

## Estimating biomass of Neotropical spiders and other arachnids (Araneae, Opiliones, Pseudoscorpiones, Ricinulei) by mass-length regressions

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**Abstract.** We sampled 505 specimens of 7 arachnid orders (313 Araneae, 65 Opiliones, 111 Pseudoscorpiones, 10 Ricinulei, 3 Schizomida, 1 Thelyphonida, 2 Scorpiones) in natural forest and agroforestry sites in central Amazonia to analyze fresh and dry mass to body length relations. The low number of schizomids, scorpions, and thelyphonids did not allow statistical analyses, but the raw data are given, because these represent the first data published for these groups from Amazonia. For all other orders general mass-length relationships for ecological studies were determined. Non-linear regressions with a power model proved to describe the relations very well and are highly significant for all taxa and groups analyzed. The resulting equations can thus be used to estimate biomass of large samples of arachnids from Amazonia based on individual body length measurements. Linear regressions of mass to length with log-transformed data also described the relation adequately, but using the resulting equations to estimate biomass of the whole spider sample caused a higher bias. This is because small biases of mass-length relation of the largest spider individuals are exponentiated. However, linear regressions behaved better for spiders smaller than 8 mm. The ratio of dry to fresh mass was around 0.3 for spiders; 0.4 for pseudoscorpions, schizomids, and thelyphonids; 0.44 for opilionids; and 0.53 for Ricinulei. A second sample of 99 spiders from a South Brazilian Atlantic Forest revealed similar mass-length relations, but a different dry to fresh mass ratio. For spiders, the usefulness of general equations to determine the biomass of bulk samples from ecological studies with certain precision requirements was further explored by using the equations from the two datasets crosswise, regarding the resulting bias and by applying equations to a further dataset from an ecological investigation. In conclusion and accordance to former studies, general equations derived from mass-length regressions of bulk samples including many specimens of different families and guilds are appropriate for an estimation of the biomass of bulk samples from ecological studies. Equations from mass-length regressions from the literature, resulting from spider samples in temperate regions, should not be used to estimate biomass of samples from neotropical spider assemblages, especially when absolute biomass is of interest and when precision is required. They underestimate biomass of tropical assemblages due to a strong bias in mass-length relation of tropical spiders larger than 10 mm. Depending on the distribution of large spiders in samples, considerable biases in single samples could affect ecological analyses.

**Resumo.** Analisamos as relações entre comprimento corporal e massa fresca e seca de 505 espécimes de sete ordens de aracnídeos (313 Araneae, 65 Opiliones, 111 Pseudoscorpiones, 10 Ricinulei, 3 Schizomida, 1 Thelyphonida, 2 Scorpiones) coletados em florestas e agroflorestas na Amazônia Central. Devido ao número baixo de Schizomida, Scorpiones e Thelyphonida nenhuma análise estatística foi possível e os dados brutos são apresentados a serem os primeiros dados publicados destes grupos para a Amazônia. Para as outras ordens análises de regressão foram feitas. Regressões não-lineares de modelo potencial demonstraram excelente descrição para as relações, sendo altamente significativas para os táxons e grupos analisados. Os coeficientes obtidos nestas regressões poderão servir de base para o cálculo de biomassa em amostras da Região Amazônica que contenham grande número de aracnídeos, utilizando-se como medida somente o comprimento total de cada indivíduo. Utilizando-se dados logaritmicamente transformados, regressões lineares de massa-comprimento também descreveram adequadamente a relação. Todavia a utilização destes coeficientes, para estimar exclusivamente a biomassa da amostra total de aranhas, apresentou resultados tendenciosos em função do efeito forte da relação exponencial a desvios pequenos em aranhas de grande porte. Regressões lineares apresentaram um comportamento estatístico mais favorável apenas para aranhas com menos de 8 mm de comprimento corporal. A relação obtida para massa seca em relação à massa fresca foi de cerca de 0.3 para aranhas, cerca de 0.4 para Pseudoscorpiones, Schizomida e Thelyphonida, 0.44 para Opiliones e 0.53 para Ricinulei. Uma segunda amostragem de 99 aranhas na região meridional da Mata Atlântica brasileira revelou relações de massa-comprimento similares, porém, com uma relação diferenciada de massa seca à massa fresca. Para a ordem de aranhas a utilidade de equações gerais para a determinação da biomassa de amostras ecológicas com devida precisão foi analisada aplicando coeficientes resultando de amostragens de outras regiões. Concluímos que coeficientes de regressões de massa-comprimento são apropriados para uso em relação à assembléia inteira de aracnídeos, desde que as amostras contenham espécimes de várias famílias e guildas diferentes. Os coeficientes obtidos na regressão da grande amostragem da Região Amazônica podem ser usadas para a assembléias de aranhas da Mata Atlântica, porém não e aconselhável uso recíproco, mais especificamente para estimativas de massa seca. A utilização de coeficientes de regressões de massa-comprimento disponíveis atualmente na literatura, resultante de amostragens em regiões temperadas, deveria ser evitada para a estimativa de biomassa em amostras de assembléias de aranhas neotropicais. Estes coeficientes subestimam a biomassa de assembléias tropicais devido a uma grande distorção na relação entre massa e comprimento corporal em aranhas maiores do que 10 mm. Desta maneira análises ecológicas podem ser altamente influenciadas pela distribuição de grandes aranhas entre as amostras individuais com distorção dos resultados.

**Keywords:** Arachnida, mass-length relationship, Brazil

Biomass data (in the sense of the weight of living animals per unit area, Bornebusch 1930; Edwards 1966) for arthropods are needed in many ecological studies, especially when these aim to analyze the role and functions of these abundant animals in ecosystems and food webs. Biomass of soil fauna is of special interest in studies of nutrient cycling involving the role of the fauna in decomposition and organic matter transformation. The importance of soil fauna has long been recognized and their function is also being studied more frequently in Neotropical ecosystems (Lavelle et al. 1997, 2001; Barros et al. 2003, 2006; Mathieu et al. 2004). The context in which we needed to estimate biomass of arachnids and other arthropods was given by two projects in the Brazilian-German research programme SHIFT (Studies on Human Impact on Forests and Floodplains in the Tropics) studying the quantitative contribution of soil fauna to decomposition in central Amazonian natural forests and different agroforestry systems (Höfer et al. 2001; Hanagarth et al. 2004; Martius et al. 2004; Brown et al. 2006).

Biomass can be obtained by direct weighing of individual living arthropods with analytical balances, but this is a very time consuming task and for very active animals it is difficult or impossible to obtain precise data. Certainly direct weighing is not a practical method in the field and for larger samples in laboratories. Most specimens in ecological studies are trapped and killed in fluids such as ethanol and it is difficult to measure preserved animals on a balance. Also, weighing fresh weight of preserved animals may provide incorrect estimations as body weight may be altered during preservation. For most studies dry mass is easier to obtain, but drying specimens or bulk samples to a constant weight, usually at 65° C or more, makes it impossible to later identify them due to their fragility. An alternative method is to use statistically verified relationships of mass with easily measurable body dimensions, such as body length or width, to estimate the biomass of each specimen. Body length might even be measured in the field or estimated with live animals so animals may not even need to be collected. Regressions using a power model (mass = a (size)<sup>b</sup>) usually adequately describe mass-length-relations for most arthropods (Rogers et al. 1976, 1977; Schoener 1980; Sample et al. 1993; Edwards 1996). They have also been shown to provide useful data for spiders from temperate regions (Brey Meyer 1967; Norberg 1978; Clausen 1983; Edwards 1996; Henschel et al. 1996a; Lang et al. 1997; Edwards & Gabriel 1998). Spiders and to a lesser extent other arachnids (opilionids, pseudoscorpions) are abundant in all terrestrial environments and are often included in functional ecological studies due to their well defined position in the food web as (arthropod) predators and their usefulness to indicate habitat quality (Jocqué 1981; Chen & Wise 1999; Wise et al. 1999; Lawrence & Wise 2000, 2004; Wise 2004). As Henschel et al. (1996a) state, it is useful and possible to use general equations for arachnid orders (e.g., spiders and opilionids) to estimate the biomass of single specimens for the whole assemblage, notwithstanding the different species-specific mass-length relationships. They suggest their equations are valid for other regions and habitats in Europe, at least for community studies involving numerous families, genera and species.

Our main interest was to derive an equation for a general relationship to estimate biomass of bulk samples to compare

soil fauna biomass at different sites in tropical South America. Thus we sampled 505 specimens of spiders and other arachnids from one location in central Amazonia and analyzed mass-length relations of this large collection (first data set) in order to obtain valid equations for the biomass estimates we needed for our studies of Amazonian forest and agroforestry systems. We tested whether these equations reliably estimated biomass of bulk samples of spiders or if different equations were necessary for different functional groups (e.g., wandering versus web building spiders), size classes (tiny spiderlings versus large mygalomorphs), or spiders with an extraordinary body shape (like *Micrathena* or *Deinopis*).

A second sample of spiders (second data set) was obtained from another region and large scale forest ecosystem of Brazil, e.g., in the southern part of the Brazilian Atlantic Forest (Mata Atlântica) and analyzed in the same way. Having two large data sets on spiders at hand and given the numerous data for this arachnid order in the literature, we explored the usefulness and limitations of general equations to determine the biomass of bulk samples from ecological studies with the required precision. This was done in three steps: 1. Determining which biases would be introduced when using equations from outside the Neotropical region for the Amazonian sample; 2. Determining the bias introduced by using the equations from the first data set (Amazonia) for the second data set (Atlantic Forest) and vice versa; 3. Determining the bias introduced by applying different equations for data from one ecological study in Amazonia and one ecological study in the Atlantic forest (application data sets) and looking for an effect of the bias on the conclusions of these studies.

## METHODS

Mass-length relations were analyzed using specimens sampled in primary and secondary forests and tree plantations within the area of the Brazilian Agricultural Research Corporation EMBRAPA in central Amazonia near Manaus (02°53'47"S, 59°59'45"W) (first data set). Sampling took place in May 1999 with the aim to obtain as many differently sized and shaped specimens from as many taxa as possible. Specimens were captured alive by hand and stored individually in vials during transport to the laboratory. They were killed by freezing for about one hour and then weighed to obtain fresh mass to the nearest 0.001 mg with a Sartorius MP2 microbalance. Body length, in dorsal view from the anterior edge of the prosoma (excluding chelicerae) to the posterior edge of the opisthosoma (excluding spinnerets), was measured with a graduated eyepiece to the nearest 0.01 mm. Numbers of specimens measured for each order and lower taxonomic levels are given in Table 1 (first data set). Lastly specimens were oven-dried for 24 h at 105° C, cooled to room temperature, and weighed to obtain dry mass. Only three of the ten Ricinulei specimens were dried because of their rarity in museum collections. The resulting ratio dry/fresh mass for these specimens was used to calculate the dry mass for the seven other specimens. From three other arachnid orders too few specimens were caught to calculate regressions (Schizomida: 3, Thelyphonida: 1, Scorpiones: 2). Results are presented in Tables 1, 2 and in Figure 3.

A second data set including 99 spiders from a South Brazilian Atlantic Forest (Mata Atlântica) (Reserva do

Table 1.—Number of specimens measured and weighed for length-mass regression, mean and range of body length (minimum and maximum in brackets) from seven arachnid orders.

Order/Infraorder/Family	First data set (Amazonia)		Second data set (Mata Atlântica)	
	Specimens	Length (mm)	Specimens	Length (mm)
Araneae	313	4.83 (0.56–36.0)	99	7.08 (1.35–28.0)
Infraorder Mygalomorphae	43	3.17 (0.78–19.1)		
Infraorder Araneomorphae:				
Amaurobiidae	1		1	8.27
Anapidae	1	1.07		
Anyphaenidae			2	6.87 (6.83–6.92)
Araneidae	8	1.89 (0.81–3.40)	18	5.77 (2.69–10.67)
Corinnidae	11	5.85 (1.85–13.9)	2	4.57 (4.52–4.62)
Ctenidae	74	12.43 (1.30–36.0)	18	16.52 (4.23–28.0)
Deinopidae			1	16.50
Linyphiidae	9	1.60 (1.20–1.90)	1	2.30
Lycosidae			2	16.85 (7.69–26.0)
Mysmenidae			3	1.73 (1.35–2.40)
Ochyroceratidae	24	1.40 (0.56–2.40)	1	1.83
Oecobiidae	2	1.75 (1.70–1.80)		
Oonopidae	68	1.46 (0.67–2.50)	1	2.31
Palpimanidae	4	3.04 (1.52–4.00)		
Pholcidae	8	2.00 (1.07–4.30)	6	2.79 (1.92–3.94)
Pisauridae	2	4.67 (3.96–5.40)	1	4.61
Salticidae	39	3.40 (1.12–6.60)	4	4.86 (3.65–5.77)
Scytodidae	5	2.57 (1.60–3.10)		
Selenopidae			1	5.00
Sparassidae	3	6.00 (5.90–6.10)	2	5.58 (3.56–7.60)
Tetragnathidae			2	5.86 (4.33–7.40)
Theridiidae	5	1.33 (1.00–2.00)	20	3.02 (1.63–10.0)
Theridiosomatidae	3	0.75 (0.62–0.83)	3	1.91 (1.49–2.69)
Thomisidae			1	7.60
Trechaleidae			3	12.53 (5.29–25.0)
Uloboridae			1	5.38
Zodariidae	4	3.60 (2.00–4.50)		
Zoridae			4	4.23 (3.85–4.81)
Opiliones	65	2.12 (0.57–6.90)		
Pseudoscorpiones	111	1.38 (0.86–2.10)		
Ricinulei	10	4.46 (2.10–5.60)		
Schizomida	3	1.62 (1.45–1.88)		
Scorpiones	2	16.30 (3.60–29.0)		
Thelyphonida	1	7.00		

Cachoeira, Antonina, Paraná: 25°25'S, 48°40'W) was obtained in 2007. Spiders (Table 1) were sampled manually at night and during the day along trails in secondary forests. Weighing and measuring procedures were the same as described above.

Tests for the effects of the bias from different equations were done with two application data sets: one from Amazonia, where spiders were sampled from 16 replicate sites of each of 7 different plantation systems (EMBRAPA central Amazonia) by means of large soil cores; and one from the Atlantic Forest, where 10 litter samples (1 m<sup>2</sup>) were taken in each of three different regeneration stages of a sub-mountain forest (Schmidt et al. 2008). From both collections all spider specimens ( $n = 441$  and  $276$ ) were individually measured (body length), so that coefficients from different regression equations could be applied to estimate the total biomass per site. Data were analyzed with Statistica 7.1 (StatSoft 2005) and graphs prepared with SigmaPlot® 8.0.2 (SPSS 2002).

## RESULTS

**Analyses of mass-length relations.**—Mass-length relationships (for both fresh and dry mass) for the arachnid orders with enough specimens sampled in the Amazonian habitats (first data set) are very well correlated with a regression model of the non-linear (power) form:  $\text{mass} = a (\text{length})^b$ . Determination coefficients are usually  $> 0.9$  (Tables 3, 4) and type I error probabilities are very low ( $< 0.001$ ) for both parameters, with the exception of the rare Ricinulei ( $n = 10$ ,  $P = 0.15$  for coefficient  $a$ ).

The mass-length relationship is almost equally well described with a linear model using logarithmic data for length and weight ( $\ln(\text{mass}) = a + b \ln(\text{length})$ ). Note that power regression results are often presented in double-logarithmic plots, but the model parameters are not the same for a power model calculated on raw data and a linear model calculated on log-transformed data. In our dataset the linear model represents the most abundant small spiders better because

Table 2.—Ratios dry/fresh mass for arachnid orders.

Order		Ratio dry/fresh mass	
Family	Guild	First data set (Amazonia)	Second data set (Mata Atlântica)
Araneae		0.29	0.21
Mygalomorphae	hunting	0.29	
Araneomorphae			
Anyphaenidae	hunting		0.25
Amaurobiidae	hunting		0.12
Corinnidae	hunting	0.29	0.27
Ctenidae	hunting	0.26	0.19
Lycosidae	hunting		0.19
Oonopidae	hunting	0.34	0.19
Oxyopidae	hunting		0.24
Palpimanidae	hunting	0.32	
Pisauridae	hunting	0.28	0.22
Salticidae	hunting	0.28	0.21
Scytodidae	hunters	0.29	
Selenopidae	hunting		0.16
Sparassidae	hunting	0.26	0.19
Thomisidae	hunting		0.18
Trechaleidae	hunting		0.20
Zodariidae	hunting	0.34	
Zoridae	hunting		0.20
Anapidae	web-building	0.24	
Araneidae	web-building	0.25	0.22
Deinopidae	web-building		0.16
Linyphiidae	web-building	0.33	0.19
Mysmenidae	web-building		0.20
Ochyroceratidae	web-building	0.31	0.19
Oecobiidae	web-building	0.29	
Pholcidae	web-building	0.27	0.20
Tetragnathidae	web-building		0.29
Theridiidae	web-building	0.28	0.21
Theridiosomatidae	web-building	0.29	0.18
Uloboridae	web-building		0.18
Opiliones		0.41	
Pseudoscorpiones		0.38	
Ricinulei		0.53	
Schizomida		0.37	
Scorpiones		0.30	
Thelyphonida		0.39	

Table 3.—Regression coefficients (a, b) and coefficient of determination in regressions of fresh mass to body length (left: power model: mass [mg] = a body length [mm]<sup>b</sup>, right: linear model:  $ln$  mass [mg] = a +  $ln$  body length [mm] b) for arachnids from Amazonia (first data set) and Mata Atlântica (second data set) ( $n$  = sample size, se = standard error,  $R^2$  = coefficient of determination). All regressions are highly significant ( $P < 0.001$ ).

	Power model				Linear model		
	$n$	a ± se	b ± se	$R^2$	a ± se	b ± se	$R^2$
Mata Atlântica: all Araneae	99	0.066 ± 0.025	3.160 ± 0.118	0.98	- 2.166 ± 0.175	2.872 ± 0.097	0.90
Amazonia: all Araneae	313	0.169 ± 0.009	2.899 ± 0.016	0.99	- 2.058 ± 0.029	2.980 ± 0.020	0.99
Araneae < 2.5 mm	225	0.085 ± 0.010	3.288 ± 0.081	0.94	- 1.958 ± 0.037	2.746 ± 0.053	0.92
Ctenidae	74	0.177 ± 0.020	2.886 ± 0.034	0.99	- 1.758 ± 0.096	2.894 ± 0.039	0.99
Oonopidae	68	0.131 ± 0.007	2.682 ± 0.076	0.94	- 2.039 ± 0.042	2.666 ± 0.099	0.96
Hunting spiders	253	0.169 ± 0.010	2.899 ± 0.018	0.99	- 2.108 ± 0.023	3.017 ± 0.015	0.99
Web-building	60	0.072 ± 0.011	3.710 ± 0.114	0.97	- 1.784 ± 0.092	2.255 ± 0.169	0.75
Opiliones	65	0.147 ± 0.028	3.622 ± 0.105	0.98	- 0.899 ± 0.048	2.984 ± 0.060	0.97
Pseudoscorpiones	111	0.156 ± 0.006	2.453 ± 0.071	0.92	- 1.892 ± 0.027	2.515 ± 0.073	0.91
Ricinulei	10	0.225 ± 0.146	2.760 ± 0.387	0.93	- 1.907 ± 0.192	3.014 ± 0.130	0.98

Table 4.—Regression coefficients (a, b) and coefficient of determination in regressions of dry mass to body length (left: power model: mass [mg] = a body length [mm]<sup>b</sup>, right: linear model:  $\ln$  mass [mg] = a +  $\ln$  body length [mm] b) for arachnids from Amazonia (first data set) and Mata Atlântica (second data set) ( $n$  = sample size, se = standard error,  $R^2$  = coefficient of determination). All regressions are highly significant ( $P < 0.001$ ).

	Power model				Linear model		
	$n$	a $\pm$ se	b $\pm$ se	$R^2$	a $\pm$ se	b $\pm$ se	$R^2$
Mata Atlântica: all Araneae	99	0.0067 $\pm$ 0.005	3.413 $\pm$ 0.245	0.96	- 3.860 $\pm$ 0.224	2.950 $\pm$ 0.092	0.93
Amazonia: all Araneae	313	0.0165 $\pm$ 0.001	3.242 $\pm$ 0.014	0.99	- 3.213 $\pm$ 0.029	2.902 $\pm$ 0.021	0.98
Araneae < 2.5 mm	225	0.028 $\pm$ 0.003	3.180 $\pm$ 0.079	0.94	- 3.121 $\pm$ 0.038	2.680 $\pm$ 0.054	0.92
Ctenidae	74	0.017 $\pm$ 0.002	3.232 $\pm$ 0.029	0.99	- 3.197 $\pm$ 0.096	2.921 $\pm$ 0.039	0.99
Oonopidae	68	0.050 $\pm$ 0.003	2.459 $\pm$ 0.094	0.90	- 3.162 $\pm$ 0.046	2.767 $\pm$ 0.108	0.95
Hunting spiders	253	0.0165 $\pm$ 0.001	3.242 $\pm$ 0.016	0.99	- 3.237 $\pm$ 0.025	2.926 $\pm$ 0.016	0.99
Web-building	60	0.017 $\pm$ 0.003	3.881 $\pm$ 0.123	0.97	- 2.997 $\pm$ 0.093	2.199 $\pm$ 0.172	0.74
Opiliones	65	0.042 $\pm$ 0.009	3.879 $\pm$ 0.119	0.98	- 1.862 $\pm$ 0.049	3.069 $\pm$ 0.062	0.97
Pseudoscorpiones	111	0.057 $\pm$ 0.003	2.589 $\pm$ 0.103	0.86	- 2.967 $\pm$ 0.037	2.771 $\pm$ 0.100	0.87

the few large spiders have a very high influence in the power model (Fig. 1). However the fresh biomass of the whole sample (313 spiders) with a mean length of 4.83 mm when estimated with the power model was closer to the observed biomass (99.8%) as when estimated with the linear model (95.7%). The same is true for dry mass estimation (power: 97.6%, linear: 86.9% of observed mass). Because different bulk samples might predominantly consist of either small or large spiders, often influenced by the sampling method, it might be useful to use either the linear model or the power model. In some cases it might even be useful to split a sample by size and use the linear model for spiders < 8 mm and the power model

for spiders > 8 mm. Therefore, we present the coefficients of both models (Tables 3, 4).

The 313 Amazonian spiders that were measured and weighed represent a large spectrum in terms of size, shape, and taxonomic and functional groups. This dataset includes tiny orb-weavers like Theridiosomatidae and Anapidae; tiny, but long-legged Ochyroceratidae; tiny, but short-legged wandering spiders like Oonopidae; median-sized jumping spiders; very small to large mygalomorphs; large ctenid hunters; as well as large, long-legged pholcids (Table 1). Very few spider specimens (the smallest spider an ochyroceratid, one ctenid, and most of the long-legged ochyroceratids) lay

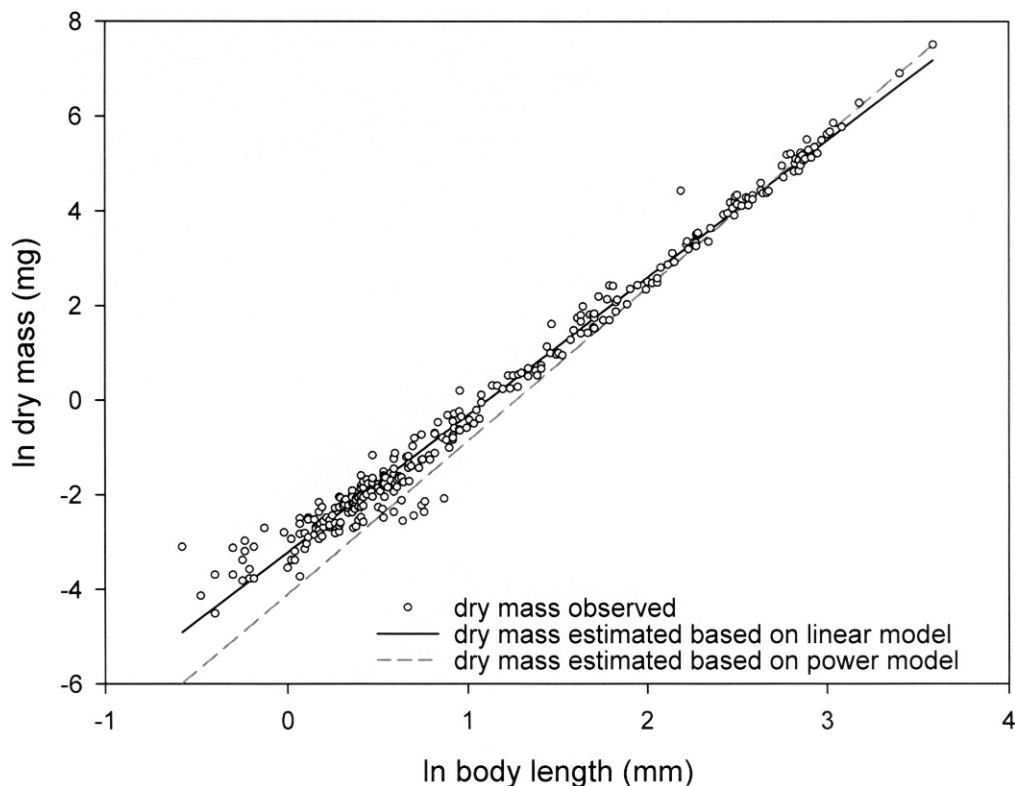


Figure 1.— $\ln$ - $\ln$  plot of dry mass (mg) vs. body length (mm) relationship of spiders in the first data set from Amazonia, showing the bias of a power model regression for small spiders as compared to a linear model regression with a bias for large spiders.

outside the 95% confidence limits of our regressions and their exclusion did not lead to considerable changes in the model parameters.

Nevertheless we calculated separate regressions for small spiders, the families Ctenidae and Oonopidae, the main hunting (or wandering) guilds; and web-building spiders because these groups might be of special interest in ecological studies (see also below); and because they always received high determination coefficients and significances (Tables 3, 4).

The strong correlations in some cases caused very high PRESS values ( $> 30,000$  for fresh mass and  $> 500,000$  for dry mass vs. length of spiders). The PRESS value (Predicted Residual Error Sum of Squares) is a gauge of how well a regression model predicts new data and often a hint to overfitting of a dataset, resulting in decreased usefulness for other datasets. To test this, we split the whole Amazonian data set by a random procedure in one learn- and one test dataset (cross-validation). For both fresh mass and dry mass the regression line of the test dataset was well inside the 95% confidence limits of the learn dataset. This shows that the strong correlation is not a result of overfitting and consequently the resulting formulae should be useful for an estimation of fresh or dry mass of bulk spider samples from the same region (central Amazonia).

The other three orders (Opiliones, Pseudoscorpiones, Ricinulei) for which regression analyses were possible were much more uniform in size and shape (Table 1). Power and linear models performed equally well and the coefficients are presented in Tables 3, 4. Mass-length relationships of these orders and also the single specimens of Schizomida, Scorpiones, and Thelyphonida are presented in Figure 3.

The mass-length regressions for spiders collected in the Mata Atlântica (second data set) were also strongly correlated and highly significant, but coefficients were slightly different (Tables 3, 4). Only one subadult deinopid and a twig-like *Argyrodes* specimen lay outside the 95% confidence limits, but they did not influence the coefficients of the power model, which produced very good estimates of fresh and dry mass (99.5% of observed value) for the whole sample. The linear model in contrast produced a considerable underestimate of fresh and dry mass (70.2% resp. 73.4%).

**Ratio dry/fresh mass.**—Fresh mass and dry mass of spiders were strongly correlated ( $R^2 = 0.99$ ,  $P < 0.001$ ) in both data sets; the ratio dry/fresh mass was on average  $0.293 \pm 0.055$  for Amazonian spiders and  $0.208 \pm 0.06$  for spiders from the Atlantic forest. There was no significant difference in ratios for the two main hunting and web-building spider guilds ( $t$ -test  $P = 0.4$ ). Anapids (tiny orb weavers) show the smallest ratio (0.24), oonopids and zodariids (small hunters, mostly strongly chitinized) the highest ratio (0.34) (Table 2). The highest variation of dry/fresh mass ratio occurred in the lowest range of body size, which is considered an effect of the decreasing precision of both length and weight measurements with decreasing size of the spiders. There was no correlation between length and the ratio dry/fresh mass.

The ratio dry/fresh for opilionids was  $0.44 \pm 0.06$  and for pseudoscorpions  $0.38 \pm 0.06$ . Both correlations are strong ( $R^2 > 0.95$ ) and highly significant ( $P < 0.01$ ). Mean ratio dry/fresh for the three ricinuleid specimens was 0.53, and for the other arachnids between 0.30 and 0.39 (Table 2).

**General usefulness of equations.**—Regarding the statistics of mass-length relationships, one certainly gets good estimates of biomass by length measurements for the Amazonian fauna using the coefficients from our equations. But how large would be the bias when using coefficients from other samples for our data or our coefficients for other data?

When using coefficients derived from spider samples from temperate regions (taken from the literature) the estimate of the total biomass of our sample of 313 spiders produced serious biases from the observed mass: 56% (fresh) and 58% (dry mass) with coefficients from the linear model of Edwards & Gabriel (1998; spiders from Massachusetts, USA); 43% (dry mass) with coefficients from the power model of Breymer (1967; spiders from Europe); 25% (dry mass) using the coefficients from the power model of Henschel et al. (1996a; spiders from Germany); 23% (fresh mass) from the power model of Norberg (1978; spiders from spruce in Sweden). These strong biases are caused by the relatively high number of spiders with a length over 12 mm (e.g., Ctenidae) and some very large individuals (24–36 mm) in our samples and the underestimation of these large spiders by formulae from temperate spider faunas (Fig. 2), which only represent spiders up to a length of 10 mm (Henschel et al. 1996a) or 8 mm (Norberg 1978). The equation of Rogers et al. (1977) from spiders (0.7–12 mm) collected from a shrub-steppe in south-central Washington suited our data set better (105% of observed dry mass).

To answer the question whether our equations are generally applicable to samples from spider assemblages in the Neotropics we tested our Amazonian equation on a spider sample (second data set) from another forest Brazilian ecosystem (Mata Atlântica) situated further south, geographically in the subtropics, and vice versa. When applying the Amazonian coefficients, the fresh biomass of the Atlantic Forest spiders was relatively well estimated (113% with power model, 110% with linear model), but the dry mass estimate was considerably overestimated (143% and 121%). This is most probably caused by the lower ratio dry/fresh mass (0.21) for the spiders sampled in the Atlantic Forest in comparison with the spiders from Amazonia (0.29) (Table 2). When using the coefficients from the Mata Atlântica data set for the Amazonian data set the following biases (underestimation) resulted for fresh respectively dry mass: 84.5% / 66.4% by power, 62.6% / 52.4% by linear model.

To obtain an idea of the effect of such biases we used one application data set from Amazonia. Fig. 4 shows box plots with means, medians and variances (percentiles) of spider biomass samples from different plantation systems, calculated with different coefficients. For most (5) systems the biomass of spiders per plot estimated with the equation from Henschel et al. (1996a) was higher than the biomass calculated with our own coefficients and showed comparable relations between medians and means and similar variance. This is due to overestimation of the dominant small spiders ( $< 4$  mm) by the Henschel equation (s.a.). In each of the systems 4 and 6, however, one larger spider (8 mm) was sampled, and these are underestimated by the Henschel equation. In consequence, for these two systems the relative position of the means change depending on the equation used. However, due to the generally high variance of spider abundance between the

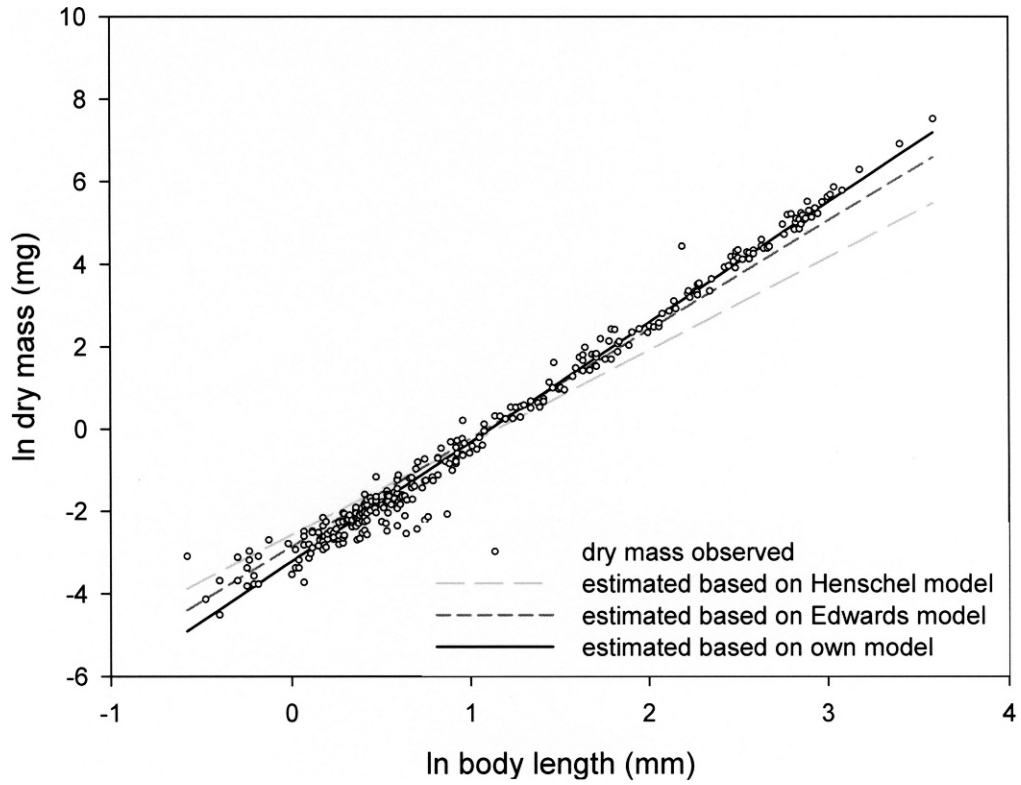


Figure 2.—*Ln-ln* plot of dry mass (mg) vs. body length (mm) relationship of spiders in the first data set from Amazonia, showing the bias when using regression coefficients (a, b) from the literature (all linear models).

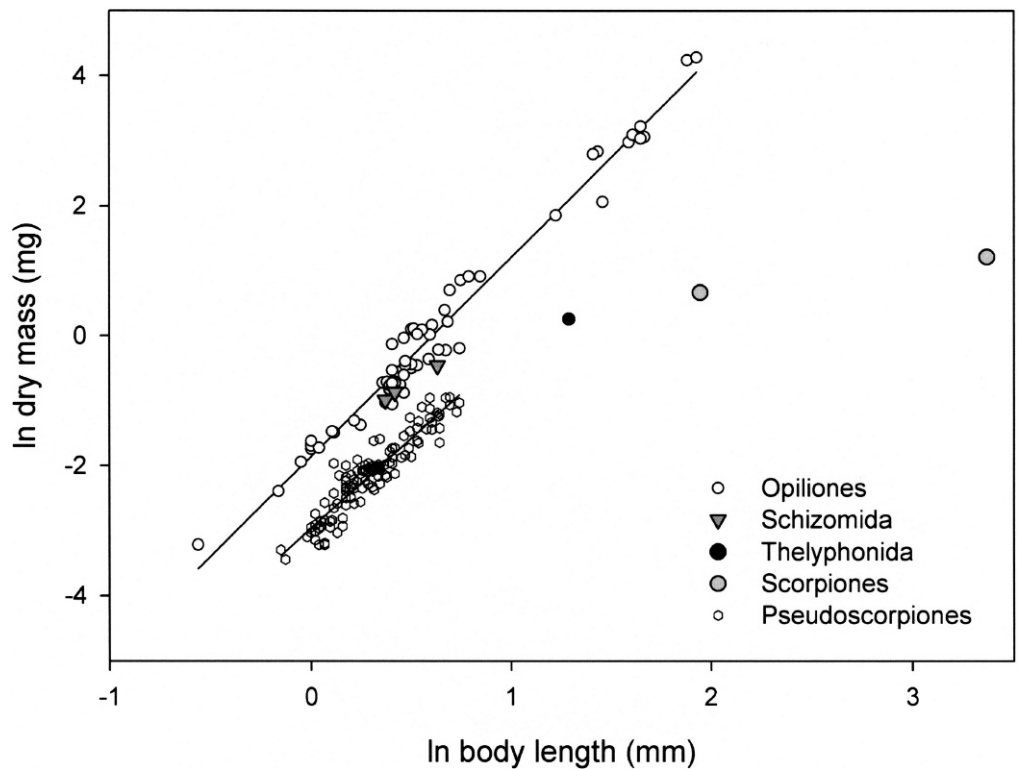


Figure 3.—*Ln-ln* plot of dry mass (mg) vs. body length (mm) relationship for other arachnid orders from Amazonia (regression lines for opilionids and pseudoscorpions from linear models).

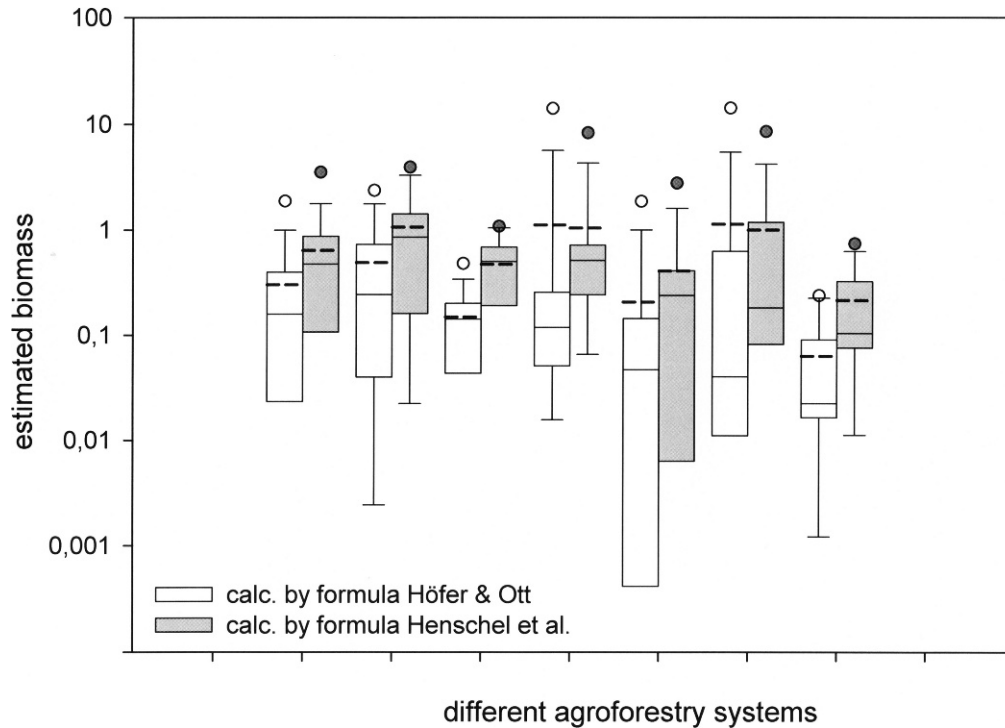


Figure 4.—Estimated total biomass of spiders in samples from seven different agroforestry systems in Amazonia (application data set), showing biases caused by applying regression coefficients originating from a data set from a temperate region in comparison with the coefficients originating from the first (Amazonian) data set. Box plots show the median (thin line), the mean (thick broken line), 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers) and outliers (circles).

replicates there are no significant differences between the systems, no matter if tested on means (ANOVA) or ranks (Kruskall-Wallis) and by both equations.

We also applied the coefficients derived from the Amazonian data set in comparison with the coefficients derived from the Atlantic Forest data set to a second application data set: 30 litter samples taken in three different regeneration stages of an Atlantic sub-mountain forest (Schmidt et al. in press). Mean dry mass values of spiders calculated by the Amazonian formula were 2.8, 5.3, 14.4 mg m<sup>-2</sup> and calculated by the Atlantic forest formula 1.5, 2.9, 8.6 mg m<sup>-2</sup>. Biomass values were significantly different (overestimated by the Amazonian formula, paired *t*-test  $P < 0.01$ ), but ANOVA for the effects of the regeneration stage on biomass gave no significant effect.

#### DISCUSSION

Mass-length regressions are a formidable solution for estimating biomass without having to destroy the specimens or handle them tediously on a microbalance, which is time-consuming and expensive. Literature and our investigation show clearly that this can be made with one measurement of body length, which can be precisely taken with a micrometer eyepiece or a vernier caliper, even for live arthropods. In view of the very high determination coefficients and very low error probabilities, power regressions of length to estimate fresh or dry mass absolutely satisfy the needs, and no further effort is necessary to estimate volume by measurements of several body dimensions. A model should also not be overfitted (see below) since it would lose its applicability to new datasets.

As mass is expected to be proportional to length cubed, in regression formulae the power (*b*) in a uniformly proportioned series of animals is expected to be close to 3. The fresh mass of spiders generally followed this relation, whereas dry mass of spiders and fresh and dry mass of opilionids increased with a power greater than 3. For pseudoscorpions, ricinuleids, and the oonopid spiders the power was less than 3. Schoener (1980) explained a power smaller than 3 for insects by a trend of longer species tending to be thinner. For our data set we suppose this to be due to different body densities (mass per volume), because all three groups represent more strongly chitinized rather than thinner animals in comparison to the other groups.

When the aim is to estimate the biomass of bulk samples including many different spider species of different sizes and shapes, one formula can be used for all spiders, although a few very extraordinary shapes (e.g., very long and thin like some *Argyrodes* or *Deinopis*) may lie outside acceptable confidence limits. Especially for tropical soil fauna communities where most specimens are not readily identifiable, often not even to genus or family level, it is desirable, if not necessary, to have one regression equation covering the taxonomic level to which the organisms can be identified (sorted) easily, which most often is the order level for arthropods (Schoener 1980; Sample et al. 1993; Henschel et al. 1996b).

Although not appearing very different, the coefficients given by other authors for estimation of spider biomass from length measurements when applied to our data produced slightly different values for single specimens, which result in consid-



erable biases for bulk samples. The adequate precision of a single mass-length regression depends upon the scientific question, and especially the variance included in the data set (e.g., how many different taxa with different body shapes were included and how strong the abundances vary in reality and in samples). As more mass-length relations of different specimens/species are included, the coefficient of determination  $R^2$  gets smaller, but unless it remains large enough to explain a considerable portion of the variation ( $> 0.8$ ) and as long as the probability of being wrong in concluding that the coefficient is not zero remains small ( $P < 0.05$ ), the regression model gains in predictability.

In community ecology data sets, the variances in invertebrate abundance between different samples and study sites are usually high (standard deviation  $> 100\%$  of the mean) and thus precision of regression factors to calculate the biomass of groups of the community must not be very high, thus allowing relatively fast and rough measures. However, a systematic bias towards certain samples should be avoided. The comparison of the coefficients extracted from the two different models fitting our own data has already shown a possible cause for such a bias: a different proportion of very small or very large spiders in different samples treated with the same equation. In our tests, bias due to the “wrong” equation used for an estimation of biomass did not produce different ecological results. If no equation for the spider assemblage of interest is available, coefficients from an equation based on samples from other regions can be used if the size distributions do not differ strongly, which is obviously the case comparing spider assemblages from temperate and tropical regions. Attention must be given to individual, very large spiders in a sample, which in addition to its already problematic outlier position can produce a king-size bias due to the power effect of the regression. But this should be resolved by statistical procedures in the ecological study.

We have shown that it is difficult if not impossible to estimate biomass from different studies (regions) using the same equation and compare the absolute values. Even within the Neotropical rainforest realm, considerable bias can result from the estimation with non-autochthonous coefficients.

We conclude from our results that our equations from the Amazonian sample are useful for biomass estimation of bulk arachnid samples from ecological studies in Amazonian rainforests and, with some restrictions, also for other neotropical forest spider assemblages. As these are often rich in species, which are represented by several developmental stages, it is valuable to have an idea of the distribution of size classes in the samples. If a wide range of sizes is represented, including spiders larger than 15 mm, the coefficients of the power functions should be used. If only smaller spiders were collected, which is often the case in soil or litter samples, the coefficients of the linear models would be more adequate or the equation resulting from the subsample of spiders  $< 2.5$  mm should be used. We also present the coefficients for specific (abundant) taxa (ctenids, oonopids) and the guilds of hunting and web-building spiders, which can be used in studies of these specific groups.

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