

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	56	4	557–568	2008
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Special paper

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BODY SIZE DISTRIBUTIONS OF EASTERN EUROPEAN DIPTERA

ABSTRACT: Weight distributions of Eastern European Diptera (estimated from 7966 species body length data compiled from Stackelberg and Nartshuk 1969, 1970) differ from respective distributions of Coleoptera and Hymenoptera. Nematoceran size distributions were predominantly right skewed while the Brachycera tended to have symmetric and left skewed distributions. Skeweness of size distributions was for Nematocera positively and for Brachycera negatively correlated with genus mean body weight. Genera of smaller mean body weight were significantly species richer than larger sized genera. Our findings are consistent with an evolutionary model that assumes body size dependent speciation and extinction rates.

KEY WORDS: Diptera, body weight, size ratios, speciation

1. INTRODUCTION

The study of animal species body size distributions (SSDs) within an ecological context has recently 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 and Marzluff 1988, Allen *et al.* 1999, Knouft and Page 2003, Ulrich

2006, 2007) 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 and Olff 2004, Ulrich 2006, 2007).

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 and Gawelczyk 2002, Smith *et al.* 2004). From this work five major patterns emerged:

- Classical niche based models (Hutchinson and 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 and Marzluff 1988, Brown 1995, Novotny and Kindlmann 1996, Kozłowski and Gawelczyk 2002, Smith *et al.* 2004, Ulrich 2006, 2007).

- 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

Table 1. Basic entries of the dipteran database. Numbers of families, genera and species included in the analysis of 35 European superfamilies of Diptera. Classification according to Pape (2004), Oosterbroek (2006), and Yeates *et al.* (2007).

Superfamily	Numbers of			
	Families	Genera	Species	Species with body length data
Anisopodoidea	2	2	9	8
Asiloidea	5	86	345	341
Axymyoidea	1	1	1	1
Bibionoidea	2	5	33	33
Blephariceroidea	1	3	5	5
Carnoidea	6	61	262	261
Chironomoidea	4	155	457	195
Conopoidea	1	11	49	49
Culicoidea	3	11	81	81
Diopsoidea	4	7	35	35
Empidoidea	5	85	910	902
Ephydroidea	5	51	240	239
Hippoboscoidea	3	12	27	26
Lauxanioidea	2	18	113	113
Muscoidea	5	106	845	804
Nemestrinoidea	2	6	18	18
Nerioidea	1	3	12	12
Oestroidea	5	268	804	801
Opomyzoidea	10	38	677	627
Pachyneuroidea	1	1	1	1
Phoroidea	2	20	361	361
Platypezoidea	1	5	23	23
Psychodoidea	1	9	92	91
Ptychopteroidea	1	1	7	7
Scatopsoidea	2	21	50	49
Sciaroidea	7	226	1206	1133
Sciomyzoidea	6	38	131	130
Sphaeroceroidea	4	23	224	223
Stratiomyoidea	2	21	94	93
Syrphoidea	2	82	460	460
Tabanoidea	2	18	130	128
Tephritoidea	7	91	351	347
Tipuloidea	3	51	363	351
Trichoceroidea	1	2	12	12
Xylophagoidea	2	2	6	6
All	111	1540	8434	7966

used with respect to the mean body size of a given taxon) (Gaston and Blackburn 2000, Kozłowski and Gawelczyk 2002, Smith *et al.* 2004). This pattern is frequently explained in terms of intra- (Kozłowski and 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 and 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 and 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 and Kitching 1991, Novotny and Kindlmann 1996, Ulrich 2005, 2006, 2007). Chislenko (1981) published size distributions of all major insect orders and reported for nearly all of them symmetric body size distributions. Recently, Espadaler and Gomez (2002) and Ulrich (2006, 2007) published regional SSDs of Iberian ant species and European Hymenoptera and Coleoptera, respectively. These three studies found hymenopteran SSDs to differ from and the beetle SSDs to be similar to the vertebrate pattern.

Beside Coleoptera and Hymenoptera, Diptera are the third major holometabolic taxon. In Europe about 18,700 species are described (Pape pers. comm.). Dipteran body size distributions are currently only poorly known. Only Chislenko (1981) compiled body length data of the Russian fauna (7331 species). A recalculation of his data gave a bi-

modal symmetric SSD with an insignificant skewness $\gamma = 0.04$. The present paper aims therefore at examining the body size distributions of the eastern European Diptera. We compiled data from the systematic work of Stackelberg and Nartshuk (1969, 1970) comprising 8434 species of Diptera from the European part of the former USSR. This work is still the most comprehensive catalog of Diptera containing body size data. From a comparison with similar work on European Hymenoptera (Ulrich 2006), Coleoptera (Ulrich 2006), and world vertebrates (Smith *et al.* 2004) we will show that taxon specific size distributions and respective evolutionary trends exist and that we have to be cautious with generalizations of patterns obtained from single taxa.

2. MATERIALS AND METHODS

The present study is based on the treatise of Eastern European Diptera of Stackelberg and Nartshuk (1969, 1970). From this work we compiled a database that contains 8434 species from 1540 genera and 111 families (Table 1). For 7966 species body length data are available (94.4%). The classification of species above the genus level follows Oosterbroek (2006) and Yeates *et al.* (2007). The classification into genera is in accordance with the Fauna Europea (Pape 2004). The database contains the following taxonomic and morphometric entries: order, infraorder, suborder, superfamily, family, subfamily, genus, species, minimum, maximum and mean body length, and body weight.

To ensure comparability to previous work on insect and vertebrate body size distributions (Smith *et al.* 2004, Ulrich 2006, 2007) the present work is based on mean species dry weight W calculated from the arithmetic mean L of available data on minimum and maximum body length using the regression equation of Ganihar (1997)

$$W[mg] = 0.032L[mm]^{2.59} \quad (1)$$

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, 2007):

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

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

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

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

with S being the number of species, x_i the respective ln transformed body weights, and h the band width. We 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) we followed Smith *et al.* (2004) and Ulrich (2007) 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). We 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 ($\sigma^2 = \mu$, cf. Ulrich 2007). 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 Diptera.

To test whether observed body weights are regularly spaced within the observed ranges, we 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). We 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 and Graves 1996). Respective confidence limits of the null models were obtained from 1000 replicates. To compare taxa we 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 (μ = mean and σ = the standard deviation of the simulated ratios). SES values below -2.0 or above 2.0 indicate approximate statistical significance at the 5% error benchmark.

Regression slopes refer to reduced major axis (RMA) regressions computed with PAST (Hammer *et al.* 2001). Errors are standard errors.

3. RESULTS

The eastern European Diptera range from less than 0.01 mg dry weight in some *Leptocera* spp. (Sphaeroceridae) and *Culicoides impunctatus* (Ceratopogonidae) to nearly 600 mg dry weight in the south-eastern European *Satanas gigas* (Asilidae) and about 300 mg in the widespread European *Tipula maxima* (Tipulidae). They span a body weight range of more than four orders of magnitude. This is about one order less than the body weight range of European Hymenoptera and Coleoptera (Ulrich 2006, 2007).

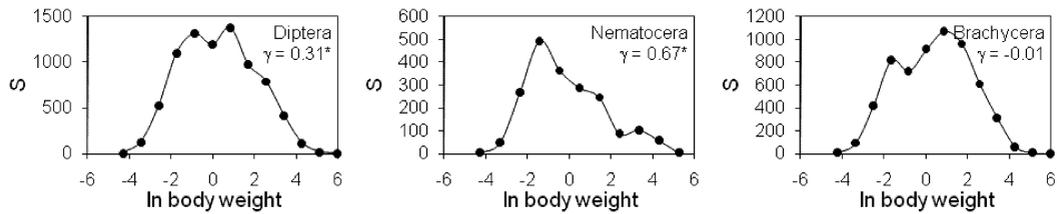


Fig. 1. Size distributions of all eastern European Diptera and the two suborders Nematocera and Brachycera. Data points denote numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk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

The body weight distributions of the all Diptera and the suborder Nematocera (Fig. 1) were significantly ($P(\gamma = 0) < 0.01$) right skewed while the respective Brachycera distribution did not show a significant skew. Three of the 13 Nematocera superfamilies had a significant right skewed SSD but none of the 22 Brachycera superfamilies. In turn, none of the Nematocera superfamilies was significantly left skewed but six of the Brachycera superfamilies. Of the 17 superfamilies with more than 100 species (Fig. 2) five had significantly left and two significantly right skewed SSDs.

We observed a similar trend for right skewed SSDs of Nematocera at the family and genus level (Fig. 3A) 17 of the 20 Nematocera families with at least five species had a positive SSD skewness and only three a negative (Fig. 3A). Of the Brachycera 34 families had a negative SSD skewness and 31 a positive. A Kruskal-Wallis test revealed a significant difference in mean skewness between Brachycera and Nematocera ($P < 0.001$). Skew was not correlated with species richness. Of 107 nematoceran genera with at least five species 43 had left and 58 right skewed SSDs (six genera had a skew of $\gamma = 0$). Of the respective 295 brachyceran genera 162 had left skewed and 131 right skewed SSDs (two times $\gamma = 0$) (Fig. 3B). A χ^2 contingency test pointed to a significant difference in skewness between Brachycera and Nematocera ($P = 0.03$). Again skew was not correlated with species richness.

The above results might indicate a trend towards pronounced skewness in higher taxa. Separate Kruskal-Wallis test for Nematocera and Brachycera comparing genera, families, and superfamilies with respect to

mean skewness gave only for the Nematocera a weak signal of increasing mean skewness with taxonomic level ($P = 0.08$).

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 we observed a significant decrease of species richness with increasing log mean body weight of genera (Fig. 3 C). Using species per genus ratios (S/G) instead of raw data strengthened this trend (Fig. 4). S/G ratios of small bodied genera were on average three to four times higher than S/G ratios of larger sized genera.

Variance – mean ratios of genus body lengths were fully consistent with a proportional rescaling pattern as predicted by Taylor' power law (Taylor 1960). The RMA scaling exponent $z = 1.99 \pm 0.02$ does not significantly deviate from the predicted value of 2 (Fig. 3D). Both ratio tests did not point to aggregated or segregated body size distributions within genera ($P > 0.5$). Further, Z standardized ratios were neither correlated with species richness nor with mean body weight of genera. Hence, body weight appeared to be randomly distributed with respect to a linear random null model.

The differences in SSD skew between Nematocera and Brachycera might be caused by a change of skewness along the body size axis. To infer such a trend we used a sliding window technique as in Ulrich (2006, 2007) and calculated mean skewness and mean body weight for a sliding window of 10 genera having more than five species ordered from smallest to largest. A significant positive correlation (Spearman' $r = 0.49$, $P < 0.0001$) between mean skewness per genus and mean ln body weight appeared for

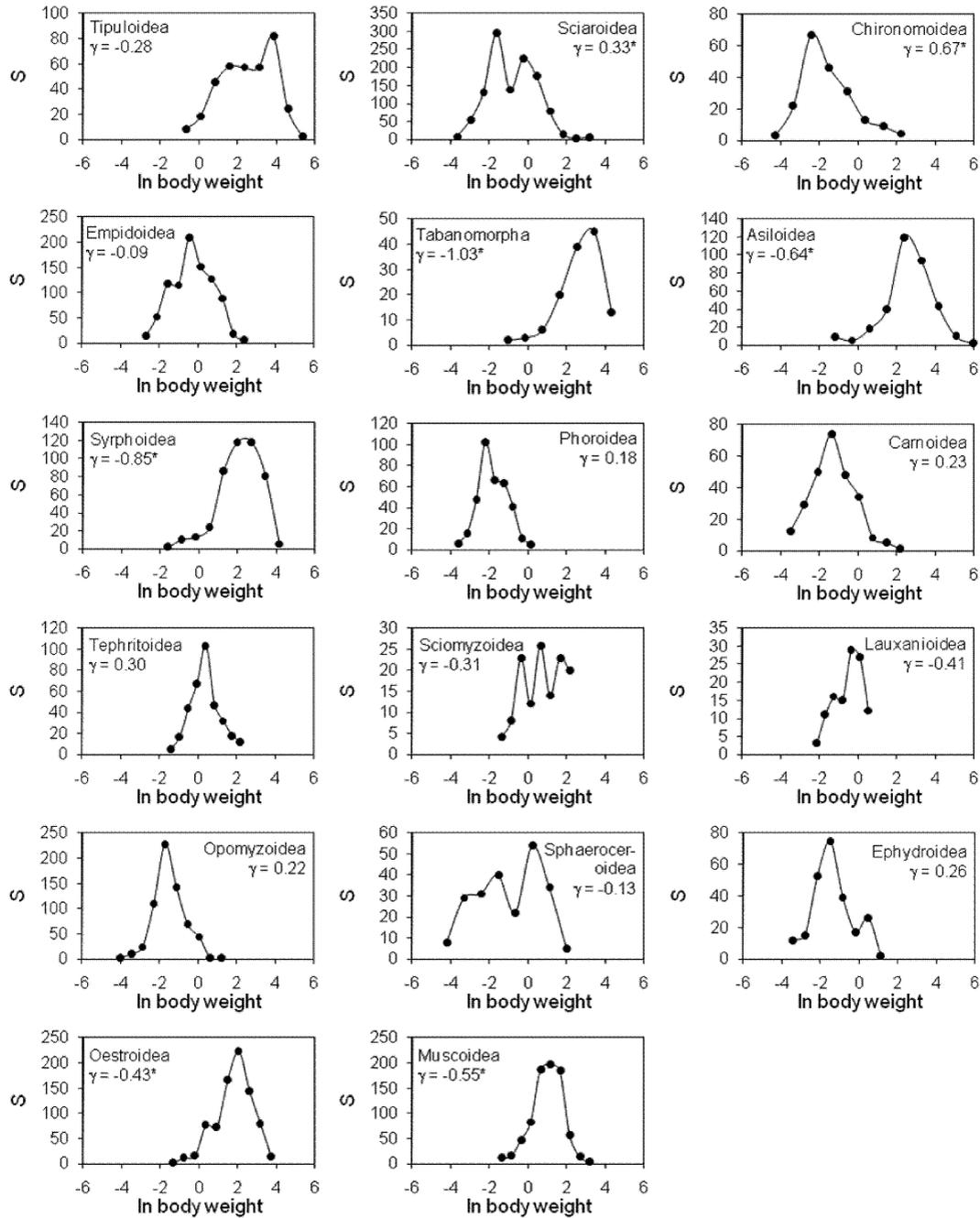


Fig. 2. Size distributions of the superfamilies of eastern European Diptera having more than 100 species. Data points denote numbers of species per size class. The number of data points reflects the number of size classes considered. Sizes are given as ln transformed body weights in mg. An asterisk after the skewness (γ) denotes that it is significant at $P < 0.01$.

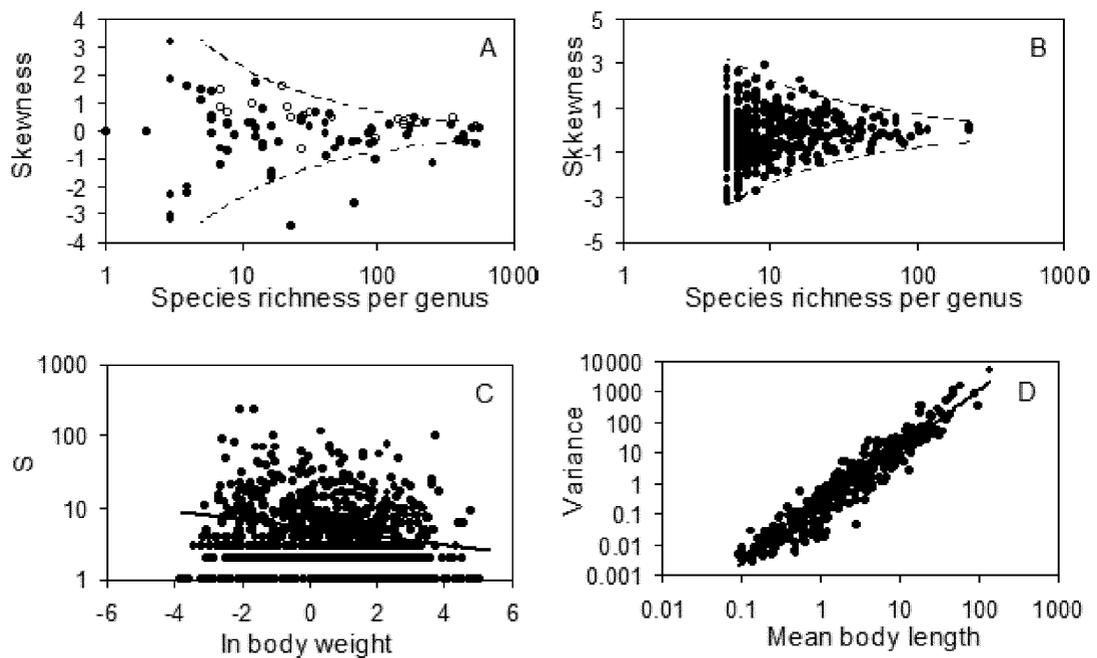


Fig. 3. A, B: Skewness of the body size distributions (ln transformed body weights in mg) of dipteran families (A) and genera (B) for all taxa with at least 5 species (S). Given are also the upper and lower 99% confidence limits according to the approximation of Tabachnick and Fidell (1996) (broken lines). Black dots in A refer to Brachycera, open dots to Nematocera. C: Species richness per genus is significantly negatively correlated with ln (mean genus body weight) ($r = -0.07$; $P = 0.006$). D: The variance – mean length relationship [$\sigma^2 = f(\mu^z)$] of central European Diptera has a RMA slope of $z = 1.99 \pm 0.02$ ($R^2 = 0.92$; $P < 0.0001$) (length is used instead of ln body weight to avoid negative values).

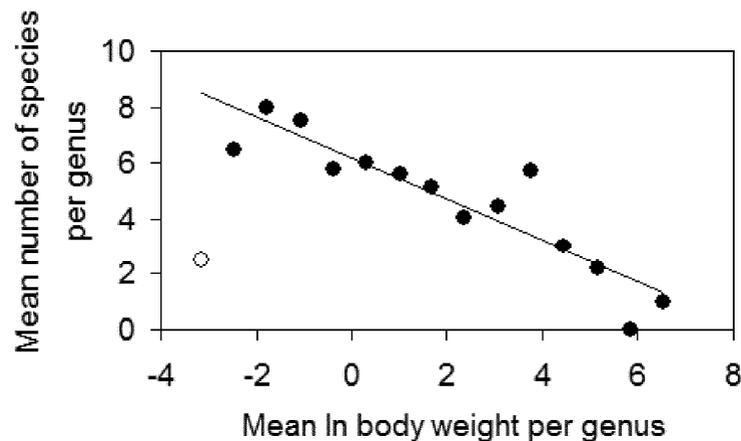


Fig. 4. Mean number of species per genus in dependence on mean ln body weight per genus for genera classified into 15 binary body weight classes. The open circle represents the lowest body weight class and is represented by only 9 genera having in total 14 species. It is not included in the regression. Regression: slope = -0.74 ; $R^2 = 0.82$; $P < 0.001$.

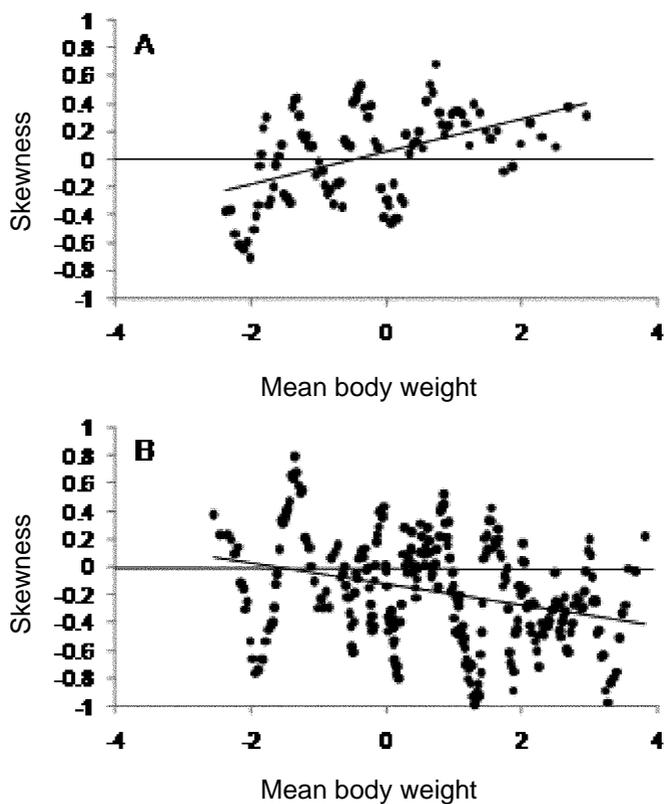


Fig. 5. Mean skewness of a sliding window of 10 genera shifted along the ranked body weights was for Nematocera (A) significantly positively (Spearman's r : 0.49 $P < 0.0001$; RMA regression slope: $z = 0.25 \pm 0.09$) and for Brachycera (B) significantly negatively (Spearman's r : -0.31 $P < 0.0001$; RMA regression slope: $z = -0.43 \pm 0.08$) correlated with mean body weight.

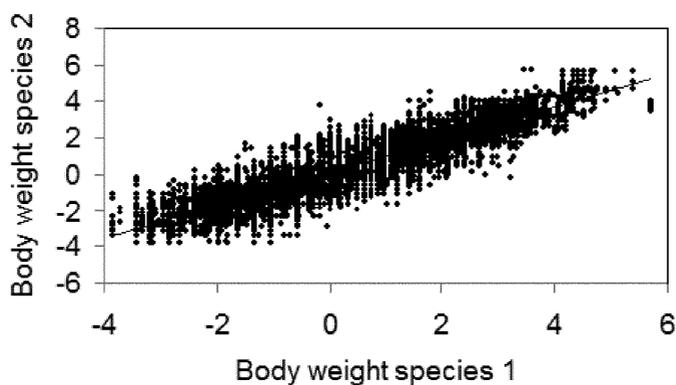


Fig. 6. Regression of body weights of congeneric species pairs for all dipteran genera with at least five species. Phylogenetic constraint (coefficient of correlation) $r = 0.91$; RMA regression slope: 0.99.

Nematocera (Fig. 5A). In turn, the mean skewness of brachyceran genera showed the opposite trend (Fig. 5B) and was significantly negatively correlated with mean genus body weight (Spearman' $r = -0.31$, $P < 0.0001$). Hence, SSDs of large sized nematoceran genera had predominately positive and those of brachyceran genera predominately negative skewness (Fig. 5).

Body size of Diptera appeared to be highly constrained when measured by the coefficient of correlation using intragenus pairwise comparisons (Fig. 6). The coefficient of correlation was $r = 0.91$. The proportional rescaling null model approaches in turn gave $r = 0.47$ and the Poisson model returned $r = 0.67$ (not shown). The observed intragenus variability in body size is therefore much lower than expected from both null models.

Of the 394 genera with at least five species and for which it was possible to determine the number of modes 34 had unimodal, 133 bimodal, 193 trimodal, 32 quadrimodal, and 2 quinquemodal SSDs. The number of modes was significantly negatively correlated with species richness ($R^2 = 0.30$, $P < 0.001$). This correlation was even more pronounced at the family level ($R^2 = 0.67$, $P < 0.001$). 40% of the families had unimodal and 30% bimodal SSDs. SSD skewness was at no taxon level correlated with the number of modes.

4. DISCUSSION

The present study is the third part of the analysis of body size distributions of European arthropods. In two previous studies (Ulrich 2006, 2007) one of us found hymenopteran SSDs to be predominantly unimodal and symmetrical (whole order $\gamma = -0.04$) while coleopteran SSDs were at least above the genus level mainly right skewed. The coleopteran pattern resembled the widespread SSD shapes of vertebrates (Kozłowski and Gawelczyk 2002, Smith *et al.* 2004).

Four major findings emerged from the present study concerning the SSDs in eastern European Diptera: 1) Nematocera and Brachycera differ with regard to the predominant shapes of their size distributions; 2), size distributions changed in an ordered manner along the body size axis; 3), intragenus variability in body size was less than ex-

pected from a random distribution pointing to certain phylogenetic constraints on body size; 4) small bodied genera tended to be species richer than genera of larger mean size.

What evolutionary factors shape size distributions? 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. In Hymenoptera Ulrich (2006) found a significant negative correlation of skewness with mean body weight per size class. Smaller sized genera had mostly negative SSD skews, large sized genera positive skews. Hymenopteran SSDs are therefore in accordance with the random diffusion model with upper and lower reflecting boundaries (Ulrich 2006). In turn, central European Coleoptera showed a very different picture (Ulrich 2007). Their skewness – body weight plots were significantly U-shaped with smaller and larger sized genera tending to have a positive SSD skewness. The present findings for eastern European Diptera reveal a third pattern (Fig. 5). We found suborder dependent negative and positive correlations between skewness and body size. This pattern is not in accordance with the diffusion model.

The above dipteran pattern might be in accordance with the hypothesis that a taxon specific speciation/extinction bias exists (Alroy 2000). According to the bias model differential extinction and speciation rates along the body size axis should result in body size dependent SSD skews (Knouft and Page 2003). Particularly higher extinction rates of larger and lower rates of smaller species should generate a trend towards left skewed SSDs at larger body sizes. If this model were to apply, genera of smaller sized species should be most species rich. This was indeed the case (Fig. 3C). Again this pattern differs from that of the Hymenoptera and Vertebrata, where genera of medium sized species are most species rich (Smith *et al.* 2004, Ulrich 2006), but also from that of the Coleoptera, where no correlation between

species richness and body size exists (Ulrich 2007).

A surprising result of the present study was the negative correlation of species richness per genus (the *S/G* ratio) with body size (Fig. 4). Such a pattern does neither occur in the previously studied Hymenopteran and Coleoptera (Ulrich 2006, 2007) nor in the Vertebrata (Smith *et al.* 2004). Of course, such a pattern might be caused by taxonomists, who split preferentially large bodied genera into smaller parts. This explanation implies fundamental differences in taxonomic practice between coleopteran, hymenopteran, and dipteran taxonomists and seems not very likely. In our view, the higher *S/G* ratios in smaller bodied genera reflect a real evolutionary trend related to a smaller morphological variability in smaller species. Detailed morphological studies have to verify this hypothesis.

As in the case of Hymenoptera (Ulrich 2006), Coleoptera (Ulrich 2007), and Vertebrata (Smith *et al.* 2004) body size of Diptera appeared to be highly constrained ($r = 0.91$; Fig. 6). Both null model approaches gave much lower values of r pointing to a lower variability in body sizes around the genus means than expected from simple statistical distributions. These and the nearly identical values for Coleoptera, Hymenoptera, and Vertebrata (Ulrich 2006, 2007, Smith *et al.* 2004) imply that the overlap in size between genera is less than expected from proportional rescaling and Poisson null models. The remarkable resemblance of r indicates that body sizes of these four very different taxa are constrained in a similar manner and possibly by similar processes.

As for Hymenoptera and Coleoptera did the intragenus variability of dipteran body sizes resemble a proportional rescaling process (Fig. 3D). The respective RMA slopes for Hymenoptera ($z = 2.30$) and Coleoptera ($z = 2.67$) are however higher than the dipteran slope ($z = 1.99$) and the theoretical expectation of $z = 2$. Hence, in Coleoptera and Hymenoptera, genera of larger bodied species have an overproportionally larger span of body weights than smaller bodied genera. Nevertheless all three patterns are consistent with speciation/extinction processes without distinct upper and lower genus specific bound-

aries in body size (although higher taxon specific upper and lower boundaries might exist). Other phyla have to be studied to see whether this finding can be generalized.

In the Hymenoptera and Coleoptera within genus variability was found to be higher in species rich genera but independent of body weight (Ulrich 2006, 2007). Hence, body weight distributions in species rich hymenopteran and coleopteran genera appeared to be more clumped than expected from the null model. The *Z*-transformed *R*-values of the ratio test were in both orders significantly positively correlated with species richness. In the present study we could not detect such a pattern for Diptera. Again Diptera differed in their size distributions from the other two large insect orders.

In summary, the present results again point to differences in body size distributions between major animal taxa. The causes of these differences are not well understood yet. Hence generalizations of patterns and models that extrapolate from findings within one taxon should be treated with caution.

ACKNOWLEDGEMENTS: Miss Hazel Pearson kindly improved our English. Thomas Pape provided information on European species richness. Paweł Trzciński helped us with the nomenclature of Syrphidae. This work was in part supported by grants from the Polish Ministry of Science (KBN, 3 P04F 034 22, 2 P04F 039 29).

5. REFERENCES

- Allen C.R., Forsy E.A., Holling, C.S. 1999 – Body mass patterns predict invasions and extinctions in transforming landscapes – *Ecosystems*, 2: 114–121.
- Alroy J. 2000 – Understanding the dynamics of trends within evolving lineages – *Paleobiology*, 26: 319–329.
- Bakker V.J., Kelt D.A. 2000 – Scale-dependent patterns in body size distributions of neotropical mammals – *Ecology*, 81: 3530–3547.
- Basset Y., Kitching R.L. 1991 – Species number, species abundance, and body length of arboreal arthropods associated with an Australian rainforest tree – *Ecol. Entomol.* 16: 391–402.
- Brown J.H. 1995 – *Macroecology* – Chicago, Univ. Press.
- Brown J.H., Marquet P.A., Taper M.L. 1993 – Spatial scaling of species composition:

- body masses of North American land mammals – *Am. Nat.* 142: 573–584.
- Calder W.A. 1984 – Size, function, and life history – Univ. Press., Cambridge.
- Chislenko L.L. 1981 – Structure of fauna and flora as dependent on organismal body size – Univ. Press, Moscow.
- Dial K.P., Marzluff J.M. 1988 – Are the smallest organisms the most diverse? – *Ecology*, 69: 1620–1624.
- Espadaler X., Gomez C. 2002 – The species body-size distribution in Iberian ants is parameter dependent – *Vie et Milieu*, 52: 103–107.
- Etienne R.S., Olf H. 2004 – How dispersal limitation shapes species – body size distributions in local communities – *Am. Nat.* 163: 69–83.
- Ganihar S.R. 1997 – Biomass estimates of terrestrial arthropods based on body length – *J. Biosciences*, 22: 219–224.
- Gaston K.J., Blackburn T.M. 2000 – Pattern and process in macroecology – Blackwell, Oxford.
- Gotelli N.J., Graves G.R. 1996 – Null Models in Ecology – Smith. Inst. Press, Washington D.C.
- Gunnarsson B. 1990 – Vegetation structure and the abundance and size distribution of spruce-living spiders – *J. Anim. Ecol.* 59: 743–752.
- Hammer O., Harper D.A.T., Ryan P.D. 2001 – PAST: Palaeontological statistics software package for education and data analysis – *Palaeontologica Electronica*, 4: 9 pp.
- Havlicek T.D., Carpenter S.R. 2001 – Pelagic species size distributions in lakes: are they discontinuous? – *Limnol. Oceanogr.* 46: 1021–1033.
- Hutchinson G.E., MacArthur R.H. 1959 – A theoretical ecological model of size distributions among species of animals – *Am. Nat.* 93: 117–125.
- Knouft J.H., Page L.M. 2003 – The evolution of body size in extant groups of North American freshwater fishes: speciation, size distributions, and Cope's rule – *Am. Nat.* 161: 413–421.
- Kozłowski J., Gawelczyk A.T. 2002 – Why are species' body size distributions usually skewed to the right? – *Funct. Ecol.* 16: 419–432.
- Kozłowski J., Weiner J. 1997 – Interspecific allometries are byproducts of body size optimization – *Am. Nat.* 149: 352–380.
- Maurer B.A., Brown J.H., Rusler R.D. 1992 – The micro and macro in body size evolution – *Evolution*, 46: 939–953.
- May R.M. 1986 – The search for patterns in the balance of nature: advances and retreats – *Ecology*, 67: 1115–1126.
- McKinney M.L. 1990 – Trends in body size evolution (In *Evolutionary trends*, Ed. K.C. McNamara) – Univ. Arizona press, Tucson, pp. 75–118.
- Morse D.R., Lawton J.H., Dodson M.M., Williamson M.H. 1985 – Fractal dimension of vegetation and the distribution of arthropod body lengths – *Nature*, 314: 731–733.
- Novotny V., Kindlmann P. 1996 – Distribution of body sizes in arthropod taxa and communities – *Oikos*, 75: 75–82.
- Oosterbroek P. 2006 – The European families of the Diptera. Identification, diagnosis, biology – KNNV Publishing, Utrecht.
- Orme C.D.L., Quicke D.L.J., Cook J.M., Purvis A. 2002 – Body size does not predict species richness among the metazoan – *J. Evol. Biol.* 15: 235–247.
- Pape T. (Ed.). 2004 – Diptera, Flies. Fauna Europaea version 1.1, <http://faunaeur.org>
- Peters R.H. 1983 – The ecological implications of body size – Cambridge, Univ. Press.
- Schmidt-Nielsen K. 1984 – Scaling: why is animal size so important? – Univ. Press, Cambridge.
- Stackelberg A.A., Nartshuk E.P. 1969 (Ed.) – Keys to the insects of the European part of the USSR – Vol V Diptera and Siphonaptera, Leningrad, part 1.
- Stackelberg A.A., Nartshuk E.P. 1970 (Ed.) – Keys to the insects of the European part of the USSR – Vol V Diptera and Siphonaptera, Leningrad, part 2.
- Silvermann B.W. 1986 – Density estimation for statistics and data analysis – Chapman and Hall, New York.
- Smith F.A. *et al.* 2004 – Similarity of mammalian body size across the taxonomic hierarchy and across space and time – *Am. Nat.* 163: 672–691.
- Strong D.R., Szyska L.A., Simberloff D.S. 1979 – Tests of community wide character displacement against null hypotheses – *Evolution*, 33: 897–913.
- Tabachnick B.G., Fidell L.S. 1996 – Using multivariate statistics – 3rd Ed. Harper Collins, New York.
- Taylor L.R. 1960 – Aggregation, variance and the mean – *Nature*, 332: 721–722.
- Ulrich W. 2005 – Die Hymenopteren einer Wiese auf Kalkgestein: Ökologische Muster einer lokalen Tiergemeinschaft – *Schriften. Forschzent. Waldökosysteme A 195*, 203 pp. (in German).

Ulrich W. 2006 – Body size distribution of European Hymenoptera – *Oikos*, 114: 518–528.
Ulrich W. 2007 – Body weight distributions of central European Coleoptera – *Eur. J. Entomol.* 104: 769–776.

Yeates D.K., Wiegmann B.M., Courtney G.W., Meier R., Lambkin C., Pape T. 2007 – Phylogeny and systematics of Diptera: Two decades of progress and prospects (In: *Linnaeus tercentenary: Progress in Invertebrate Taxonomy*, Eds. Z.-Q. Zhang, W.A. Shear) *Zootaxa* 1668, pp. 565–590.

Received after revising June 2008