

Body weight distributions of central European Coleoptera

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Abstract. Species number – body weight distributions are generally thought to be skewed to the right. While this pattern is well documented in vertebrates, comparative studies on species rich invertebrate taxa are still scarce. Here I show that the weight distributions of central European Coleoptera (based on 8257 species body weight data compiled from Freude et al., 1964–1994) are predominantly right skewed. Skewness and species richness per taxon were positively correlated. The number of modes of the body weight distributions was negatively correlated with species richness. 273 of the 558 genera had bimodal distributions. Species richness per genus did not significantly depend on mean genus body weight. In general the coleopteran size distributions differed from those of European Hymenoptera but were similar to the respective distributions of vertebrates. I conclude that we should be cautious when generalizing patterns found in one taxon.

INTRODUCTION

The study of animal body sizes has a long tradition in ecology (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Gotelli & Graves, 1996). Recently, species size distributions (SSDs) have regained interest after the notion that there are taxon specific differences in SSDs that might be explained by differential patterns of speciation and extinction (Dial & Marzluff, 1988; Allen et al., 1999; Knouft & Page, 2003; Ulrich, 2006) and by evolutionary trends towards larger or smaller body sizes (Orme et al., 2002; Smith et al., 2004). Hence, SSDs might be tools to link evolutionary processes to ecological patterns (Etienne & Olf, 2004; Ulrich, 2005, 2006).

Our current knowledge about the ecological implications of animal body sizes stems mostly from studies of vertebrate taxa (cf. Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Brown, 1995; Kozłowski & Gawelczyk, 2002; Smith et al., 2004). From this work five major patterns emerged:

– Classical niche based models (Hutchinson & MacArthur, 1959; May, 1986) and theoretical work based on fractal geometry (Morse et al., 1985) predict the lower weight classes to be most species rich. The empirical evidence rather points to medium size classes as being most diverse and therefore to unimodal humped distributions (Dial & Marzluff, 1988; Brown, 1995; Novotný & Kindlmann, 1996; Kozłowski & Gawelczyk, 2002; Smith et al., 2004; Ulrich, 2006).

– SSDs (based on log body weight or log body length) appeared to be considerably right skewed with 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 & Blackburn, 2000; Kozłowski & Gawelczyk, 2002; Smith et al., 2004). This pattern is frequently explained in terms of intra- (Kozłowski & Weiner, 1997) and interspecific (Brown et al., 1993) body

size optimization or body size dependent speciation and extinction rates (McKinney, 1990; Maurer et al., 1992).

– Mammal size distributions become more symmetrically distributed at small geographic scales (Bakker & Kelt, 2000). Such a pattern implies a selective species assembly caused either by an accumulation of larger species at these scales or by a selective loss of smaller species.

– The degree to which SSDs are skewed appears to depend on taxonomic level. Higher levels were found to have a more pronounced skew and therefore a higher proportion of small species (Kozłowski & Gawelczyk, 2002). This implies a positive correlation of SSD skew and species richness (Ulrich, 2006).

– Body size within vertebrate taxa seems to be phylogenetically constrained. The study of Smith et al. (2004) on constraints on mammalian body size showed that these constraints (measured as the coefficient of correlation of congeneric species pairs) are strongest in medium size classes.

SSDs of terrestrial invertebrates are much less studied (Gunnarson, 1990; Basset & Kitching, 1991; Novotný & Kindlmann, 1996; Ulrich, 2005, 2006). Chislenko (1981) published size distributions of all major insect orders and reported for nearly all of them symmetric body size distributions. Recently, Espadaler & Gomez (2002) and Ulrich (2006) published regional SSDs of Iberian ant species and European Hymenoptera, respectively. Both studies found hymenopteran SSDs to differ from the vertebrate pattern. At all taxonomic levels and irrespective of taxon species richness SSDs appeared to be symmetric. Further, body size is less constrained than in vertebrates (Ulrich, 2006). In turn, irrespective of taxonomic level medium size classes appeared to be most species rich and unimodal SSDs dominate.

Coleopteran body size distributions are currently only poorly known. Chislenko (1981) reported a unimodal

symmetric SSD (skewness $\gamma = 0.08$, n.s.) for the Coleoptera known to him (4875 species). However, this work used a rather heterogeneous ensemble of species from different geographical regions. Novotný & Kindlmann (1996) analyzed data on parts of the central European Coleoptera (5790 species) contained in Reitter (1908–1916) to assess skewness and the number of modes. They found a weak trend towards right skewed SSDs but concluded that this skew might be significant mainly due to the large number of species analyzed. The present paper aims to examine the body size distributions of the central European Coleoptera as contained in the systematic work of Freude et al. (1964–1994) comprising more than 8700 species. From a comparison with similar work on European Hymenoptera (Ulrich, 2006) and world vertebrates (Smith et al., 2004) it will be shown that taxon specific size distributions exist and that we have to be careful when generalizing based on single taxon patterns.

MATERIAL AND METHODS

The present study is based on the treatise of central European Coleoptera of Freude et al. (1964–1994). From this work I compiled a database that contains 8727 species from 1685 genera and 112 families (Table 1). For 8257 species body length data are available (94.6%). The classification of species above the genus level follows the tree of life project (<http://tolweb.org/tree/>). The database contains the following taxonomic and morphometric entries: suborder, superfamily, family, subfamily, genus, subgenus, species, minimum, maximum and mean body length, and body weight.

Because most studies use body weight as the basic measure of size (cf. Gaston & Blackburn, 2000, Kozłowski & 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 Ganihar (1997)

$$W[mg] = 0.038L[mm]^{2.46} \quad (1)$$

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. Skewness γ is computed as in Ulrich (2006):

$$\gamma = \frac{n}{(n-1)(n-2)} \sum_{i=1}^n \left(\frac{w_i - \bar{w}}{\sigma_w} \right)^3 \quad (2)$$

where w_i is the ln-transformed body weight of species i . I calculated the standard error of γ according to Tabachnick & Fidell (1996): $SE(\gamma) = (6/n)^{1/2}$.

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

$$f_h(x) = \frac{1}{Sh\sqrt{2\pi}} \sum_{i=1}^S \text{Exp}\left(-\frac{1}{2}\left(\frac{x-x_i}{h}\right)^2\right) \quad (3)$$

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

$$h = 1.06S^{-0.2} \min(\sigma_x; \text{range}/5.36) \quad (4)$$

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 whether within genus body weights are constrained within upper and lower limits (phylogenetic constraint) I fol-

TABLE 1. Basic entries of the coleopteran database. Numbers of families, genera and species included in the analysis of 18 European superfamilies of Coleoptera.

Superfamily	Numbers of			
	Families	Genera	Species	Species with body length data
Bostrychoidea	4	50	155	146
Buprestoidea	1	27	133	129
Byrrhoidea	1	12	39	39
Cantharoidea	5	19	118	116
Caraboidea	7	131	1002	978
Chrysomeloidea	3	182	961	925
Cleroidea	3	49	143	135
Cucujoidea	38	334	1281	1215
Curculionoidea	9	298	1482	1449
Dascilloidea	4	11	44	44
Dermestoidea	4	16	59	59
Dryopoidea	5	18	64	60
Elateroidea	4	68	215	201
Histeroidea	2	38	112	107
Hydrophiloidea	4	25	198	178
Lymexyloidea	1	2	8	3
Scarabaeoidea	4	58	245	241
Staphylinoidea	13	347	2468	2232
All	112	1685	8727	8257

lowed Smith et al. (2004) and Ulrich (2006) and computed the regressions of ln transformed body weights between congeneric species pairs. For genera having two to ten species, all pairs were included; for larger genera, 20% of all species pairs were randomly selected. The coefficient of correlation r is then a measure of how much body size is constrained within a given taxon (Smith et al., 2004). I tested r against two null model approaches and assigned species body weights within each genus using a normal random distribution around the observed mean according to a proportional rescaling process ($\sigma^2 = \mu^2$) and according to a Poisson distribution ($\sigma^2 = \mu$). It should be emphasized that such a comparison is not a true phylogenetic analysis where body size distributions are compared with respect to the underlying phylogenetic tree. Such an analysis is still impossible due to the low phylogenetic resolution of the Coleoptera.

To test whether observed body weights are regularly spaced within the observed ranges, I computed the ratios of log-transformed body weights ($R = \ln W_n / \ln W_{n-1}$) and raw body weights ($R = W_n / W_{n-1}$) 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 a null model, where species body lengths were randomly placed inside the respective range (two species were placed at the upper and lower observed length or weight, cf. Gotelli & Graves, 1996). Respective confidence limits of the null models were obtained from 1000 replicates. To compare taxa I calculated the standardized effect size SES of R as a Z-transformed score [$Z = (R - \mu) / \sigma$] to compare the observed index R to the distribution of simulated indices ($\mu =$ mean and $\sigma =$ standard deviation of the simulated ratios). SES values below -2.0 or above 2.0 indicate approximate statistical significance at the 5% error level (1-tailed test).

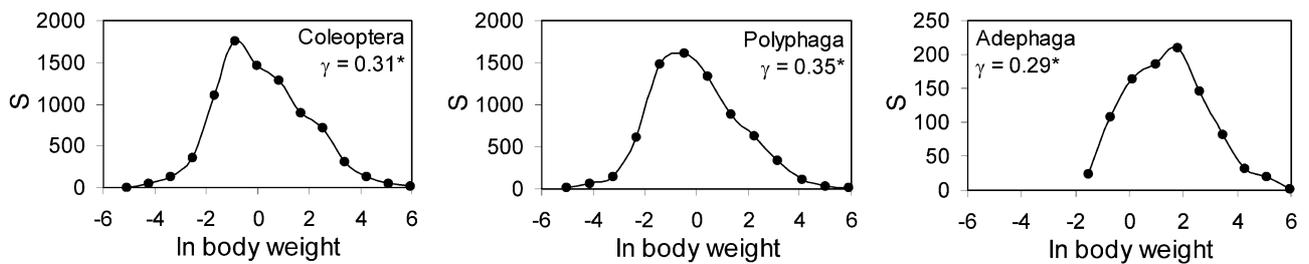


Fig. 1. Size distributions of all central European Coleoptera and the two suborders Polyphaga and Adephaga. Data points denote numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk after the skewness (γ) denotes that it is significant at $p < 0.01$.

Regression slopes refer to ordinary least squares regressions computed with the multiple regression and the non-linear estimation modules of Statistica 7 (Statsoft, 2005). Errors are standard errors.

RESULTS

The central European Coleoptera range from about 0.004 mg dry weight [*Scaphisoma* (Scaphidiidae) and *Oligella* (Ptilidae) species] to more than 500 mg dry weight in *Procerus gigas* (Carabidae) and *Lucanus cervus* (Lucanidae). They span a body weight range of more than five orders of magnitude.

The body weight distributions of the suborders and all Coleoptera (Fig. 1) were significantly [$p(\gamma = 0) < 0.01$] right skewed. Eleven of the 18 superfamily SSDs (Fig. 2) were significantly right, and five significantly left skewed. The Chrysomeloidea were significantly right skewed ($p < 0.05$) and bimodal, a pattern that mainly reflects that it is composed of two families (Chrysomelidae and Cerambycidae).

12 of the 77 family skewness values were significantly positive, five negative (Fig. 3A). Eight of the 18 families with more than 100 species had significantly ($p < 0.001$) right skewed SSDs. Of 403 genera with at least five species 196 had left and 207 right skewed SSDs (Fig. 3B). These values do not differ from the null expectation of a random distribution around zero [$p(\chi^2) > 0.1$]. 28 genera (6.9%, Fig. 3B) ranged outside the 99% confidence limits of the skewness.

The above results might indicate a trend towards positive skewness in higher taxa. A Kruskal Wallis ANOVA comparing genera, subfamilies, families, and superfamilies with respect to mean skewness did not point to increasing mean skew with taxonomic level ($P > 0.5$). However, there was a highly significant positive correlation ($p < 0.001$) between skewness and ln species richness per family (Fig. 3A). This correlation remained when genera, subfamilies, and superfamilies were included ($R^2 = 0.06$; $p < 0.001$). Using the subfamily to order levels only strengthened the correlation to $R^2 = 0.16$ and $p < 0.0001$ (Fig. 4). Of 34 taxa above the genus level with at least 100 species 26 had a positive SSD skewness. All but one taxon with more than 200 species (14 taxa) had a positive skew, 12 of these were statistically significant at the 1% error level.

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

lowermost or the uppermost size class the species richest. Nevertheless the species richness – log mean taxon body weight plots were at the superfamily, family and genus level (Fig. 3D) not significantly unimodal. All quadratic and linear terms of fits of quadratic algebraic functions to the data sets (using ln transformed species numbers) were not significant [all $p(t) > 0.05$]. Further, seven genera of the first body weight quartile (mean weight < 0.19 mg, in total 51 genera) had more than 20 species, whereas from the overall frequency distribution ten such genera were expected (Fig. 3D). Six genera of the fourth quartile (mean weight > 10 mg, in total 51 genera) had more than 20 species although again ten were expected. Both deviations from expectation are statistically not significant (binomial test $P > 0.5$). Hence, the unimodal impression of Fig. 3D is not corroborated by the statistical analysis and arises due to a higher number of genera of intermediate size.

Variance – mean ratios of genus body lengths were consistent with a proportional rescaling pattern (Taylor's power law, Taylor, 1960) with a scaling exponent $z = 2.23$ (Fig. 3C). The ratio test pointed to clumped distributions in ln body weight within coleopteran genera. In 84 of the 403 genera with at least five species (20.8%) the observed variance of the ln weight ratios $\ln W_n / \ln W_{n-1}$ was above the upper 95% confidence level of the null model. Using raw body weight ratios W_n / W_{n-1} resulted in only 34 genera (8.4%) above the 95% null model confidence level. Hence, body weight appeared to be randomly distributed with respect to a linear random null model. Further there was a strong positive correlation between effect size Z and species richness ($R^2 = 0.50$; $P < 0.0001$). Of 38 genera with more than 30 species 31 had positive Z-values > 1.96. Their body length distribution was therefore aggregated.

Body size of Coleoptera appeared to be highly constrained when measured by the coefficient of correlation using intragenus pairwise comparisons (Fig. 5A). The coefficient of correlation was $r = 0.91$. The two null model approaches in turn gave $r = 0.47$ (rescaling, Fig 5B) and $r = 0.67$ (Poisson variability, Fig 5C). The observed intragenus variability in body size is therefore much lower than expected from both null models.

Of the 558 genera with at least five species 45 had unimodal, 273 bimodal, and 85 trimodal SSDs. The number of modes was significantly negatively correlated with

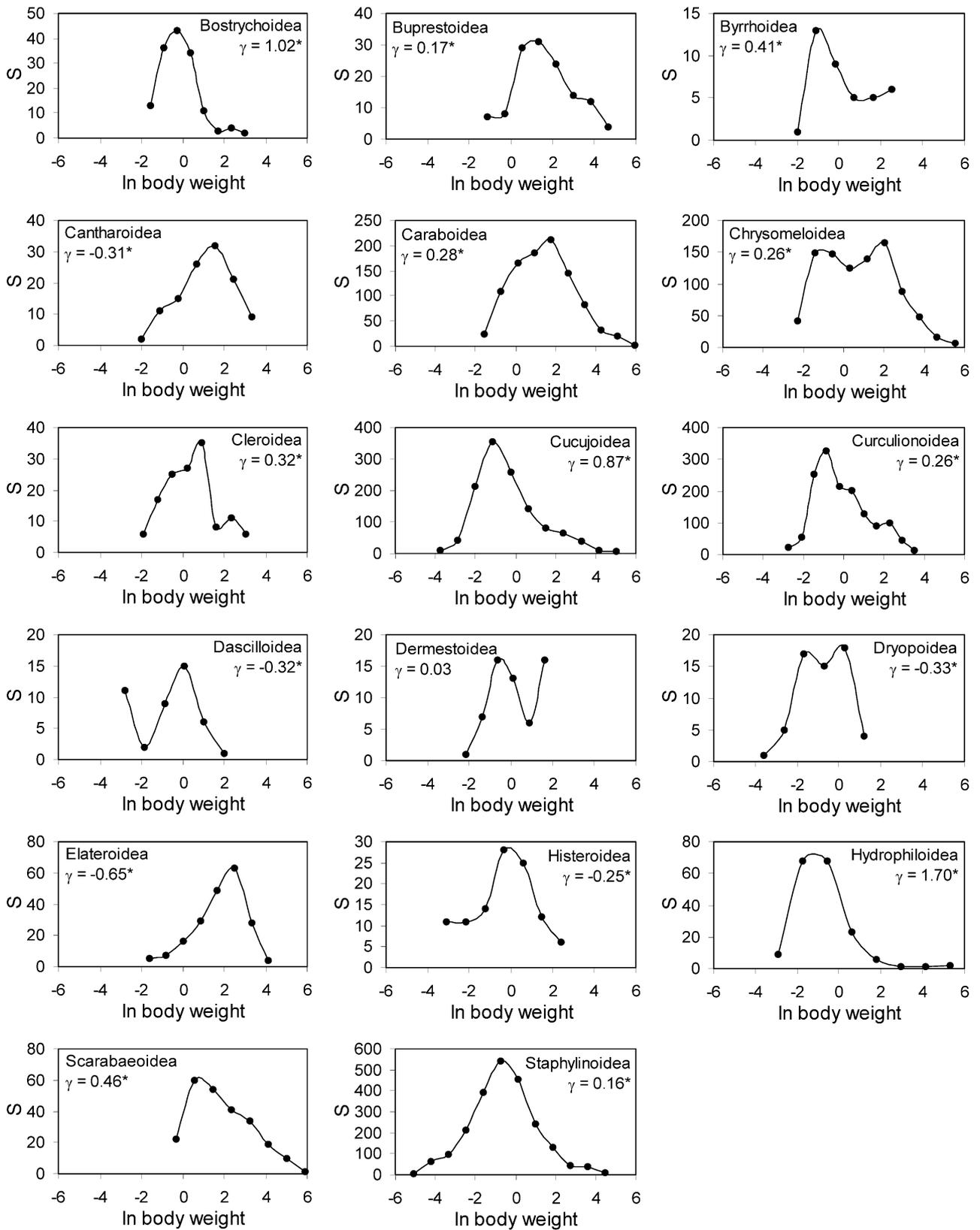


Fig. 2. Size distributions of the superfamilies of central European Coleoptera having more than 30 species. Data points denote numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk after the skewness (γ) denotes that it is significant at $p < 0.01$.

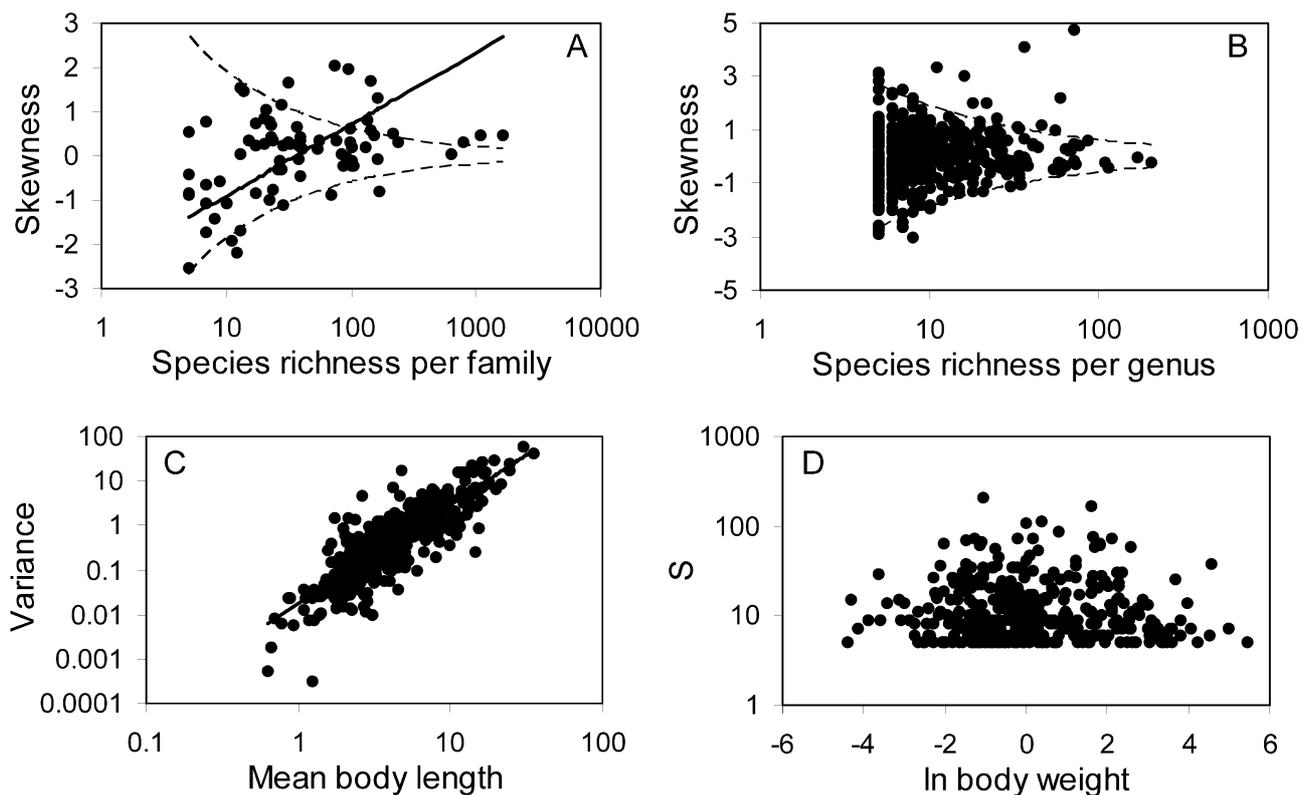


Fig. 3. A, B: Skewness of the body size distributions (ln transformed body weights in mg) of coleopterans families (A) and genera (B) for all taxa with at least 5 species (S). Given are also the upper and lower 99% confidence limits according to the approximation of Tabachnick & Fidell (1996) (broken lines). The full line in A shows the RMA regression $\gamma = -2.52 + 0.70 \ln(S)$; $R^2 = 0.14$; $p < 0.001$. C: The variance – mean length relationship ($\sigma^2 = \mu^z$) of central European Coleoptera follows closely Taylor's power law with a slope of $z = 2.23$ ($R^2 = 0.70$; $p < 0.0001$) (length is used instead of ln body weight to avoid negative values). D: The species number – ln mean body weight relationship of genera. Included are all genera with more than five species.

species richness ($R^2 = 0.11$, $P < 0.001$). The respective correlations for subfamilies ($R^2 = 0.21$, $P < 0.0001$) and families ($R^2 = 0.22$, $P < 0.0001$) were also highly significant. Both, subfamilies (54%) and families (53%) had mostly bimodal SSDs.

DISCUSSION

Three major findings emerged regarding SSDs in central European Coleoptera: first, coleopteran size distributions are predominantly right skewed; second, size

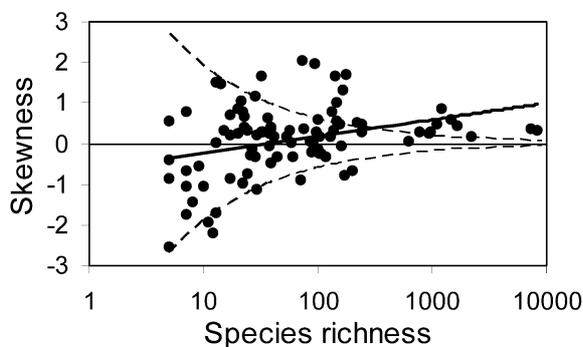


Fig. 4. Skewness values of subfamilies, 112 families, 17 superfamilies, 3 suborders, and all Coleoptera dependent on the species richness of the respective taxonomic level. $R^2 = 0.12$; $p < 0.0001$.

distributions appeared to be taxon specific, which implies that we must be careful when generalizing about possible causes of observed distributions; third, intrataxon variability in body size is less than expected from a random distribution pointing to certain phylogenetic constraints on body size.

The present study also allowed for the first time a detailed comparison of body size distributions of two large European arthropod taxa. In a previous study (Ulrich, 2006) I found hymenopteran SSDs to be predominantly unimodal and symmetrical (whole order $\gamma = -0.04$). Chislenko (1981) and Espadaler & Gomez (2002) reported a very similar pattern. The central European Coleoptera of the present study deviate from this pattern. Their size distributions are at least above the genus level predominantly right skewed (Figs 1–3). Novotný & Kindlmann (1996) have reported already a skew of $\gamma = 0.27$ ($P < 0.001$) for central European Coleoptera, a value very similar to the present one ($\gamma = 0.31$). Further, I found at different taxonomic levels significant positive correlations between skewness and species richness. Such a pattern does not exist in the Hymenoptera (Ulrich, 2006) but resembles the one known from vertebrates (Kozłowski & Gawelczyk, 2002, Smith et al., 2004).

Many evolutionary and ecological scenarios have been proposed to explain right skewed SSDs (reviews in

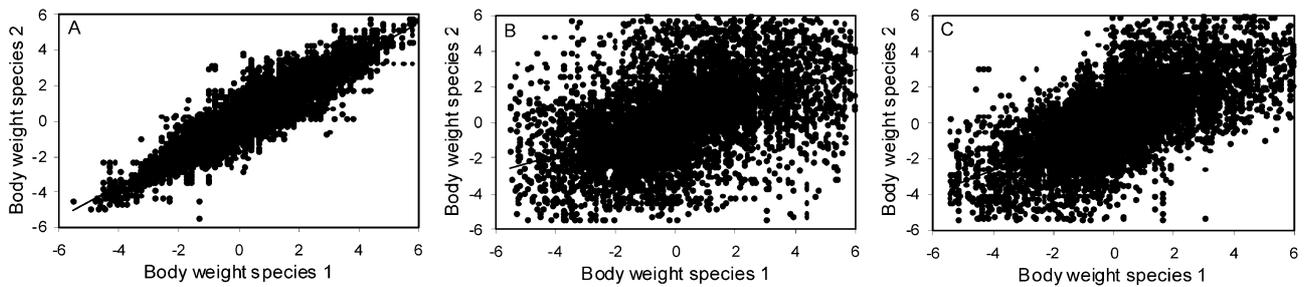


Fig. 5. A: Regression of body weights of congeneric species pairs for all coleopteran genera with at least five species. Phylogenetic constraint (coefficient of correlation) $r = 0.91$. B: The same regression for the null model where within genus body weights were randomly assigned with a variance of $\sigma^2 = \mu^2$ (proportional rescaling): $r = 0.47$. C: The same regression for the null model having a Poisson distribution of body weights ($\sigma^2 = \mu$): $r = 0.67$.

Brown, 1995; Gaston & Blackburn, 2000; Kozłowski & Gawelczyk, 2002). 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 boundaries of body size (modelled as reflecting boundaries) result in SSD skews to the opposite direction. If the boundary model were to apply, the genera close to these boundaries should exhibit SSD skews in opposite directions. For the Hymenoptera I found size class specific SSDs in accordance with the random diffusion model (Ulrich, 2006). Using a sliding window technique to infer a trend in mean skewness a highly significant ($R^2 = 0.07$, $p < 0.0001$) negative regression between mean skewness per genus and mean \ln body weight (slope = -0.05 ± 0.006) appeared. Applying the same technique to Coleoptera resulted in a very different picture (Fig. 6). A significant U-shaped distribution came up with the genera of the lower and upper size classes having mainly positive SSD skews and the middle ranking sizes classes negative skews. This pattern is at least for the upper size classes not in accordance with the diffusion model where symmetrical or left skewed SSDs are predicted.

However, the pattern might be in accordance with the hypothesis that a taxon specific speciation/extinction bias exists (Alroy, 2000). According to the bias model higher speciation rates of smaller species and/or higher extinc-

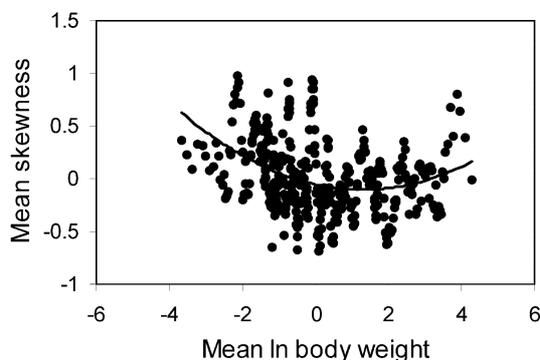


Fig. 6. A plot of mean skewness for a sliding window of 10 genera shifted along the ranked body weights was significantly U-shaped as inferred from the significance level ($p < 0.0001$) of the quadratic term of a second order algebraic function fitted to the data. $R^2 = 0.13$.

tion rates of larger species should result in a right skewed SSD (Knouft & Page, 2003). If this model were to apply, genera of smaller sized species should be most species rich. This was not the case (Fig. 3D). Species richness did not significantly differ between genera of different mean size. Again this pattern was different from that of the Hymenoptera, but also from that of the Vertebrata, where genera of medium sized species are most species rich (Smith et al., 2004; Ulrich, 2006).

As in the case of Hymenoptera (Ulrich, 2006) and of vertebrates (Smith et al., 2004) body size of Coleoptera appeared to be highly constrained ($r = 0.91$; Fig. 5A). Both null model approaches gave much lower values of r (Figs 5B and C) pointing to a lower variability in body sizes around the genus means than expected from simple statistical distributions. Smith et al. reported $r = 0.89$ for vertebrates and I found a very similar value of $r = 0.91$ for Hymenoptera. These high values imply that the overlap in size between genera is less than expected from both null models. The remarkable resemblance of r indicates that body sizes of these three very different taxa are constrained in a similar manner and possibly by similar processes.

Smith et al. (2004) argue 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. The variability of hymenopteran body sizes resembled more a proportional rescaling process (Fig. 3F; $\sigma^2 \propto \mu^{1.81}$). The coleopteran pattern (Fig. 3C; $\sigma^2 \propto \mu^{2.23}$) deviates even more from a Poisson distribution indicating that genera of larger bodied species have a proportionally larger span of body weights than smaller bodied genera. Both arthropod patterns are consistent with speciation/extinction processes without distinct upper and lower genus specific boundaries in body size.

In the Hymenoptera within genus variability is higher in species rich genera but independent of body weight (Ulrich, 2006). Hence, body weight distributions in species rich hymenopteran genera appear to be more clumped than expected from the null model. In the Coleoptera I found the same pattern. The Z-transformed R-values of the ratio test were significantly positively correlated with species richness. Both results are consistent with the existence of subgenera that serve as new

centres of body size (Ulrich, 2006). However, within genus body size distributions differed between Coleoptera and Hymenoptera. In the Hymenoptera log body weight distributions do not differ from the expectation of a linear random null model (5.9% of genera above the 95% null model confidence limit) while raw body weight ratios appear to be clumped (185 genera above the 95% confidence limit) (Ulrich, 2006). In the Coleoptera this pattern was reversed. For raw body weight ratios 8.4% and for log body weight ratios 20.8% of the genera ranged above the 95% confidence limit.

This difference might have implications for the question about the unit of evolutionary change. The size distributions of the European Hymenoptera did not deviate from the expectation of a linear random assortment of log body weight (\approx body length) whereas Coleoptera did not deviate when using raw body weight. This result points to taxon specific scales as being the most appropriate for the study of body size distributions. The result indicates that we should be cautious when using evolutionary models to explain these distributions using standard null model approaches (Gotelli & Graves, 1996).

In summary, the present results point to differences in body size distributions between major animal taxa. Hence generalizations of patterns and models that extrapolate from findings within one taxon should be treated with caution.

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