

Body weight distributions of European Hymenoptera

Werner Ulrich

Ulrich, W. 2006. Body weight distributions of European Hymenoptera. – *Oikos* 114: 518–528.

Species number–body weight distributions are generally thought to be skewed to the right. Hence it is assumed that the number of relatively small species is larger than the number of relatively large species. While this pattern is well documented in vertebrates, comparative studies on larger invertebrate taxa are still scarce. Here I show that the weight distributions of European Hymenoptera (based on 12 601 species body weight data compiled from major catalogues) do not exhibit a general trend towards right skewed species–body weight distributions. Skewness did not depend on the number of species per taxon. Species richness peaked at intermediate body weights irrespective of taxonomic level. Kernel density analysis revealed that hymenopteran taxa had between one and four peaks in their size distributions with larger taxa having fewer peaks. Within genus variability in body weight was allometrically related to mean body weight ($\sigma^2 = \mu^{1.81}$) in line with a proportional rescaling pattern. These results call for a rethinking about the generality of current vertebrate centred models of body size evolution.

W. Ulrich, Dept of Animal Ecology, Nicolaus Copernicus Univ. in Torun, Gagarina 9, PL-87-100 Torun, Poland (ulrichw@uni.torun.pl).

The study of animal body sizes has a long tradition in ecology (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Gotelli and Graves 1996). Body sizes were used as proxies for patterns of resource allocation (Holling 1992) and ecological niches (Hutchinson 1959) and the distributions of body sizes in local communities or species pools above the local scale served to study effects of competition (Brown and Nicoletto 1991), food webs (Cohen et al. 2003), evolutionary trends (Orme et al. 2002, Smith et al. 2004), dispersion (Etienne and Olf 2004), or patterns of speciation and extinction (Dial and Marzluff 1988, Allen et al. 1999, Knouft and Page 2003).

Our current knowledge about the ecological implications of animal body sizes stems mostly from studies of vertebrate taxa (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Brown 1995, Kozłowski and Gawelczyk 2002, Smith et al. 2004) and pelagic size distributions (Havlicek and Carpenter 2001). Much less is known

about terrestrial invertebrate size distributions in temperate (Gunnarsson 1990, Novotny and Kindlmann 1996) and tropical habitats (Schoener and Janzen 1968, Basset and Kitching 1991, Agosta and Janzen 2005). Although more than 300 species–body size distributions (SSDs) have been published (Loder 1997) nearly of them dealt with local SSDs and, due to the often limited species numbers and size differences, resulted in a wide variety of SSDs and associated patterns (Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002). A notable exception is the work of Chislenko (1981), who published size distributions of all major insect orders based on the species known to him (in total 21 374 species). His figures (based on \log_{10} body length data) point for nearly all insect orders to symmetric body size distributions. Other regional to continental size distributions of taxa other than vertebrates were provided by Novotny and Kindlmann (1996; part of the central European beetles and some lepidopteran, dipteran, and hemipteran taxa),

Accepted 27 February 2006
Subject Editor: Stig Larsson

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ISSN 0030-1299

Fenchel (1993; free living aquatic animals) and parasites (Poulin and Morand 1997). A regional hymenopteran SSD was reported by Espadaler and Gomez (2002) for 242 Iberian ant species.

A number of predictions about regional to continental animal body size distributions and their ecological implications have been derived from these studies. First, in vertebrates species number–log body weight distributions (species number–log body length, respectively) appeared to be unimodal and considerably right skewed with many more small than large bodied species (small and large is here always used with respect to the mean body size of a given taxon) (Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002, Smith et al. 2004). A series of models has been developed to explain unimodality (McKinney 1990, Maurer et al. 1992, Brown et al. 1993, Kozłowski 1996, Kozłowski and Weiner 1997, Kozłowski and Gawelczyk 2002). These invoke either some sort of optimization that favors medium sized species (Kozłowski and Weiner 1997) or are based on the central limit theorem of statistics that predicts a normal distribution for instance after a random drift in species body size evolution (the random diffusion model of McKinney 1990). On the other hand, Havlicek and Carpenter (2001) and Cumming and Havlicek (2002) argued for multimodal distributions in accordance with Holling's (1992) texture hypothesis.

Gaston and Blackburn (2000) and Kozłowski and Gawelczyk (2002) summarized the knowledge about the skewness of body size distributions and argued for right skews as the prevailing pattern of animal taxa. However, the reviews were mainly based on vertebrate data. Whether the pattern can be generalized to invertebrate taxa is still a matter for discussion (Chislenko 1981, Novotny and Kindlmann 1996, Espadaler and Gomez 2002).

At least in vertebrates skewness was found to depend on geographic and on taxonomic scale (Brown and Nicoletto 1991, Kozłowski and Gawelczyk 2002). Bakker and Kelt (2000) showed that mammal size distributions become more symmetrically distributed at small geographic scales. Such a pattern might imply an accumulation of larger species at these scales and a selective species assembly. However, for the majority of all animal taxa, in particular the most diverse insect orders, detailed studies are still missing.

A body of theoretical work based on fractal geometry predicted at least for terrestrial systems the smallest size classes to be the most species rich (Morse et al. 1985, May 1986, Gaston and Blackburn 2000, Brown et al. 2004). The empirical evidence points instead either to medium size classes as being the most diverse (Dial and Marzluff 1988, Novotny and Kindlmann 1996, Kozłowski and Gawelczyk 2002, Smith et al. 2004) or to independence of diversity and body size in the case of whole phyla (Orme et al. 2002). However, a major

concern about the interpretation of SSD patterns is that for a series of hyperdiverse taxa like Nematoda, Acarina, Coleoptera, Diptera, or Hymenoptera many extant species are unknown (May 1978) and that new descriptions involve mostly small bodied species (Gaston et al. 2001). Therefore, detailed studies of these taxa at different spatial scales are needed to assess the validity of current fractal and scaling models about species-body size distributions (Kindlmann et al. 1999, Kozłowski and Gawelczyk 2002, Orme et al. 2002).

Body size within vertebrate taxa seems to be constrained. The study of Smith et al. (2004) about phylogenetical constraints on mammalian body size showed that these constraints (measured as the coefficient of correlation of congeneric species pairs) are highest in medium size classes. Again, invertebrate data of a comparable resolution are still missing.

The present paper aims to examine the body size distributions of a large part of the European hymenopteran fauna contained in a database comprising more than 15 000 species. It will be shown that hypotheses inferred from vertebrates cannot uncritically be transferred to arthropod taxa. The present results also emphasize the importance of ecological factors like guild membership and life history for a proper interpretation of body size distributions and phylogenetical constraints.

Materials and methods

The present study is based on a compilation of European hymenopteran species from major recent catalogues and revisions. In total the database contains 15 004 species in 2107 genera, 73 families, and 18 superfamilies of Hymenoptera. These species represent 88% of the estimated 17 000 described European species (Ulrich 1999a, 2005) and 60% to 75% of the assumed total number of European Hymenoptera (20 000 to 25 000 species; Ulrich 1999a, 1999b, 2001, K. Horstmann, pers. comm.). For 12 601 of them sufficiently precise body length data and information about hosts (in the cases of parasitoids) and life histories were available. Taxonomic entries in the database and the literature used for compilation are given in Table 1. The classification of species into families and superfamilies follows Gauld and Bolton (1988). Above the superfamily level the paraphyletic Symphyta and the probably monophyletic Aculeata s. str. and Parasitica s. str. (without Ichneumonoidea) were considered. The Ichneumonoidea probably form a monophyletic basal branch of the Aculeata s. l. (Whitfield 1998, Ronquist 1999, Vilhelmsen 2001).

It should be emphasized that this compilation cannot be a representative description of the European fauna. It is biased towards better studied taxa like the Vespoidea, Apoidea, or Chrysoidea that contain higher proportions of larger species. For instance, it contains only 3716

Table 1. Basic entries of the hymenopteran database. Numbers of families, genera and species of 18 European superfamilies of Hymenoptera. Given are the works used for compilation of the data.

Superfamily	Numbers of			Sources
	Families	Genera	Species	
Apoidea	2	122	1358	Tobias 1978
Cephoidea	1	7	28	Tobias and Zinoviev 1988
Ceraphronoidea	2	12	116	Trypitsyn 1978
Chalcidoidea	18	637	3544	Trypitsyn 1978, 1989, Graham 1969, 1987, 1991
Chrysoidea	6	56	213	Tobias 1978
Cynipoidea	6	82	646	Dalla Torre and Kiefer 1910, Eady and Quinlan 1963, Quinlan 1978
Evanoidea	3	7	23	Tobias and Zinoviev 1988
Ichneumonidea	4	808	6604	Kasparyan 1981, 1990, Yu and Horstmann 1997, Tobias 1986a, 1986b, Fischer 1972, 1973, 1976, 1996
Megalodontoida	2	6	48	Tobias and Zinoviev 1988
Orussoidea	1	1	1	Tobias and Zinoviev 1988
Proctotrupoidea	4	74	489	Trypitsyn 1978, Townes 1977, Townes and Townes, 1981
Scelionoidea	3	65	587	Trypitsyn 1978, Kozlov and Kononova 1990
Siricoidea	2	6	20	Tobias and Zinoviev 1988
Stephanoidea	1	3	4	Tobias and Zinoviev 1988
Tenthredinoidea	5	86	773	Tobias and Zinoviev 1988
Trigonalvoidea	1	1	1	Tobias and Zinoviev 1988
Vespoidea	11	132	543	Tobias 1978
Xyeloidea	1	2	6	Tobias and Zinoviev 1988
All	73	2107	15004	

species of Ichneumonidae, whereas recent estimates range from 5000 to even 7000 European species (Ulrich 1999a, K. Horstmann 2002, pers. comm.). On the other hand, of the 2800 described Aculeata s. str. (Ulrich 1999a, 2005) 2114 (76%) species are contained in the database. However, within families body size spectra should not be significantly biased due to unseen species (Gaston and Blackburn 2000). Hence, the compilation does not allow for direct comparisons of absolute numbers of species or taxa above the family level. Such comparisons are omitted and the present work concentrates on comparisons of intrataxon distributions of size spectra.

The database contains the following taxonomic and morphometric entries: suborder, superfamily, family, subfamily, genus, subgenus, species, minimum, maximum, and mean recorded body length, and body weight. Non-parasitoids are classified according to their feeding type as phytophages, predators or omnivores. Additional entries for parasitoids are main host order, hyperparasitoid host order, main host family, host guild (ectophytophages, gallers, miners, mycetophages, omnivores, parasitoids, predators, saprophages, sap-suckers, and wood-borers in accordance with the classification in Ulrich 1999a,b, 2001), stage of attack (egg, larva, pupa, imago/adult), parasitoid type (idiobiontic-not allowing for further host development to the next developmental stage or koinobiontic-allowing for further host development to the next developmental stage).

Because most studies used body weight as the basic measure of size (Gaston and Blackburn 2000, Kozłowski and Gawelczk 2002) the present work is based on mean species dry weight calculated from the arithmetic mean of available data on minimum and maximum body length using the regression equation of Ulrich (2001)

$$W[\text{mg}] = 0.01 L[\text{mm}]^{2.84} \quad (1)$$

This regression explained 92% of body weight variance of 100 randomly chosen Hymenoptera species representing the whole body size spectrum (Ulrich 2001). Of course, in the majority of species the literature-based mean lengths will only be rough estimates. However, these inaccuracies are counterbalanced by the large number of data points used for the analysis. Body weight distributions (in the following the term SSD refers always to the species-body weight distribution) are based on ln-transformed weights.

To assess the number of modes of the body weight distributions I used a normal kernel density estimator according to Havlicek and Carpenter (2001):

$$f_h(x) = \frac{1}{Sh\sqrt{2\pi}} \sum_{i=1}^S \text{Exp}\left(-\frac{1}{2}\left(\frac{x_i - x}{h}\right)^2\right) \quad (2)$$

with S being the number of species, x_i the respective ln transformed body weights, and h the band width. I used a smooth bandwidth according to Silvermann (1986) of

Table 2. Analysis of variance of within parasitoid genus skewness dependent on main host guild, host order, type (koinobiontic or idiobiontic), stage of attack (egg, larva, pupa, imago/adult), and superfamily membership.

Variable	Effect		Error		F	p(F)
	df	MS	df	MS		
Host guild	9	6.49	423	1.79	3.62	0.0001
Host order	14	0.52	424	1.14	0.46	0.96
Type	1	0.36	477	1.11	0.32	0.57
Attack of stage	3	1.37	473	1.10	1.24	0.29
Superfamily	13	1.08	543	1.11	0.98	0.47

$$h = 1.06S^{-0.2} \min(\sigma_x; \text{range}/5.36) \quad (3)$$

with range being the range of ln transformed body weights. The step width x was in all cases $h/5$. Kernel density estimates were done for all genera with at least five species.

To study phylogenetical constraints on body weight I followed Smith et al. (2004) and computed the regressions of ln transformed body weights between congeneric species pairs. For genera between two and ten species, all pairs were included; for larger genera, 20% of all species pairs were randomly selected. The coefficient of correlation is then a measure of how much body size is constrained within a given taxon (Smith et al. 2004).

To test whether observed body weights are regularly spaced within the observed ranges, I computed the ratios of log-transformed body weights ($\ln W_n / \ln W_{n-1}$) and raw body weights (W_n / W_{n-1}) of subsequent species on the rank order of species for all genera with more than five species (the ratio test of Strong et al. 1979). I compared the variance of these ratios with the expectation from two null models, where species body lengths or weights were randomly placed inside the respective range (two species were placed at the upper and lower observed length or weight, Gotelli and Graves 1996). Respective confidence limits of the null models were obtained from 1000 replicates. In the case of a regular spacing the observed variance should be significantly smaller than the null model variance (Strong et al. 1979).

Regression slopes refer to ordinary least squares regressions computed with the multiple regression and the non-linear estimation modules of Statistica 7 (Statsoft 2005). Logarithmic transformations always refer to natural (ln) logarithms. Errors refer to standard errors.

Results

The European Hymenoptera range from about 0.0002 mg dry weight (some Mymarid species of *Alaptus*, *Sphelliga* and *Camptoptera* and Encyrtid species of *Aphyculus* and *Stemmatocerus*) to as much as 400 mg dry weight in some *Megarhyssa*, *Urocerus*, *Ammophila* and *Bombus*. They span a body weight range of more than six orders of magnitude.

The body weight distributions within genera, families, superfamilies, suborders, and all Hymenoptera (Fig. 1 and 2) revealed neither a consistent pattern in skewness nor scale dependence. The SSD of all Hymenoptera was bimodal with an insignificant negative skewness ($\gamma = -0.04$, $p(\gamma=0) > 0.05$). The SSD of the suborder Symphyta was right skewed ($\gamma = 0.45$, $p(\gamma=0) < 0.01$) but those of the Parasitica and Aculeata s. str. left skewed ($\gamma = -0.15$, $p(\gamma=0) < 0.01$ and $\gamma = -0.58$, $p(\gamma=0) < 0.001$, respectively) (Fig. 1). Five of the superfamily SSDs (Fig. 2) were left, and seven right skewed. The Scelionoidea were significantly right skewed ($p < 0.05$), a pattern that mainly reflects its composition

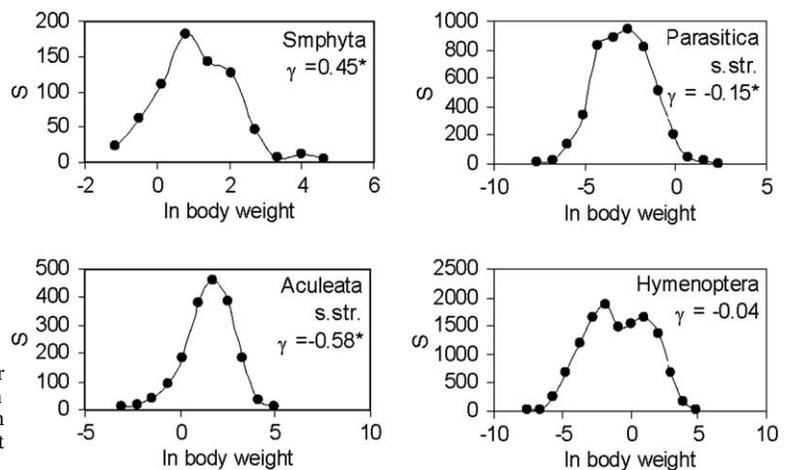


Fig. 1. Size distributions of the three suborders Symphyta, Aculeata s. str. and Parasitica s. str. (without Ichneumonoidea) and of all Hymenoptera. Data points denote the numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk after the skewness γ denotes that γ is significant at $p < 0.01$.

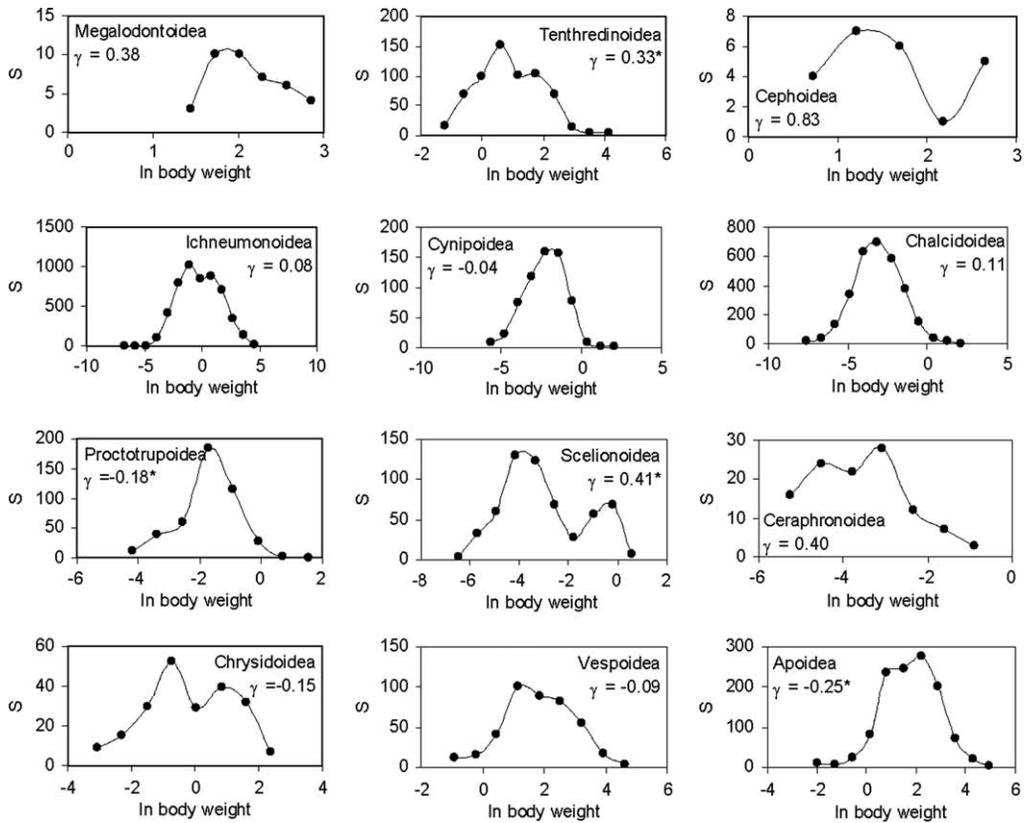


Fig. 2. Size distributions of all hymenopteran superfamilies having more than 20 species per size class. Data points denote numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk after the skewness γ denotes that γ is significant at $p < 0.01$.

of two families (Scelionidae and Platygasteridae). Interestingly, the three Aculeata SSDs were left skewed although this was statistically significant only for the Apoidea ($p(\gamma = 0) < 0.01$).

Skewness of family and genus based SSDs also did not deviate from a random expectation (Fig. 3A, 3B). Thirty-one of 63 family skewness values were negative, 32 positive (Fig. 3A). Of 558 genera with at least five species 284 had left and 274 right skewed SSDs (Fig. 3B). These values do not differ from the null expectation of a random distribution around zero ($p(\chi^2) > 0.5$). 7 families (11%, Fig. 3A) and 16 genera (2.9%, Fig. 3B) ranged outside the 99% confidence limits of the skewness.

If skewness were more pronounced at a higher taxonomic level as had been hypothesised by Kozłowski and Gawelczyk (2002) skewness should correlate with taxon species richness. This was not the case. A correlation between skewness per taxon and ln species number including all families, superfamilies, suborders, and the whole order did not explain any part of variance ($R^2 < 0.001$, $p > 0.5$, Fig. 3A, 3B).

In none of the superfamilies (Fig. 2) and families (data not shown) with at least five species was the lowermost

or the uppermost size class the species richest. The same pattern can be seen in the genera (Fig. 3C). No genus below a mean body weight of $\exp(-6) = 0.0067$ mg (in total 88 genera) had more than 20 species whereas from the overall frequency distribution seven such genera were expected. On the other hand, no genus above a mean body weight of $\exp(3) = 20.1$ mg (in total 82 genera) had more than 20 species although five were expected. Additionally I fitted a quadratic algebraic function to the data set (using ln transformed species numbers). The quadratic term $a = -0.01$ was highly significant ($p(t) = 0.001$) indicating a unimodal distribution. Hence most species rich were intermediate size classes.

The ratio test did not point to regular or to clumped distributions in ln body weight within hymenopteran genera. In 31 of 525 of the genera (5.9%) the observed variance of the length ratios L_n/L_{n-1} deviated from the null model expectation at the 5% error level. In turn, in 256 (49%; 185 genera above and 71 genera below the model expectation) genera the respective body weight variance deviated from the model expectation.

I further tested whether the intragenus variability in ln body weight changed with species richness and body weight. Figure 3D indicates that within genus variability

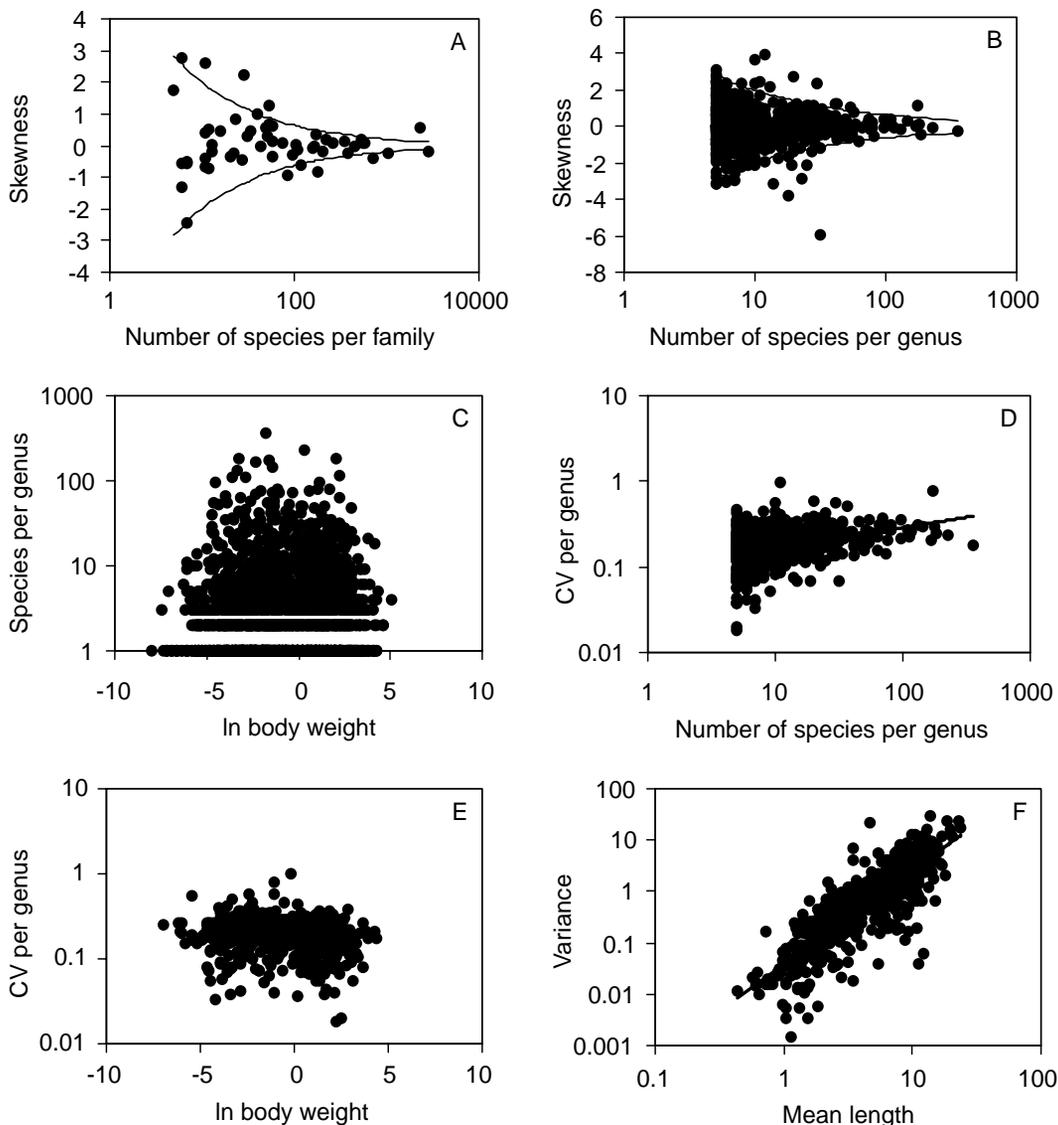


Fig. 3. Skewness of the body size distributions (ln transformed body weights in mg) of hymenopteran families (A) and genera (B) for all taxa with at least five species. Given are also the upper and lower 99% confidence limits according to the approximation of Tabachnick and Fidell (1996). (C) The species number–ln body weight relationship of European Hymenoptera. (D, E) The dependence of the coefficient of variation in mean ln body weight per genus on the number of species per genus (D) and the ln mean body weight per genus (E). (F) The variance–mean length relationship ($\sigma^2 = \mu^z$) of European Hymenoptera follows closely Taylor's power law with a slope of $z = 1.81$ ($R^2 = 0.62$) (length is used instead of ln body weight to avoid negative values). The same regression of the variance–mean body weight relationship gave $z = 1.89$ ($R^2 = 0.94$) (data not shown).

(measured by the coefficient of variation CV) is higher in species rich genera but independent of body weight (Fig. 3E). Hence, body weight distributions in species rich genera appeared to be more clumped than expected from the null model. The variance–mean ratio was for raw and log-transformed body weights consistent with a proportional rescaling pattern (Taylor's power law, Taylor 1960) with a scaling exponent $z = 1.81$ (Fig. 3F).

Because most genera have species numbers below 30 and CV is negatively biased at lower sample sizes the correlation between body size variability and species

richness of Fig. 3D might be caused by this bias. To test for this I assigned for each genus linearly randomly distributed ln body weights inside the observed range and computed the expected CV under this null model. 199 of 243 genera with more than 20 species had an observed CV higher than expected from this null model ($p(\chi^2) < 0.0001$). For comparison I also compared observed and expected CVs using raw body weights instead of ln transformed and found the same pattern although less pronounced. Now, 151 of 243 genera with more than 20 species had an observed CV higher than

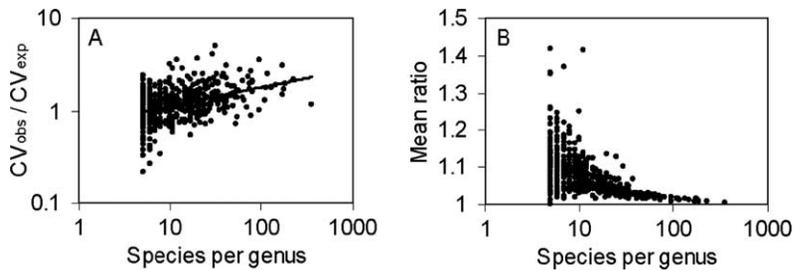


Fig. 4. (A) Within genus variability of body length dependent on the species number S per genus. Variability is given as the quotient of observed CV divided by the expected CV (mean of 1000 replicates) under the assumption that body weights are linearly randomly distributed inside the observed body length range of the genus. Regression: $\text{Var} = 0.71S^{0.20}$; $R^2 = 0.16$; $p < 0.0001$. B: Mean values of L_n/L_{n-1} of body lengths dependent on species number per genus. Regression: $\text{ratio} = 1.18S^{-0.035}$; $R^2 = 0.24$; $p < 0.00001$.

expected from the null model ($p(\chi^2) < 0.01$). Further, there was a highly significant correlation between the quotient of observed and expected CV and species richness per genus (Fig. 4). Hence, a significant trend towards underdispersion in larger genera remained.

I used the residuals of the regression between observed through expected CV and species number in Fig. 4 to study whether within genus \ln body weight variability of parasitoid genera depended on ecological characteristics. An ANOVA revealed, even after Bonferroni corrected experiment wise error levels, a strong signal for host guild ($F_{9,512} = 3.27$; $p = 0.0002$) with hyperparasitoids and parasitoids of sap-suckers having a significantly higher and parasitoids of wood-boring insects a lower within genus variability than expected from the above null model (Table 2). However, stage of attack ($F_{3,439} = 2.28$; $p = 0.06$), parasitoid type ($F_{1,443} = 3.14$; $p = 0.08$), and main host order ($F_{14,390} = 1.48$; $p = 0.11$) did not significantly influence within genus variability.

Of the 558 genera with at least five species 115 had unimodal, 319 bimodal, 123 trimodal, and 1 tetramodal SSDs. There was a significant negative correlation between the number of modes and the species richness with SSDs of species rich genera tending to be unimodal (Fig. 5). The number of modes did not significantly depend on guild membership, stage of attack, host order, and parasitoid type (parasitoids only) (genus based ANOVA: $p(F)$ in all cases > 0.1).

Lastly, I looked whether constraints on body size (congeneric pairwise correlations of body weight)

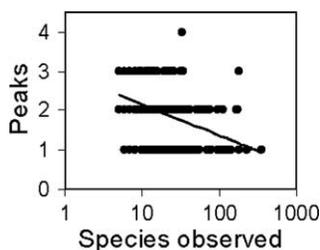


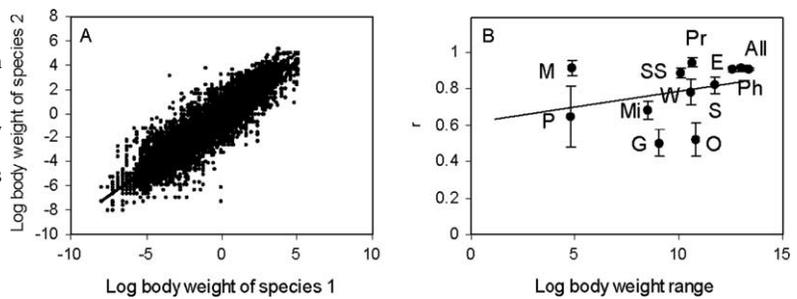
Fig. 5. The number of peaks of the kernel density estimates of \ln body weight distributions of hymenopteran genera is significantly negatively correlated with the number of species (indicated by the regression lines). $R^2 = 0.19$; $p < 0.01$; ANOVA: $F = 17.18$ ($df = 3$), $p < 0.0001$.

differed between ecological groups. Congeneric species appeared to have very similar body weights. The coefficient of correlation r for all hymenopteran genera was 0.91 (Fig. 6A). This coefficient was slightly lower when comparing taxa or guilds spanning smaller size ranges (Fig. 6B). Body size constraints instead appeared to be guild specific. An ANCOVA using the residuals of the regression in Fig. 6A as predictors and the body size range per guild a covariate pointed to highly significant guild specific differences in body size constraints ($F_{9,16226} = 43.7$; $p < 0.00001$). The body weight of the parasitoids of miners and gall-makers and of the omnivorous parasitoids was significantly (p (mean residual < 0) < 0.01) less constrained than expected from the overall regression. Hence in these guilds the ranges of body sizes within genera were larger than expected from the overall pattern. In contrast congeners of parasitoids of ectophytophages and of mycetophages were more similar than expected (p (mean residual > 0) < 0.01). A comparison for koino- and idiobiotic parasitoids gave a significant although weaker signal for less constrained body sizes in idiobiotic Hymenoptera ($F_{2,25922} = 9.6$, $p < 0.001$). On the other hand, phytophagous and parasitic Hymenoptera did not significantly differ (Fig. 6B).

Discussion

There is already a series of studies dealing with invertebrate body size distributions on the local scale. (Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002). However, the present study is the first that deals with continental wide body size distributions of a large arthropod taxon in detail. Comparable is only the study by Chislenko (1981), who compared size distributions of insects and found for most orders more or less symmetric SSD shapes. For Hymenoptera ($S = 1599$) his data imply an insignificant positive SSD skew of $\gamma = 0.09 \pm 0.06$, a value close to the present one. Novotny and Kindlmann (1996) used parts of the central European Coleoptera (5790 species) to assess skewness. They fitted a lognormal SSD to body length data and showed that the Coleoptera as a whole had a slight but

Fig. 6. (A) Regression of ln body weights of congeneric species pairs for all hymenopteran genera with more than two species. Phylogenetical constraints (coefficient of correlation) $r = 0.91$. (B) Constraints dependent on mean ln body size range (ln max - ln min) for 10 parasitoid guilds and the phytophagous Hymenoptera. Host guilds: Ectophytophages (E), Gallers (G), Miners (Mi), Mycetophages (M), Omnivores (O), Parasitoids (P), Predators (Pr), Saprophages (S), Sap-suckers (SS), Wood-borers (W), Phytophages (Ph), and all parasitoid species (All). Error bars denote three standard errors of r . There might be a weak dependence of r on the body size range ($R^2 = 0.096$, $p = 0.33$; without Mycetophages: $R^2 = 0.33$, $p = 0.06$).



significant right skew. On the other hand species rich coleopteran subtaxa and other species rich arthropod families exhibited a variety of distributions. Espadaler and Gomez (2002) provided the only available regional hymenopteran SSD for 242 Iberian ant species. Although they do not explicitly report the skewness their Fig. 1A implies a symmetric distribution ($\gamma = 0.01$). The present analysis based on 165 mainly central and eastern European ants agrees with this result ($\gamma = -0.10 \pm 0.19$, ns).

A general prediction from vertebrate studies was that whole taxa SSDs above the local scale based on body lengths or log body weights should be right skewed at least above the family level (Brown 1995, Poulin and Morand 1997, Gaston and Blackburn 2000, Gaston et al. 2001, Kozłowski and Galweczyk 2002, Knouft and Page 2003, Smith et al. 2004). The present results clearly contradict this prediction. For none of the taxonomic levels did a clear trend towards a right skew appear although some taxa had significant skews. Further, skewness did not depend on taxonomic hierarchy as suggested from vertebrate studies (Kozłowski and Gawelczyk 2002, Smith et al. 2004). Hence, the present data (based on more than 12 500 species representing 15% to 20% of the total European arthropod fauna) call for a rethinking of certain generalities in species body size patterns. Novotny and Kindlmann (1996) rightly remark that their Coleoptera skewness was significant ($p < 0.0001$) mainly due to the mass of data points (5790 species) in their analysis. Any deviation from zero will become significant if we only enlarge the sample size. Hence the present, albeit limited, evidence from larger arthropod taxa does not point to significantly right (or left) skewed SSDs in invertebrates above the local scale. It might be that the skewness in vertebrate SSDs exhibits mainly some vertebrate specific evolutionary trends.

Many evolutionary and ecological scenarios have been envisioned to explain right skewed SSDs (reviewed by Brown 1995, Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002). Most prominent are McKinneys'

(1990) and Maurer et. al.'s (1992) models about biases in speciation and extinction probabilities for large and small bodied species. According to these models even slightly higher speciation and lower extinction rates of smaller species will result in right skewed SSDs, in particular if available niche space is taken into account (Kozłowski and Gawelczyk 2002).

Many animal taxa exhibit explicit trends in body size evolution and according to the bias models SSDs should reflect these trends (for instance Cope's rule about the trend towards larger body sizes in mammals) (McShea 1998). In all major parasitoid superfamilies and in the Symphyta there is a clear trend towards smaller body sizes in evolutionary derived lineages although a detailed evolutionary study is still missing. Basal species of most species rich parasitoid families are larger than their derived counterparts (Gauld and Bolton 1988). According to the bias model this higher speciation rate of smaller species should result in a right skewed SSD (Knouft and Page 2003). This was not the case. The superfamilies in which the size reduction trend is most obvious (Ichneumonoidea, Chalcidoidea, Cynipoidea) were not significantly skewed (Fig. 1). Of the larger families with the most pronounced size reduction trends the Pteromalidae ($\gamma = 0.19$), Eulophidae ($\gamma = 0.09$), Cynipidae ($\gamma = 0.07$), and Tenthredinidae ($\gamma = 0.08$) were slightly right skewed and the Ichneumonidae ($\gamma = -0.21$), Diapriidae ($\gamma = -0.26$), and Encyrtidae ($\gamma = -0.22$) slightly left skewed.

Smith et al. (2004) favoured the idea that mammal taxa have a characteristic body size. Formalizing this statement implies that the variability of genus or family body sizes should more or less follow a Poisson distribution with a variance/mean ratio of about 1 as indicated by some data of these authors. It was therefore a surprise to see that the variability of hymenopteran body sizes resembled more a proportional rescaling process (Fig. 3F; $\sigma^2 \propto \mu^{1.81}$). Such a pattern is consistent with speciation/extinction processes without distinct upper and lower genus specific boundaries in body size.

Upper and lower limits of body size might result in skewed SSDs. McKinney (1990) assumed that body weight evolution can be modelled by a random walk process and termed this the random diffusion model. In such a process upper or lower reflecting boundaries result in SSD skews to the opposite direction. In Hymenoptera the smallest species of only 0.25 to 0.4 mm body length are probably close to the lower size boundary of insects. Some Mymaridae and Encyrtidae are the smallest insects known (flightless males of *Dicopomorpha echmepterygis* are as little as 0.14 mm long, Gahlhoff 1998). On the other hand it is interesting that several species from very different families (Apidae, Sphecidae, Siricidae, and Ichneumonidae) reach about four cm body length. This might be the upper limit for Hymenoptera in temperate regions. If the boundary model were to apply, the genera close to these boundaries should exhibit SSD skews in opposite directions. Of the 22 genera (parasitoids only) with more than five species and a mean body length of less than 1 mm, 10 had a positive and 12 a negative skew. The mean skewness was $\gamma = 0.16 \pm 0.25$. Of the 13 genera (phytophages and parasitoids) above a mean length of 15 mm, 11 had a positive and 2 a negative skew (mean $\gamma = 0.65 \pm 0.16$). However, both results might be influenced by the small number of data points used. Therefore, I applied a sliding window technique to infer a trend in mean skewness and computed the regression of mean body weight and mean skewness for a sliding window of 10 genera shifted over the whole data set of generic mean sizes and skews. A weak but highly significant ($R^2 = 0.07$, $p < 0.0001$) negative regression (slope = -0.05 ± 0.006) appeared (Fig. 7). 127 of 226 windows above five mm mean body length were negative (mean $\gamma = -0.13 \pm 0.25$) and 227 out of 296 genera below five mm mean length were positive (mean $\gamma = +0.12 \pm 0.21$). This pattern is in accordance with the random diffusion model but not with a simple version of speciation/extinction bias models that assumes similar biases across the body size spectrum.

Brown et al. (1993) and Kozłowski and Weiner (1997) developed models of inter and intraspecific body size

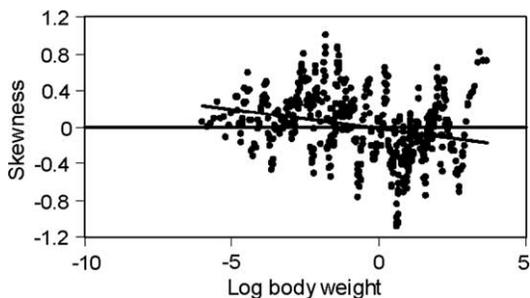


Fig. 7. A plot of mean skewness for a sliding window of 10 species shifted along the ranked body weights resulted in a significant negative correlation. $R^2 = 0.08$; $p < 0.0001$.

optimization. These models do not explicitly refer to SSDs and theoretically allow for a wide range of SSD shapes. The simulations of Kindlmann et al. (1999), however, showed that the Kozłowski and Weiner model of intraspecific body size optimization produces under most parameter settings strongly right skewed SSDs (modal skewness values > 1). That Hymenoptera and probably Coleoptera too-containing together more than 30% of the whole European fauna (Ulrich 1999b)-do not conform to this pattern might stem from taxon specific peculiarities. However, it is also possible that energetic optimization models refer more to large bodied vertebrate species and are less applicable to arthropods. Further data on regional arthropod SSDs are needed to clarify whether Hymenoptera are an exception from the general rule or whether the prevalence of smaller species is vertebrate specific.

Etienne and Olff (2004) showed that ecological drift (Hubbell 2001) within guilds of species with similar body weights combined with between guild allometric scaling of abundance, dispersal, and speciation on body weight is able to produce unimodal right skewed SSDs under a wide variety of parameter settings if only larger species disperse over larger distances than smaller species. While this model strictly applies only at the metacommunity scale it has potential implications for whole taxon distributions as well. A positive dispersion-body size relationship is consistent with the common positive occupancy-body size relationship (Gaston and Blackburn 2000). If this holds for Hymenoptera too, the Etienne and Olff model might serve as an explanation for the above results without invoking optimization processes or selection driven speciation biases. However, a critical test needs additional data on regional species abundances and spatial distributions.

A critical point of all comparative studies is that there is still no standard for measuring body sizes and different studies used either body weights (May 1986, Brown et al. 1993), log body weights (Gardezi and da Silva 1999, Gaston and Blackburn 2000), body length (Hutchinson and McArthur 1959) or log body length (Fenchel 1993, Novotny and Kindlmann 1996). Each such transformation changes the skewness and other parameters of the distribution. Most often used were log body weights and log body lengths. If body weight W scales to length L to a constant slope the skewness of both SSDs should be identical ($\gamma(\ln L) = \gamma(\ln W)$). However, if many taxa are involved the results can differ due to different scaling exponents. Hence these measurement uncertainties might explain at least some part of the observed variability in body size distributions. Surely they prohibit direct comparisons of published SSDs and make it difficult to draw unequivocal generalisations. Additionally, the problem which measure to use is closely connected with the question about the basic unit of body size evolution and of respective evolution-

ary models. There is apparently no study to test for these differences and to define the most appropriate unit for models of body size evolution although this would be very welcome for a more reliable comparison of different studies.

The variability in body size has surely gained as much attention as the SSD shapes (reviewed in Gotelli and Graves 1996). Early competition orientated models predicted a regular spacing of sizes inside the realized range (Hutchinson 1959, Holling 1992) whereas most recent studies failed to detect regularities in size distributions (Gotelli and Graves 1996). Frequently null models are applied to study observed size ratios with randomized ones. While such comparisons heavily depend on the model algorithms a better approach would be to compare local and regional whole taxon ratios or to adjust null models to observed whole taxon patterns. The present results show that the size distributions of the European Hymenoptera do not deviate from the expectation of a linear random assortment of body sizes (Fig. 3D, 4) if dealing with body length data. This result might indicate that body length (or log transformed weight) might be the most appropriate scale for the study of body size distributions. That species rich taxa showed a trend towards underdispersion even after correcting for Poisson errors (Fig. 3D, 4) is consistent with the existence of subgenera that serve as new centres of body size. Smaller genera, however, appear to be more homogeneous.

Body size appeared to be highly constrained (Fig. 5). This result is very similar to the pattern Smith et al. (2004) reported for mammals. Additionally, the analysis showed that this pattern is also guild dependent. Parasitoids of endophytophagous (miners and galls) and of omnivorous (often also endophytophagous) hosts were less constrained in body size than parasitoids of ectophytophagous hosts. The latter are mainly larger sawflies, beetle and lepidopteran caterpillars. Hence phylogenetical constraints in body size appeared to be affected by ecological traits. While such a pattern seems not improbable, it has not been previously reported. The guild dependence of phylogenetical constraints in parasitoids contrasts to a certain extent with the fact that the overall shapes of the SSDs were surprisingly unaffected by ecological traits like guild and host taxon membership, or parasitoid type.

Acknowledgements – I thank A. Makarieva for her critical and valuable suggestions on the manuscript. She also drew my attention to the work of L. Chislenko on body size distributions. Miss Hazel Pearson kindly improved my English. This work was in part supported by a grant from the Polish Science Committee (KBN, 3 F04F 034 22).

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