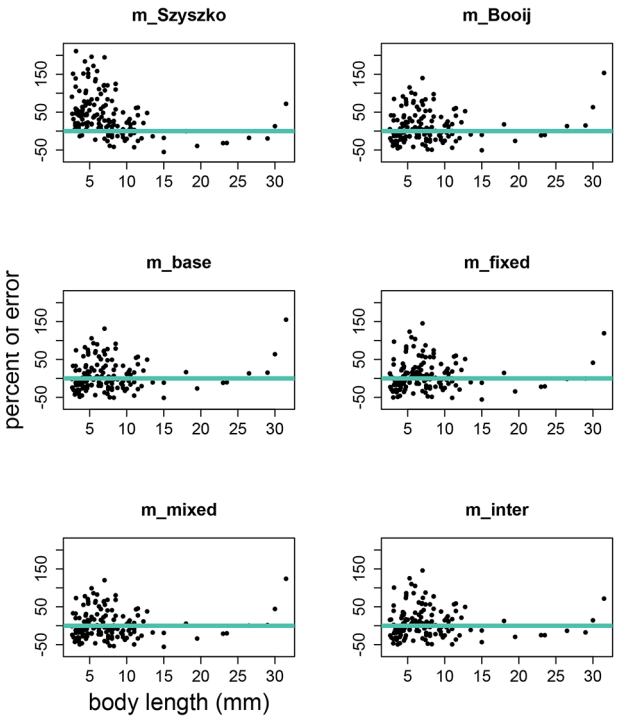

Fig. 3 Deviation graphs of all six models showing the relative deviation as percentage of observed weight on the y-axis against size (body length) on the x-axis. The line (y = 0) represents the observed weights for reference

untransformed weights. In contrast, m_{Booij}, predicted more accurately for smaller carabid species, with no significant changes in intercept and slope during OP-regression with log-transformed weights. It tended to overestimate larger species. Consequently, its predictions significantly differed from the reference during the OP-regression with untransformed weights. It also yielded a lower R^2 value compared to $m_{Szyszko}$. Despite the mentioned imprecision and the limited representation of larger carabid species in our validation dataset, we are confident that our results reveal systematic patterns in the two models' weight predictions, which likely originate from the two models' varying methodological background. Several studies emphasise the specific applicability of size-weight equations in terms of certain regions or habitats (Sabo et al., 2002; Gruner, 2003; de los Santos Gómez, 2013). Our validation data featured some of the same species as the data used by Booij et al. (1994) and was possibly recorded in similar habitats but originated from a different geographical region ("various locations" in the Netherlands vs. the German Baltic Sea coast). $M_{Szyszko}$ was developed using carabids caught with pitfall traps in Polish forests (Szyszko, 1983), while, in contrast, Booij et al. (1994) collected carabids by hand also at "various locations" in the Netherlands. One likely contributing aspect is the varying assemblages of carabids across climatic zones or between different habitats (Thiele, 1977); for example, larger species tend to be more abundant in forests (Schreiner, 2011; Schwerk and Szyszko, 2011; Šerić Jelaska et al., 2011). Yet another important aspect are the different sampling methods. It is known that smaller species are well represented in hand catches, while pitfall traps tend to predominantly capture larger species (Boetzl et al., 2018; Knapp et al., 2020). We see that smaller carabid species were over-represented in the data of Booij et al. (1994) (Fig. 2), and although we did not have access to the original data from Szyszko (1983), we can assume that it featured comparatively larger carabid species. The different regions and habitats, as well as different catching methods, therefore led to different representations of sizes and taxa in the two models' training data.

We found that taxonomic parameters are capable of improving weight predictions of size-weight models for carabids. Our model candidates m_{fixed}, m_{mixed} and mjnter featured 'subfamily' as fixed effect, random effect or interaction term, while m_{base} featured no taxonomic parameters and served as a reference model fitted to the exact same training dataset. Relative deviation graphs and OP-regression indicated that the inclusion of taxonomic parameters can increase the accuracy of predicted weights for independent data. Just as with m_{Booij}, the four models showed no significant changes in intercept and slope during OP-regression with log-transformed weights. During OP-regression with untransformed weights, both m_{fixed} and m_{mixed} showed significantly different slopes compared to the reference. However, changes in slope were less pronounced than with m_{base}. M_{fixed} and m_{mixed} also yielded larger R^2 values, thereby indicating improved predictions for larger carabid species. Overall, m_{mixed} performed marginally worse than m_{fixed} in terms of R^2 values, which is due to the fact the predictions of m_{mixed} were made on the population level only (excluding the estimated random effect). Although subfamily had no significant effects in the fitted model (Table 2), m_{inter} was the most accurate model for both smaller and larger species, showing no significant changes in intercept or slope and yielding the largest R^2 values in both OP-regression approaches. Sabo et al. (2002) observed that the accuracy of size-weight models for insects improves with increasing taxonomic specificity, while Gruner (2003) found that the inclusion of an additional width-parameter can enhance (dry) weight predictions for carabids. Mroczyński and Daliga (2016) used the differentiation of morphological types to improve size-weight models for beetle larvae. Consequently, different taxonomic groups in carabids (here subfamilies) could also have certain shape characteristics, which result in modifications to the general size-weight relationship. Our findings support this hypothesis, as additional taxonomic parameters were capable of improving model

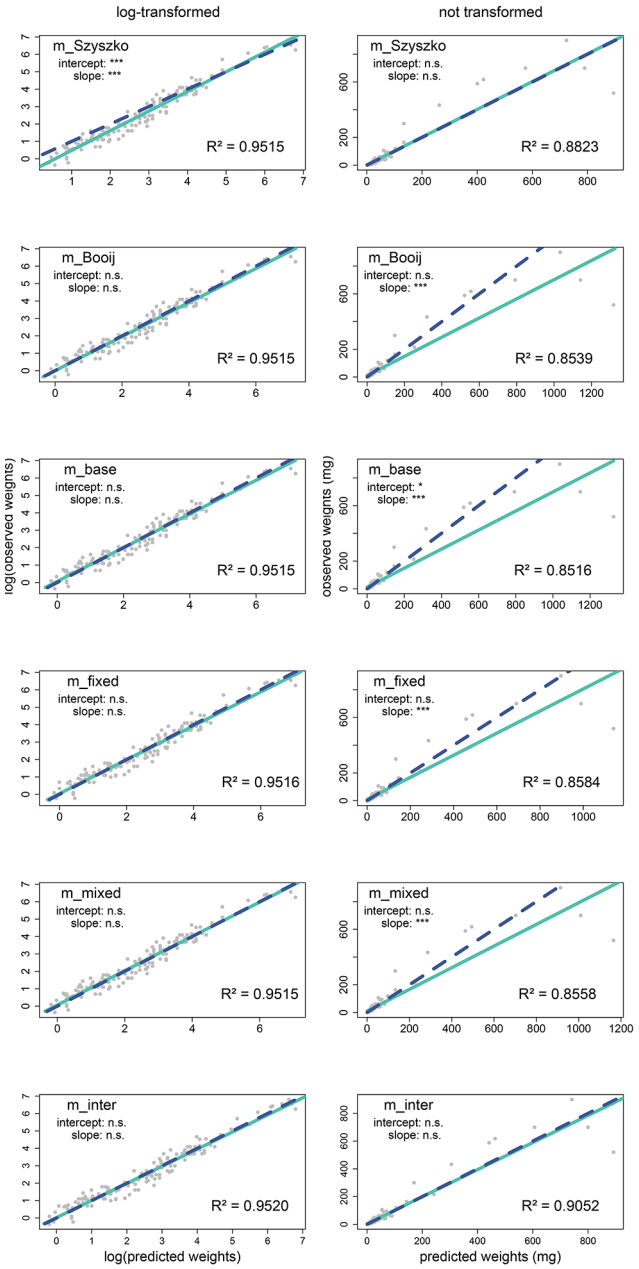

Fig. 4 Observed weights plotted against predicted weights for all six models on the log-scale (left) and the original scale (right), showing the reference line 1:1 (dashed) and the individual regression line (solid). Take note of the different scales on the x-axis. Significance codes for intercept and slope are: *** (< 0.001), ** (< 0.01), * (< 0.05)

accuracy in our study. Another possible explanation in this regard could be that the different subfamilies represent specific size ranges. For example, species belonging to Carabinae are typically relatively large, while Trechinae species are usually comparatively small. Figure 1b indicates that the relationship between log-transformed body length and log-transformed fresh weight may not be perfectly linear. In this case, an additional taxonomic parameter would improve the model by adding flexibility. Owing to the limitations of the two datasets used in our study, we estimated model coefficients for only six subfamilies, which considerably limits the practical applicability of the models described herein. Nevertheless, we believe that the inclusion of a taxonomic parameter as a random effect could be a promising approach to formulating size-weight models that are less biased by their training data - and therefore less restricted in their applicability. Such models would not require specific taxonomic predictors when applied to independent data.

It needs to be mentioned that size-weight models for carabids have disadvantages and limitations. M_{Booij} and our approach are based on training data that contain certain inaccuracies. This might also be the case for $m_{Szyszko}$, as the original reference does not provide detailed information in this regard (Szyszko, 1983). Furthermore, size-weight models are usually fitted on the logarithmic scale; therefore, prediction errors for larger species translate exponentially into relatively large absolute errors. This general problem was described by Koch and Smillie (1986) for hydrological models, but it also applies to size-weight models for insects (e.g. Rogers et al., 1976). Another sensitive aspect is determining which sizes are used when applying size-weight models. There are intraspecific differences in size between different regions and habitats (Szyszko et al., 1996; Baranovská and Knapp, 2014; Baranovská et al., 2019). Individual size usually also varies between females and males of the same species (Riecken and Raths, 1996; Knapp, 2012; Baranovská and Knapp, 2014), while both the magnitude of this sexual dimorphism and the abundance ratio of male and female beetles can vary spatially - within the same species and population (Yarwood et al., 2021). Additionally, the size of carabid imagos is affected by conditions during larval development and can therefore vary considerably (Szyszko et al., 1996; Baranovská and Knapp, 2014; Tseng et al., 2018). Moreover, size-weight models cannot account for phenological variations in biomass within the same species at different times of the year: carabids are usually lighter after overwintering or as teneral imagos, but they increase in weight towards reproduction (Grüm, 1975; Booij et al., 1994; Szyszko et al., 1996). In the context of the described limitations and the imprecision of the aggregated data in this study, the predicted weights and calculated relative deviations (Fig. 3) should not be taken literally; instead, they should be considered as a whole, in order to reveal systematic patterns in the weight predictions of the different models.

After all, size-weight equations are models and therefore only approximations of reality. We thus recommend directly measuring carabid fresh weights, whenever feasible. This represents a considerable amount of work and requires very specific methods (Booij et al., 1994; Knapp, 2012), as

Table 3 Estimated model coefficients of the observed vs. predicted regression models (sensu Pineiro et al. 2008) for log-transformed predictions (left) and not transformed predictions (right). R^2 was calculated as adjusted pseudo-R^2 (Nagelkerke, 1991)

	Observed vs. predicted regression					
	log-transformed			**not transformed**		
	Estimate	CI	p	Estimate	CI	p
(Intercept)	0.00	-0.10–0.10	1.000	0.00	-8.06–8.06	1.000
predicted weight	1.00	0.97–1.03	**< 0.001**	1.00	0.95–1.05	**< 0.001**
[m_szyszko]	-0.64	-0.80 – -0.49	**< 0.001**	1.49	-9.93–12.91	0.798
[m_booij]	0.00	-0.14–0.14	0.975	10.91	-0.38–22.21	0.058
[m_base]	0.06	-0.07–0.20	0.367	11.45	0.16–22.74	**0.047**
[m_fixed]	0.04	-0.09–0.18	0.531	8.72	-2.60–20.04	0.131
[m_inter]	0.02	-0.11–0.16	0.727	3.39	-7.99–14.76	0.560
[m_mixed]	0.06	-0.07–0.20	0.358	10.43	-0.88–21.73	0.071
pred. weight * [m_szyszko]	0.13	0.08–0.18	**< 0.001**	0.00	-0.08–0.08	0.974
pred. weight * [m_booij]	-0.02	-0.07–0.02	0.333	-0.31	-0.38 – -0.24	**< 0.001**
pred. weight * [m_base]	-0.03	-0.08–0.01	0.173	-0.31	-0.38 – -0.24	**< 0.001**
pred. weight * [m_fixed]	-0.03	-0.07–0.20	0.249	-0.20	-0.27 – -0.13	**< 0.001**
pred weight * [m_inter]	-0.02	-0.06–0.03	0.461	-0.02	-0.10–0.06	0.571
pred weight * [m_mixed]	-0.01	-0.06–0.03	0.540	-0.22	-0.29 – -0.15	**< 0.001**
Observations	1043			1043		
Degrees of freedom	1029			1029		
R^2	0.958			0.885		
F statistic (p)	1828 (< 0.001)			619.7 (< 0.001)		

commonly used catching and storing fluids can introduce some bias (Braun et al., 2009, 2012; Knapp, 2012). However, if this is neither feasible nor possible (e.g. for historic or archived data), size-weight models are a suitable solution. We explicitly advise against obtaining the weights of certain species directly from the literature because they can underlie substantial variations. Carabid (mean) sizes should be measured directly (see Šerić Jelaska et al., 2011) and only be substituted from the literature when this is also neither feasible nor possible. Researchers should preferably use size-weight functions from the same region and habitat, if available. However, special attention should be paid to the methodological background of both the size-weight model and one's own data. Generally, we recommend the combined application of the models of Szyszko (1983) and Booij et al. (1994), with the former used for larger and the latter for smaller carabid species. The two models intersect at approximately x = 2.4655, y = 4.2801 on the log-scale, which converts to 11.77 mm and 72.25 mg, respectively. We therefore recommend the use of m_{Booij} for carabids < 11.8 mm and $m_{Szyszko}$ for carabids ≥ 11.8 mm. Furthermore, it should be noted that biomass data from different studies should only be compared when they were derived with the same method, which also means that they should have been predicted with the same model (or a combination of models).

Conclusions

We found the size-weight model provided by Booij et al. (1994) is more accurate for smaller carabids, while the model of Szyszko (1983) is more accurate for larger carabids when tested against independent data. Additional taxonomic parameters have the potential to improve the weight predictions of size-weight models and may lessen restrictions in terms of applicability. Although it is preferable to measure the biomass of carabids directly, estimating weights with size-weight models is generally less work-intensive, and sometimes it is the only available method. For further application, we recommend a combined use of the models of Booij et al. (1994) and Szyszko (1983), with the former used to predict the weights of smaller carabids (< 11.8 mm) and the latter to predict the weights of larger carabids (≥ 11.8 mm).

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Data availability We declare that the data used in this research is not our own. It has been previously published by Booij et al. (1994) and Schultz (1996) and can be found in these publications. Carabid species included in this research, their respective source publication and the modelling results of this research are provided in the Supplementary Material (Table S1).

Code availability The R code is available at https://github.com/fabio-weiss/carabid_biomass.

Declarations

Conflict of Interest/Competing interests All involved authors declare that they have no conflicts of interest.

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