# Estimating biomass from body size of European spiders based on regression models

Anja Penell<sup>1</sup>, Florian Raub<sup>2</sup> and Hubert Höfer<sup>2</sup>: <sup>1</sup>Am Zündhütle 18, D-76228 Karlsruhe, Germany; <sup>2</sup>State Museum of Natural History Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe, Germany; E-mail: florian.raub@smnk.de

**Abstract.** There is a need for reliable and standardized methods to measure functional species traits. Body mass is just one dimension of body size, a most important morphological trait, because it is directly linked with metabolic rate and affected by environmental conditions. However, it is still not widely used due to the difficulties and constraints of direct measures. Weighing many (small) animals (i.e., arthropods) is laborious, time consuming and biased when using preserved material. Therefore, the applicability of general equations for estimating mass from body size of spiders was tested. We calculated linear regressions to estimate fresh and dry mass of spiders from different body measures (i.e., body length, carapace length and width) of 189 spiders sampled in southern Germany. We compared these regressions with each other and with equations from the literature and tested the impact of taxa, sex and habitat on the accuracy of biomass estimates using an independent test dataset of 166 spiders. All size-fresh mass regressions were highly significant with R<sup>2</sup> values between 0.81 and 0.98. The slope of the ln-transformed body mass - body size relationship ranged between 2.51 and 2.95. The regressions including total body length always showed higher R<sup>2</sup> values, i.e., they provide better predictions of body mass/fresh mass was 0.22. Taxon-, sex- or microhabitat-specific regressions did not produce better estimates than general regressions. Therefore, we strongly recommend the use of general regressions in the context of biomass estimation of assemblages and propose parameters from our regressions to be used for European spiders.

Keywords: Araneae, morphological traits, practical use, fresh mass

Biomass is an important parameter in population and community studies because it is directly related to nutrient and energy availability at each trophic level in all ecosystems (Vucic-Pestic et al. 2010; Chapin et al. 2012). It is also an important morphological and functional trait, correlated with the individual's metabolic rate and food requirement (Peters 1983; Hudson et al. 2013), scaling with many life-history traits (Moretti et al. 2016). Body size and mass are determinants of the interactions of any organism with its abiotic and biotic environment. Both are quantitative and measurable under standardized conditions and therefore among the traits recommended for terrestrial invertebrates (Moretti et al. 2016).

Directly determining the mass of living arthropods by weighing is technically elaborated, laborious, time consuming and error-prone. In ecological studies, spiders and other arthropods are usually caught in different preserving agents and transferred to ethanol for identification and voucher depositing, causing unpredictable changes in fresh mass and prohibiting desiccation for dry mass. Therefore, alternative methods to estimate the body mass have repeatedly been developed and tested (e.g., for aquatic invertebrates: Johnston & Cunjak 1999; Miserendino 2001; Sabo et al. 2002; for terrestrial invertebrates: Rogers et al. 1976, 1977; Sage 1982; Sample et al. 1993; Hódar 1996; Wardhaugh 2013). The most common and approved method is to calculate statistically tested regressions of mass and body size measures. Although body volume would be the logical predictor of mass (Moretti et al. 2016) direct measures of volume or the body diameter are rather difficult to take. Therefore, calculations of fresh or dry mass based on easily measured body size dimensions such as length or width are clearly preferable. Previous publications often propose the power model as the best model to describe the size-mass relationships (Breymeyer 1967; Rogers et al. 1976; Gowing & Recher 1984; Ganihar 1997; Brady & Noske

2006; Höfer & Ott 2009; Martin et al. 2014), but often use it in its linearized form (Ganihar 1997; Wardhaugh 2013). Linear models based on logarithmic data have also been used to describe the relationship (Rogers et al. 1977; Ganihar 1997; Höfer & Ott 2009).

Spiders are a diverse group and although their bodies' physical structure is rather uniform (i.e., oval prosoma and opisthosoma, chitinized carapace) across all developmental stages and life forms, body shapes vary, e.g., in the ratio prosoma-opisthosoma or the ratio body-leg size. It is therefore important to know if regressions of body size-mass across multiple species (herein called general equations) can be used for all spider assemblages, at least in the same biogeographical/climatic region. In Central Europe, there are very few extreme shapes, as for example in ant-mimic spiders (Synageles Simon, 1876, Myrmarachne MacLeav, 1839) or the mygalomorph Atypus Latreille, 1804 with their compact legs and big chelicerae. Within a species, body size and mass (of adults) can vary considerably and not only by sexual dimorphism (Mikhailov 1996; Foellmer & Moya-Laraño 2007; Wunderlich 2008; Logunov 2011). Size (and mass) of adults depend on their sexual maturity, i.e., the developmental stage of eggs in females. Ecological factors causing size and mass variation are nutritional conditions during the development and life cycle (Jocqué 1981a; Jakob et al. 1996), related to climatic-geographical (Entling et al. 2010; Bowden et al. 2013) and habitat conditions (e.g., microclimate, structure, disturbance; Jocqué 1981a, b). Deviations of the size-mass relationship, i.e., caused by different densities of body mass could result from extraordinarily strong chitinization, occurring in several families (e.g., Atypidae, Corinnidae, Thomisidae, Araneidae, Linyphiidae, Theridiidae), or from opisthosoma content (eggs, guanine), but is expected to be low in comparison with the existing size variation.

Although the necessary accuracy or tolerable error of a biomass estimate certainly depends on the scientific question, it is desirable to have reliable general equations for mass estimation by regression of body size and this seems feasible for spiders (Henschel et al. 1996; Lang et al. 1997; Höfer & Ott 2009).

The global spider community has recently been estimated to equal 25 million tons and to consume between 400 and 800 million tons of prey per year on a global level (Nyffeler & Birkhofer 2017). This study however, also shows the scarcity of available reliable and comparable biomass measures worldwide. For the global impact assessment, a total of only 65 values of spider biomass  $m^{-2}$  were gathered from the literature – for all terrestrial biomes (Nyffeler & Birkhofer 2017).

For spiders of temperate zones in North America, there are equations for fresh and dry mass from a large sample of different species (Edwards & Gabriel 1998); for Europe (Central Europe, Palearctic) there are only few general equations for (dry) mass from body length from Breymeyer (1967: 3 lycosid species); Clausen (1983: 8 species from Denmark); Henschel et al. (1996: 138 spiders of 11 species from southern Germany); Hódar (1996: 18 spiders from arid zone of southeastern Spain) and Lang et al. (1997: 17 linyphiid and 6 lycosid species from arable land).

In this study, we wanted to (1) derive body mass-size relationships from a larger and diverse sample of European spiders (creation dataset, 189 specimens), (2) identify the body size measure that predicts biomass best and (3) test if taxon, sex or microhabitat influence the mass estimation to an extent that makes the use of specific regressions necessary. The latter was done applying the parameters from the creation dataset to a second independent sample of spiders (test dataset, 166 specimens). As a result, we propose regression parameters for three body size measures to estimate biomass of Central European spider assemblages.

## **METHODS**

Sampling.—For the calculation of the regressions, 189 spiders (creation dataset) were sampled during five collection events in the surroundings of Karlsruhe, Baden-Württemberg, Germany between 12 April and 9 May 2016. Additionally, spiders from the Swabian Alp and from Bavaria were included. Spiders were captured manually or with a modified hand-held vacuum cleaner during visual searching, by beating vegetation, sifting litter and pitfall traps in order to cover the whole range of spider types in the sampling locations (Supplementary material Table S1, online at http://dx.doi. org/10.1636/JoA-S-17-044.s9). To test the regressions, we used a second dataset of 166 spiders (test dataset) sampled within a radius of 50 km around Karlsruhe in June 2016 and April and September 2017 (forests, open areas in the Black Forest) (Supplementary Material Table S1). All spiders were captured alive and stored individually in vials for a maximum of 24 hours until weighed.

Weighing and measuring.—Specimens were anesthetized with  $CO_2$  and weighed to the nearest 0.01 mg with a microbalance (Sartorius Supermicro S4). Subsequently, the spiders were killed and preserved in 75% ethanol. Body size measurements were taken from the preserved specimens with a

micrometer eyepiece to the nearest 0.05 mm: 1. Total body length, from above, excluding chelicerae and spinnerets = BL; 2. Length of the carapace (dorsal part of the prosoma) = CL; 3. Width of the carapace = CW. Thereafter the spiders were identified, juvenile specimens at least to genus or family and all adults to species. Nomenclature is based on the World Spider Catalog (2017), version 18.0 (online at http://wsc.nmbe.ch). Specimens were deposited in the collection of the State Museum of Natural History Karlsruhe (SMNK-ARA, SMNK-STUD). The body length measurement of 30 spiders was repeated after one year's storage in 75% ethanol to check for the influence of the preservation process on the size. This effect was tested using a paired t-test. To calculate a regression for body length-dry mass in order to enable dry mass estimation and - more important - to enable comparison with equations in the literature (almost exclusively for dry mass), we dried these 30 specimens in a laboratory oven at 70 °C for 48 hours and weighed them on the same microbalance. These measurements also served to calculate a ratio of dry/ fresh mass.

**Regression analyses.**—In preliminary tests we estimated the body mass of the 189 specimens comparing the power model (mass = a (size)<sup>b</sup>), exponential model (mass =  $a + (e)^{b(size)}$ ) and linear model (ln (mass) =  $a + b \ln$  (size)). We selected the linear model as the best fitting one based on the residual standard errors and the R<sup>2</sup> values.

Linear regressions for fresh mass were then calculated (using the creation dataset, 189 spiders) for each of the following data subsets: (1) all spiders, (2) lycosids, (3) males/ females, (4) ground/vegetation dwelling spiders. For each of these groups, regressions were calculated based on the size measurements mentioned above: total body length (BL), carapace length (CL), carapace width (CW) and the product of body length x carapace width (BL x CW). A regression for body length-dry mass was calculated for the 30 dried specimens. All regression analyses were performed in R 3.3.0 (R Development Core Team 2016) with the function "lm". The adjusted  $R^2$  and the standard deviations of the residuals are presented as goodness-of-fit and regression parameters a and b for the linear model mass = exp(a + b) (ln body measure)) with standard errors to be used for future estimates. Plots show the individual values, regression lines and 95% prediction intervals of the regression. In contrast to the oftenused confidence interval (which is an estimate of the "true" population mean of the actual observed sample), the prediction interval uses the observed sample statistics of mean and standard deviation to estimate an interval in which future observations will fall with a certain probability. Therefore, it is more appropriate to graphically represent the range in which the regression can be used.

**Comparison of the regressions.**—We tested the influence of taxon, sex and microhabitat using the different regressions (1-4) to estimate the mass of the test sample (166 spiders) by:

(a) applying the parameters of the lycosid-specific (2) and the general regressions (1) to the 71 lycosid spiders of the test sample to compare the resulting estimates.The taxon Lycosidae was selected based on a sufficient number in both samples and the fact that lycosids usually predominate the very common pitfall trap samples due to

their high activity density and comparatively large body size.

- (b) applying the parameters of the sex-specific (3) and the general regressions (1) to the 76 adult spiders of the test sample to compare the resulting estimates.
- (c) applying the parameters of the microhabitat-specific (4) and the general regressions (1) to the 97 ground-dwelling spiders and the 69 vegetation dwelling spiders of the test sample to compare the resulting estimates.

We used ANOVA to compare the results of the different regression models. If this test showed a significant effect, Tukey's HSD post-hoc test was applied. All ANOVA and post-hoc analyses were carried out in Statistica 9.0 (StatSoft 2009).

# RESULTS

Sampling.—A total of 189 spiders was sampled, weighed and measured for the regression analyses. 120 (63.5%) spiders were adult (50 males, 70 females), 105 specimens were sampled on the ground, 83 from vegetation (herb or shrubs), one specimen was caught in a house. The sample represented 47 species of 17 families (Supplementary Material Table S1, online at http://dx.doi.org/10.1636/JoA-S-17-044.s9). Wolf spiders (Lycosidae) dominated the sample with 58 individuals (31%) of 5 genera and 10 species. Total body length of the spiders ranged from 1.15 mm (a juvenile linyphild) to 16.8 mm (an adult female of Eratigena atrica (C. L. Koch, 1843)), body mass ranged from 0.25 mg to 432.8 mg (same specimens). The body shape (ratio CW/BL) was rather similar for all spiders (mean: 2.7) except for the specimens of the genus Tetragnatha Latreille, 1804 (4.2), sampled in vegetation (Supplementary Material Table S2, online at http://dx.doi.org/10.1636/JoA-S-17-044.s10).

**Regressions.**—Comparing the different regression models (BL all spiders) the linear model (using ln transformed data) showed the least residual standard error (0.31, back-transformed 1.36) in comparison to the power model (2.17) and the exponential model (2.29) and also the highest  $\mathbb{R}^2$  values (Linear: 0.96, Power: 0.95, Exponential: 0.93). The estimated total body mass of the 189 spiders differed by only 3% from the weighed value using linear regression, but 4% using the power model and 17% using the exponential model. Therefore, we decided to use linear regression analyses, based on Intransformed measures of body size and mass values in order to reduce heteroscedasticity. The use of a linear regression has the strong advantage that  $\mathbb{R}^2$  can be used as goodness-of-fit in comparisons of the different regressions (Anderson-Sprecher 1994).

All size-fresh mass regressions (Fig. 1; Supplementary Material, Figs. S1–S5, online at http://dx.doi.org/10.1636/JoA-S-17-044.s1 through dx.doi.org/10.1636/JoA-S-17-044.s5) were highly significant (P < 0.0001) with R<sup>2</sup> values between 0.806 (CW of Lycosidae) and 0.984 (BL x CW of male spiders) and standard deviations of the residuals of 0.17–0.42 (Table 1). The regression parameters a (intercept) and b (slope) are presented in Table 2 with their standard errors. The slope parameter b ranged from 2.51 to 2.95 for regressions based on single body measures. Only two of the 24 regressions showed a fit R<sup>2</sup> < 0.9, but 13 a fit R<sup>2</sup> > 0.95.

The body length-dry mass regression was also highly significant (a = -3.1726, b = 2.6296,  $R^2 = 0.91$ , SD = 0.42). The ratio dry mass/fresh mass was between 0.13 and 0.34 with a mean of 0.220 ( $\pm$  0.05) for the weighed values and between 0.20 and 0.23 with a mean of 0.213 ( $\pm$  0.01) for the estimated values.

The repeated measurement of body length of 30 spiders after one year in 75 % ethanol resulted in a mean difference of -0.056 mm (1.2%), not significant (t = 2.093; P = 0.08, paired t-test).

**Comparison of the regressions.**—The application of the lycosid specific regressions showed a weakly significant effect of (a) taxon-specific regressions (F (8, 630) = 2.234, P = 0.024) for biomass estimation, but a post-hoc test showed no significant differences between single regressions (Supplementary Material Fig. S6, online at http://dx.doi.org/10.1636/JoA-S-17-044.s6).

There was no significant influence of (b) sex (F (8, 666) = 1.110, P = 0.354) or (c) microhabitat (F (8, 1485) = 1.218, P = 0.284) on the body mass estimates (Supplementary Material Figs. S7 & S8, online at http://dx.doi.org/10.1636/JoA-S-17-044.s7 and http://dx.doi.org/10.1636/JoA-S-17-044.s8).

The total dry mass of the 30 spiders was 102.4 mg. Our own dry mass regression underestimated these spiders by 14%. Regressions from literature either underestimated or overestimated the mass by 19–38% (Supplementary Material Table S3, online at http://dx.doi.org/10.1636/JoA-S-17-044.s11).

## DISCUSSION

In contrast to other studies which described the power model to be best suited for most insects and spiders (Ganihar 1997: Brady & Noske 2006), the linear model was more appropriate in our study showing the least residual standard error, the highest  $R^2$  value and the smallest difference between estimated and weighed mass. A power model is better adjusted to spiders at the upper end of the size spectrum whereas a linear model better estimates the mass of the small spiders (see Höfer & Ott 2009: Fig. 1). Using a linear model to estimate a sample including large spiders (which is more frequent in tropical assemblages) may result in a large bias of the total estimate, although the mass of most of the (smaller) spiders is well estimated. Analogous to Ganihar (1997) and Brady & Noske (2006), the exponential model was suboptimal for body mass calculation of our German data set. Because linear models show further advantages in the comparison and interpretation of graphs, we decided to use linear regression models on log-transformed data for all further regression analyses and propose this procedure and the resulting regression parameters.

Comparing the goodness-of-fit, the regressions including body length and carapace width showed the highest  $R^2$  values, lowest standard deviations, and also the smallest prediction intervals (Table 1, Fig. 1). The regressions based on BL showed a better fit than the ones using carapace measures. This is certainly caused by the fact that the opisthosoma contributes most to the variation in size and mass within the species, depending mainly on the nutritional status and the development of the sexual organs (Jakob et al. 1996). If this variation is included, the regression becomes more precise. On the other hand, the use of a carapace measure of adult spiders



Figure 1.—Scatter plots of spider body size measures/fresh mass and regression lines with prediction intervals (outer lines) calculated for all spiders (n = 189): a. Body length/mass. b. Carapace length/mass. c. Carapace width/mass. d. Body length x carapace width/mass.

might reflect the mean biomass of a species better. Of the carapace measures, CL performed slightly better than CW.

Although the use of general equations is desirable and was repeatedly proposed, there is concern that the length-mass relationship might differ between taxa (i.e., with different body shapes), between regions (latitudes, climatic zones, temperate versus tropical faunas; see Schoener 1980; Gowing & Recher 1985; Höfer & Ott 2009; Martin et al. 2014), or

Table 1.—Regression statistics for the different regression equations of the form mass = exp (a + b (ln body measure)): sample size (N), range of body length (BL) in mm, adjusted determination coefficient (adj.  $R^2$ ), standard deviation of residuals (SD), BL = body length, CL = carapace length, CW = carapace width; all regressions highly significant (p < 0.0001).

				BL	,	CL	,	CW	7	BL*CW	
	Group	Ν	BL range [mm]	adj. R <sup>2</sup>	SD						
	All spiders	189	1.15 - 16.8	0.959	0.31	0.933	0.39	0.928	0.41	0.972	0.26
	Ground spiders	105	1.10 - 12.6	0.981	0.22	0.950	0.36	0.944	0.37	0.977	0.24
Fresh mass	Vegetation spiders	83	1.10 - 9.0	0.919	0.38	0.908	0.40	0.898	0.42	0.960	0.26
	Males	59	1.15 - 9.2	0.968	0.26	0.953	0.31	0.954	0.31	0.984	0.18
	Females	73	1.30 - 16.8	0.975	0.26	0.944	0.38	0.946	0.38	0.976	0.25
	Lycosidae	58	2.85 - 9.8	0.930	0.17	0.845	0.25	0.806	0.28	0.924	0.18
Dry mass	All spiders	30	1.15 - 8.3	0.911	0.42						

Table 2.—Parameter estimates (a - intercept, b - slope) with standard errors (SE) for the different equations of the form mass = exp (a + b (ln body measure)), BL = body length, CL = carapace length, CW = carapace width.

		BL				CL				CW				BL*CW			
	Group	а	SE	b	SE	а	SE	b	SE	а	SE	b	SE	а	SE	b	SE
	All	-1.72389	0.06	2.69638	0.04	0.47993	0.04	2.51877	0.05	1.04109	0.04	2.66434	0.05	-0.40055	0.04	1.38032	0.02
Fresh mass	Vegetation	-1.50235	0.00	2.51147	0.04	0.58644	0.05	2.57141	0.00	1.08888	0.05	2.81913	0.00	-0.3910	0.05	1.40548	0.02
	Females	-1.89589	0.10	2.83422 2.71443	0.07	0.16993	0.06	2.60587 2.56124	0.08	0.72575	0.05	2.78296	0.08	-0.26268	0.05	1.43728	0.02
Dry mass	Lycosidae All	-1.79359 -3.17260	0.17 0.23	2.78452 2.62960	0.10 0.15	-0.1380	0.18	2.9514	0.17	0.7208	0.15	2.8807	0.19	-0.77771	0.15	1.50278	0.06

between habitat types. Most studies agree that taxon-specific regression equations on the level of orders are necessary (see Hódar 1996; Wardhaugh 2013).

In order to decide which method and equation to choose for the respective scientific question, it would be of particular interest to recognize the reliability and predictive power of general versus specific equations. The applicability of the different regressions for the biomass estimation of spiders has therefore been tested using a test dataset of 166 spiders sampled at different locations and during different seasons of the year to minimize local or seasonal effects.

Lycosids were selected for taxon-specific regressions for several reasons. First, they were sufficiently represented in our samples, due to their abundance and activity. For the same reason, lycosids often (strongly) dominate pitfall trap samples and pitfall trapping is a very common sampling method in ecology. Where wolf spiders are abundant (i.e., in grassland, Jocqué & Alderweireldt 2005), these relatively large spiders dominate the biomass of predators and are supposed to have a considerable impact on both prey and predator assemblages of the ground. So, it seemed reasonable to test a proper regression for this family to increase accuracy. In contrast to our expectation, the estimates using parameters from the taxon-specific regressions differed stronger from the weighed mass than the estimates from general regressions, probably reflecting the lower goodness-of-fit and a resulting lower predictability. The use of habitat specific or sex specific regressions did not produce significantly different biomass estimates. We therefore conclude that a further identification or a separation in male/female or habitat groups is not necessary in order to improve the estimated biomass values.

The taxon-specific (lycosid) regressions showed a lower goodness-of-fit due to the narrow size range and body mass range. Although lower  $R^2$  values are not inherently bad as far as predictions are made for specimens within the same range, estimating the mass of spiders outside of the small range used for regression creation can lead to a considerable bias. It is important to remember that the predictive power comes from the inclusion of many data points distributed over the whole range of size, shape and size-mass relation. A sample size of n = 10 can be adequate to find a significant relationship of size-mass with high  $R^2$  values (Hódar 1996), but the probability that the regression is useful for most of the different species/ shapes is low, due to low predictive power.

Our sample of 189 specimens including 47 species from 17 families, collected in different habitats and strata represents

most of the guilds and life-history types occurring in temperate European habitats, i.e., sheet, space and orb web weavers, ambush, ground and other hunters (Cardoso et al. 2011). Very few Central European spiders fall outside the size range represented by our sample. Based on this and the goodness-offit results, we expect our regressions to be useful for spider assemblages at least in temperate regions of Europe.

The slope parameter b (power coefficient) of our regressions based on single body measures ranged between 2.51 and 2.95 for fresh mass (2.63 for dry mass), thus being close to 3 as expected for animals with isometric growth (Suter & Stratton 2011). The values differed only slightly from regressions for Neotropical spiders (Mata Atlântica 2.87, Amazonia 2.98 for all spiders, but 2.2 for Amazonian web-building spiders; Höfer & Ott (2009), Supplementary Material Table 3, online at http://dx.doi.org/10.1636/JoA-S-17-044.s11).

Comparing length-dry mass relationships of assemblages from temperate and tropical zones, Schoener (1980) found that tropical insects usually have smaller power regression coefficients. No difference was found between temperate habitats located far apart from each other (Gowing & Recher 1985). Martin et al. (2014) also showed a positive relation between the absolute latitude of the sample and length-dry mass power regression coefficients. Höfer & Ott (2009) determined parameter estimates from regression analyses for Neotropical arachnids and showed that parameters from different tropical regions within Brazil are close enough to be used, but parameters from temperate zones were not useful for the Neotropical fauna. The slopes of the regressions of Brazilian spiders are higher than the slopes of the regressions of the German spiders. Using the parameters of the linear regression calculated by Höfer & Ott (2009: subtropical Brazil), the relative difference of the estimated to the weighed body mass was 9% higher than using the equation of this study. The use of equations from the tropical region led to 7 -24% higher differences (Supplementary Material Table 3, online at http://dx.doi.org/10.1636/JoA-S-17-044.s11). Thus, equations from different climatic zones should not be used for mass estimation, while equations from the same zone might be used outside the geographic region.

The ratio between dry and fresh mass measured in this study (0.13–0.34, mean 0.22) was comparable to other studies: Edwards & Gabriel (1998): 0.25–0.39 (mean 0.314), Höfer & Ott (2009): 0.12–0.29 (mean 0.21) in spiders from southern Brazil and 0.24–0.34 (mean 0.29) in spiders from Amazonia. The preservation of spider specimens in 75% ethanol for one

year did not significantly alter body length in this study, although there was a trend towards shrinking. This could become relevant over longer periods of preservation time (Greenstone et al. 1985; Edwards 1996; Simmons 2014), but the bias should not be large and does not matter when comparing specimens sampled and measured at the same time. Anticipating that the soft-skinned opisthosoma is more affected by shrinking or swelling than the strongly chitinized prosoma, regressions based on carapace measures could be applied when using long term conserved material.

Biomass is a good proxy for metabolic rate, food requirement, competitiveness etc., and in the case of spiders as predators also for the impact on prey populations and possibly the carrying capacity (Seidl & Tisdell 1999) of an ecosystem. We therefore suggest our regression parameters as useful for estimating the biomass of spider assemblages in Germany, probably also for the Central European or even Palearctic fauna. Their usefulness for specific questions and precision levels can easily be tested and confirmed, weighing and measuring few specimens from the population, environment or region under study. The slopes of our regressions can also be used to estimate fitness through body condition indices involving size and mass measurements (see Jakob et al. 1996 and following discussion in Kotiaho 1999 and Marshall et al. 1999).

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Manuscript received 19 June 2017, revised 12 April 2018.