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Size structure of epigeic communities of spiders, carabids and staphylinids (Araneae; Coleoptera: Carabidae, Staphylinidae)

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A b s t r a c t : The present study focuses on the size structure of whole communities and local faunas of epigeic spiders, carabids and staphylinids in Czechoslovakia. The size distribution of number of species is apparently lognormal in carabids and staphylinids. For spiders only, the size distribution of number of species has two peaks. In all groups the most abundant species of communities are species of certain size clases. The mutual size ratio of species of neighbouring size groups is discussed and amounts in three groups studied on average the value 1. 6.

INTRODUCTION

Hutchinson (1959) has drawn attention to the problem of different sizes of pairs of related sympatric species. From several examples he calculated the average length ratio of the larger to the smaller and obtained a value of 1.3. This gave impetus to the study of the size ratios for sympatric species in communities. In the sixties and seventies, several papers were published giving evidence that a regularity exists in the sequence of sympatric species size. This regularity was referred to as „the 1.3 rule". Lovtrup et al. (1974) made the regularity of the sequence with a coefficient of 1.26 ($\sqrt[3]{2}$), the basis of their concept of evolution by quantum steps (but see Roff, 1977). Summarizing a large volume of data, Roth (1981) and Simberloff and Boecklen (1981) found no statistical support that the 1.3 size ratio is a rule of nature. A lucid review of the problem was published by Wiens (1982).

The initial incentive by Hutchinson (1959) arose from his investigation of water bugs of the genus *Corixa*; later studies, however, were largely based on the examination of vertebrates – birds and mammals, viz. of pairs, less frequently groups of three or four sympatric species. Actually, the species were investigated on their own, separated from the community and their whole living environment, and disregarding their abundance. It is species rather than populations that have been subject to study. However, taking into account the fact that the size distribution in a community mirrors to a degree also competitive interactions, it is clear that the size ratios between species should be considered in the context of their relative densities (Wiens, 1982). Wiens stresses two fundamental prerequisites for the study of the size distribution: the species examined must be sympatric and they must use generally similar resources. Still, the size distribution is determined also by a number of factors other than competition. For arriving at some conclusions in this complex situation, communities with a high frequency of species occurrence have to be studied; five to ten species in a community (such as spider crabs – Hines, 1982; bumblebee – Ranta and Tiainen, 1982) are insufficient for establishing the trends in the size distribution. Therefore, we centered our attention on whole communities or a whole local fauna of epigeic spiders, carabids and staphylinids (Růžička, 1985; Boháč and Růžička, 1990).

Many researchers divide species into groups with respect to their size, often, however, in a simple integer arithmetic series (Waldorf, 1976; Nentwig, 1982). Ploeg (1980) claims that „there is no unambiguous way to divide any spider community into size classes". In spite of the critical sound of papers from the eighties, we suppose that a regularity in the size distribution in some communities does exist, though this regularity is of a type different from what has been so far considered: a regularity based on the ecological successfulness of species, on their relative abundance.

METHODS

The size structure of communities can be analysed in three ways:

1. The basic approach consists in determining some measure as mass, length of the body or a body part, etc., for all individuals from a representative sample of the community.

2. A similar but more schematic presentation of the size structure is obtained by plotting of the abundance of each species against its average size. In this manner, published data on communities can be handled if the species and their abundances are listed.

3. The third approach for surveying the size structure of the fauna of a larger area consists in handling size and abundance data for all species from the group examined in a given region.

To each size interval is attributed the number of species belonging to this interval by their mean size. This given a survey on the size pool. The distribution of abundant species in the entire fauna can be also evaluated. Classification of the abundance of species is a representation of the degree of species dominance in communities. This is, naturally, an approximation dependent on the author's personal experience, biotopes included in the territory and on the species size, as discussed previously (Růžička, 1985; 1987). Questionable, however, is the evaluation of rather rare species. Classifying a species as abundant implies that in the area studied, this species ranks among the foremost in some communities as far as its dominance is concerned. The number of species of the highest category of abundance (very abundant, very common species) in the individual size intervals then may exhibit the same maxima as the abundance in communities.

If the analysis reveals that the abundance values in dependence on size are centered into maxima about certain values whose positions are independent of the biotope or season of the year, the abundance minima can be conceived as forming boundaries, and all species can be divided into size groups separated by these boundaries.

RESULTS

We examined the size structures of the carabid fauna (379 species) over the territory of Czechoslovakia (data by Kult, 1947). The numbers of species in dependence on the body length exhibit an approximately symmetric distribution with

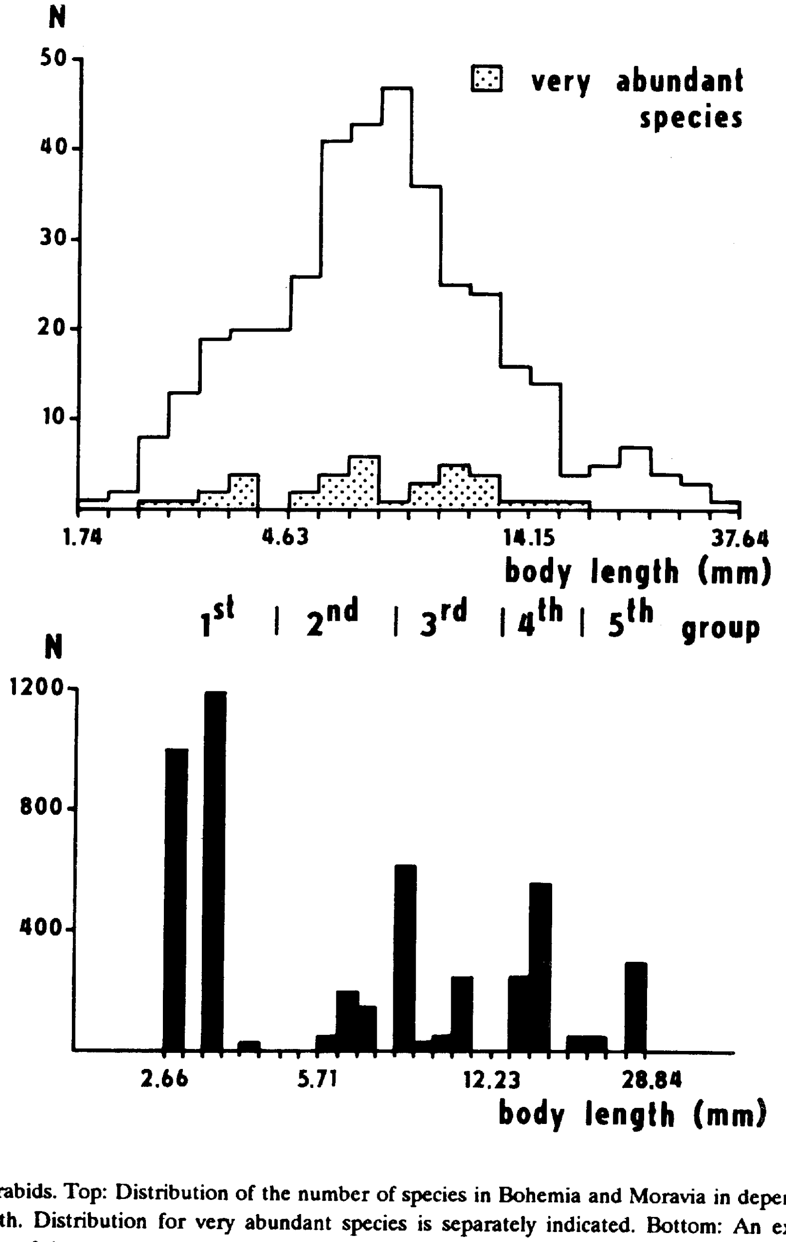

Fig. 1: Carabids. Top: Distribution of the number of species in Bohemia and Moravia in dependence on body length. Distribution for very abundant species is separately indicated. Bottom: An example of distribution of the number of individuals in a community in dependence on body lenght; Lowland forest, pitfall trapping (Obrtel, 1971).

a marked maximum at 7.5 mm. The number of common and very common species (9.3 % of all species) display three maxima (Růžička, 1985). By evaluation of published data of communities from various biotopes and correction with respect to the measurement of the size of the dominant species in the community samples, five body length groups were established, viz. up to 4.5 mm, 4.6 – 8.0 mm, 8.1 – 13.0 mm, 13.1 – 20.0 mm, and larger than 20.0 mm (Fig. 1).

The first group is represented in the communities, e. g., by species of the genera *Bembidion* and *Trechus*, the second, by species of the genera *Agonum*, *Amara*, the third and fourth, by species of the genera *Harpalus, Pterostichus*, and the fifth, by species of the genus *Carabus*.

We also examined the size structure of the fauna of staphylinid beetles (1 697 species) living in central Europe (data by Freude et al., 1964; 1974). The number of species in dependence on the body length exhibit a distribution slightly elongated to the right, with a single expressive maximum. This maximum coincides with that of the number of species of the most abundant subfamily Aleocharinae. The second most abundant subfamily, Staphylininae, assumes the region of larger body lengths (Boháč and Růžička, 1990).

By evaluation of published data of communities from various biotopes and data correction with respect to the measurement of the size of dominant species on the community samples, five body length groups were established, viz. up to 3.0 mm, 3.1 – 4.5 mm, 4.6 – 7.0 mm, 7.1 – 11.0 mm and larger than 11.0 mm. The first size group can be divided into two subgroups with a boundary at 2.0 mm, the largest species can be separated off by a boundary at 17.0 mm (Fig. 2).

The first group is represented in the communities predominantly by species of the subfamily Aleocharinae, the second, by species of the subfamily Steninae, the third, by species of the subfamilies Omaliinae, Oxytelinae, the fourth, by species of the genera *Philontus*, *Quedius*, *Lathrobium*, the fifth, by the biggest species of the genera *Staphylinus*, *Ocypus*, *Othius* and others.

Furthermore we examined the size structure of the fauna of epigeic spiders (522 species) living on the territory of Czechoslovakia (data by Miller, 1971). The species number distribution in dependence on the length of the cephalothorax exhibits two clear maxima. The maximum at 1.15 mm coincides with that of the number of species of the most abundant family Linyphiidae s. l., the maximum at 2.85 mm coincides with that of the number of species of the second most abundant family Lycosidae. An expressive minimum of the number of species occurs at 1.65 mm. The number of very abundant species (12.8 % of all species) display four maxima. The difference in the size of males and females of the same species is insignificant and only manifests itself in the position of the last maximum (Růžička, 1985). By measuring about 4 000 individuals in samples of communities, in conjuntion with the evaluation of published data of communities from various biotopes, four size groups with respect to the cephalothorax length were established: up to 1.3 mm, 1.3 – 2.0 mm, 2.1 – 3.2 mm, and larger than 3.2 mm. The first group can be divided into two subgroups, below and above 0.8 mm (Fig. 3).

The first group is represented in communities mostly by species of the family Linyphiidae, the second, by species of the genera *Pachygnatha*, *Oxyptila*, the third, by species of the genera *Pardosa*, *Pirata*, the fourth, by species of the genera *Alopecosa*, *Trochosa*.

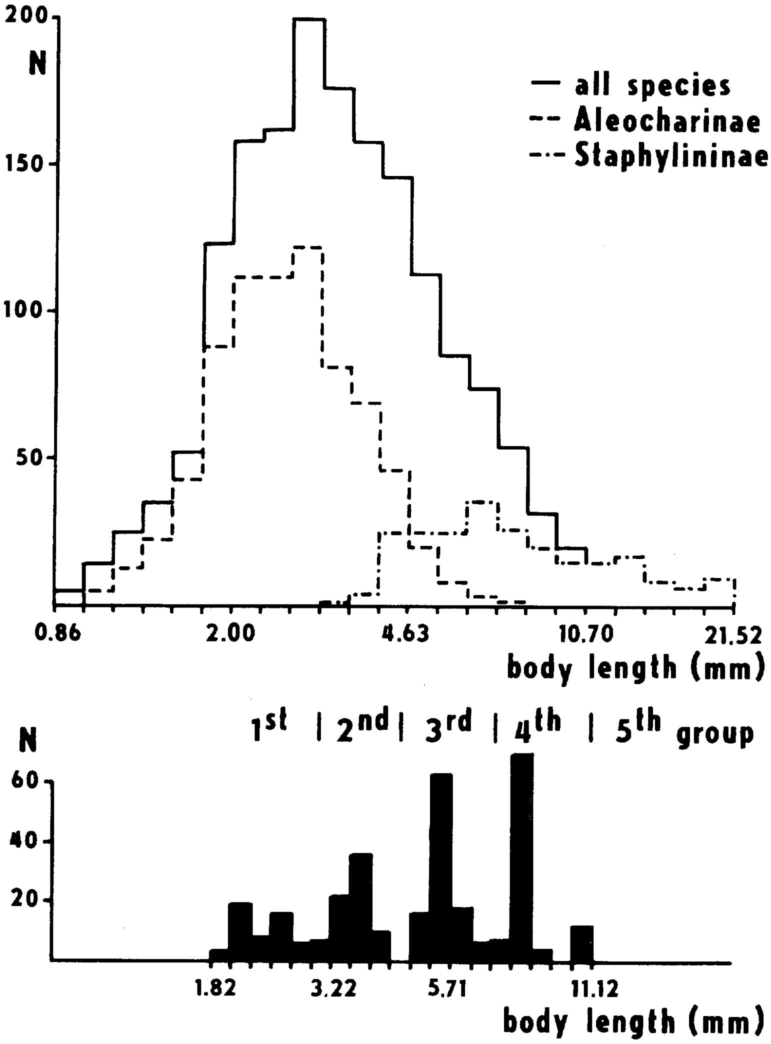

Fig. 2: Staphylinids. Top: Distribution of the number of species in Central Europe in dependence on body length. Distribution for the subfamilies Aleocharinae and Staphylininae is separately indicated. Bottom: An example of distribution of the number of individuals in a community in dependence on body length; pond littorals, quadrat sampling (Boháč and Růžička, 1990).

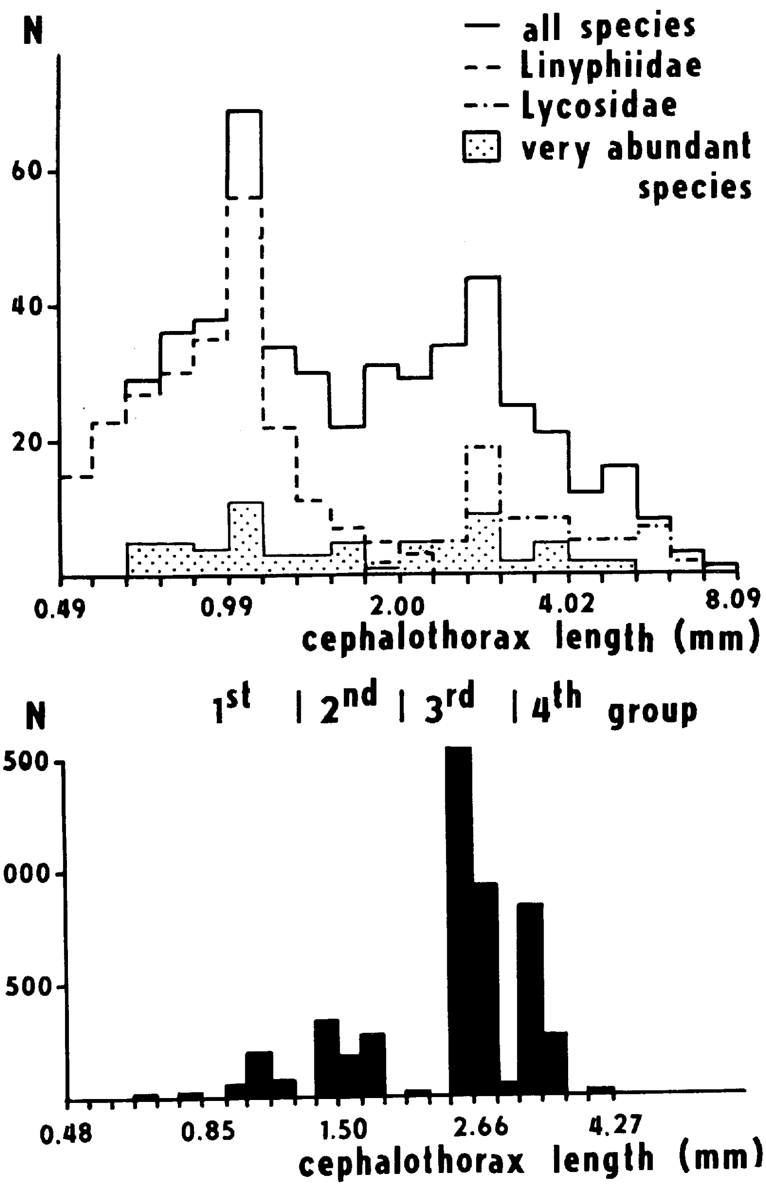

Fig. 3: Epigeic spiders. Top: Distribution of the number of species in Czechoslovakia in dependence on cephalothorax length. Distribution for the families Linyphiidae and Lycosidae and for very abundant species is separately indicated. Bottom: An example of distribution of the number of individuals in a community in dependence on cephalothorax length; meadows, pitfall trapping (Buchar, 1968).

DISCUSSION

Distribution scale

In 1959, Hutchinson and MacArthur suggested that it is „reasonable to adopt a geometric measure to the size function". Only the use of a geometric progression scale ensures an appropriate evaluation of the distribution of the abundance as well as the number of species in the regions of both low and high values; really a cephalothorax length ratio between two spider species, say 1 : 2, is as significant for small species with cephalothorax lengths of 0.4 and 0.8 mm as for big species with cephalothorax lengths of 2.2 and 4.4 mm. For low values the arithmetic progression scale division is too coarse whereas for high values this scale is too fine, and the value distribution is merkedly elongated to the right (e. g. Stanley, 1973: Fig. 1)

The use of different geometric progressions (with different quotients) does not affect the positions of the abundance maxima, their density, however, is different. Hutchinson and MacArthur (1959) advise employing a quotient of 1.3. Actually, however, this value is too coarse so that the abundance maxima in a graphical representation are not separated. For predators, for instance, the quotient should be chosen low enough to allow manifestation of minima between groups of species between which the predator-prey relation can play an important role. When studying the size structure of spider communities the quotient used must not exceed 1.10. For example, for lycosids the minimum at 3.2 mm separating the medium size and large size groups ceases to be apparent if a higher quotient is employed; and the size difference of the two groups is just sufficient for the predator-prey relationship between them to come into force (Schaefer, 1972). When handling species number data, the total number of species of the taxon under study must be, of course, also taken into account when choosing the quotient implies distribution of a low number of data into many size intervals. The details of the distribution then also depend on the choice of the scale origin. Geometric progressions with quotients of 1.10, 1.15 and 1.20 are feasible for the practice.

Adequacy of the choice of a geometric progression scale is borne out by the size groups obtained encompassing approximately the same number of size intervals.

Although several choices of body size measure exist, we selected the body length or cephalothorax length, owing to the ease of their measurement. Other measures that might suit better, such as the weight, are in an approximately exponential relationship to the length for the groups examined.

Size Pool

Hemmingsen (1934) demonstrated that for a given insect taxon on a given geographical area, the relationship between number of species and size can be approximated by a lognormal function. This confirmed also for other groups of animals by Hutchinson and MacArthur (1959). This lognormal distribution is apparently the primary representation of the size distribution.

For epigeic spiders, two clear-cut size types have developped. The maxima of the number of species coincide with the first and the third size groups, represented in communities mainly by species of the families Linyphiidae and Lycosidae. The second size group falls into the region of the species number minimum, with the cephalothorax length about 1.5 mm. This group encompasses the least number of species and is not very abundant in communities; species involved are those of the small genus *Pachygnatha*.

The size distribution in taxonomic subgroups exhibits identical features for staphylinid beetles and spiders. For the former, the most abundant in the number of species is the subfamily Aleocharinae, involving predominantly small species. The next subfamily in the species abundance sequence is Staphylininae, comprising species large in size. The spider family most abundant in species is Linyphiidae s. l., comprising species small in size, the next is the family Lycosidae, containing species large in size. For spiders, this seems to support the hypothesis that the previously separate families Micryphantidae and Linyphiidae, s. s., both comprising species small in size and having similar ways of life, hence, living in the same size niche, actually constitute a single family Linyphiidae s. l. (see Millidge, 1977).

Selection for small size (Peters, 1983, in Craig, 1987) has been suggested for spiders on three levels:

1. Levi (1980) proposed that there is an evolutionary trend toward small size for spiders in the superfamily Araneoidea. The spiders in the families Araneidae and Tetragnathidae (species with the most primitive morphologies) are significantly larger than spiders in the other families. In contrast, the Anapidae, Mysmenidae, Symphytognathidae, and Theridiosomatidae (families containig species with the most derived morphologies) are significantly smaller. Nesticidae, Linyphiidae and Theridiidae fall between these two groups in total size and morphology (Craig, 1987).
2. The most species-rich and most abundant spider family in central Europe is the family Linyphiidae, containing the smallest species.
3. Millidge (1984) divide the Linyphiid species in two major groups: Haplotracheate (with simple unbranched median tracheae) and Desmitracheate (with probably synapomorphic median tracheae trunks which branch into two bundles of narrow tracheae). Derived Desmitracheate contains the smaller species and there are species richer than Haplotracheate.

The situation is less clear with carabids. The most abundant in species are the subfamilies Harpalinae and Pterostichinae. Both comprise species of diverse body lengths (Harpalinae, 2.25 – 15 mm), the maximum of the numbers of species lies at a body length of approximately 7 mm for both subfamilies. The third in the species number sequence is the sufamily Bembidiinae. The most abundant in the number of species is the genus *Bembidion*, the second in this sequence is the genus *Harpalus*.

A completely opposite situation was found by Hutchinson and MacArthur (1959) for the fauna of dragonflies of the north-east of the USA. Large Anisoptera are represented by more species than the small Zygoptera. As against the evaluated approximately 190 species, only 65 species live in Czechoslovakia (Teyrovský, 1959). Although it is difficult to evaluate so low a number of species, the situation seems to be alike. The most abundant in species is the family Libellulidae (Anisoptera – big species), the second in this order is the family Agrionidae (Zygoptera – small species).

Our evaluation of the number of species in taxonomic subgroups also depends on the choice of the taxonomic level. Taxonomic evaluation, though, varies frequently, mirroring not only the objective reality but also the degree of our knowledge and our subjective opinion. Some trends may emerge from the evaluation of a greater number of groups, these trends, however, may not be generally valid. The situation in different groups of animals may develop in different ways.

Species Distribution into Size Groups

Abundance distribution in dependence on size may be different in different communities. For the total adult individuals in sweep samples of the insects of forest understories in Costa Rica and Massachusetts, Schoener and Janzen (1968) found the same lognormal distribution in dependence on body length as for the total number of species. Cloudsley-Thompson (1983), on the other hand, observed two definite size types for spiders in desert areas, viz. large burrow inhabiters and small nomadic hunters.

The size spectrum and its practical realization in communities depend on moisture conditions, length of the growing season (Schoener and Janzen, 1968), and on the biotope occupied and its stratum. In soil ground communities the interactions between species are apparently stronger than in other strata. This seems to be the reason why in these communities, species of a certain size are found to be preferred. For instance, for carabids the body length region of 4.02–4.63 mm encompasses approximately 20 species, similarly as the regions of 3.04–3.50 and 3.50–4.02 mm. Although the same number of species is offered, this region of 4.02–4.63 mm is not occupied to a significant extent; none of the species from this size region is classed as very abundant, a marked minimum in abundance in communities being observed in this range (Fig. 1).

The size of the organisms relates to a great many features of their life history: clutch size, age at maturity, gestation time, growth rate, life span, foraging behaviour, predation vulnerability, thermal tolerance, energy demands, etc. (Wiens, 1982). For spiders of the family Linyphiidae the size of the adults may be limited by the characteristic way of their propagation – ballooning. All these, in a more general sense, may be aspects of the r-K strategy (Pianka, 1970). Moreover, the established preference of species of a certain size pertains to adults, while interactions between species also concern beetle larvae and spider juveniles during their whole development.

The distribution of species into size groups, naturally, is not rigid and should be only construed as a trend. This distribution is unambiguous for dominant species, with respect to which the size groups have been established. Many less abundant species from the continuous pool, however, lie directly on the borders of the size groups. When classifying them into particular groups for practical purposes of coenological study, additional evaluating criteria such as the overall constitution of the body, length and strength of limbs and mouth organs, etc., are adopted.

Size Ratios

The ratios of the higher to the lower limits of the size groups are 1.63, 1.54, 1.60 for spiders, 1.78, 1.63, 1.54 for carabids and 1.50, 1.50, 1.56, 1.55 for staphylinids, hence, in average, 1.59, 1.65 and 1.54 for spiders, carabids and staphylinids, respectively. These mean values may be, however, questionable. With regard to the physique and other factors, the size group ratios may not be identical for all groups of animals. Also, the limits of these groups are determined not only theoretically but also practically; there are rounded. For practical reasons, fewer size groups were established than as actually exist. For spiders, for instance, the subgroup with cephalothorax length up to 0.8 mm is not very abundant in communities, and thus its establishment is of little value for practical coenological studies. The facts found for the three examined groups of invertebrates do not allow general conclusions to be drawn; it can only be claimed that the mutual size ratio of dominant species of nieghbouring size groups of spiders, carabids and staphylinids is in average 1.59, which is $\sqrt[3]{4}$.

Practical Application

The relative abundance (dominance) for invertebrate animals is largely calculated for species within the framework of the entire taxon. Frequently, species differing in size by an order of magnitude are thus interrelated. This is about the same as if the densities were compared for the bank voles and the stags in Central European forests. While for vertebrates the inadequacy of such an approach is apparent at first glance, for invertebrates the disproportion of their size is mostly disregarded although the proportion of 1 mm to 0.5 mm is as significant as the proportion of 1 m to 0.5 m.

The need to classify animals into groups by their size has been stressed in the Introduction. Such a division can be important for the study of trophic relations. Thus, grasshoppers, webworms or cutworms are commonly eaten by the big spider species of the family Lycosidae but they cannot serve as food to the small species of the family Linyphiidae.

Vertebratologists conventionally work with the notion of „small mammals" as a group. It can be expected that for invertebrates, also, the use of size groups may lead to coenological characteristics with a higher explanatory power.

CONCLUSIONS

In the beginning of their development, animal taxons rich in species obviously exhibit lognormal distribution of species number in dependence on body size. In the course of phylogenetic development, all properties of species including their body size are formed by many factors of the surrounding environments. The size acquired by a particular species is influenced (within the physiological limits) by the competition of other species, by food availability, by the possibilities of escape or shelter from predators etc. As a result of cumulative effects of all these factors it may occur that the species of particular size, i. e. those which are able to adapt themselves best to the selective pressure of the environment, become the most abundant species of communities. On the contrary, certain sizes prove to be „disadvantageous" from the viewpoint of assertment in the community, and there exist no species of these sizes which would be more abundant in the community. Under Central European conditions, this situation was observed in epigeic communities of carabids, staphylinids and spiders. Large offer within the size pool provides that the size structure of communities can change in the course of evolution. In relation to evolution of community size structure, the size pool can differentiate as well.

On the basis of understanding these regularities we can divide the species of a particular taxon into natural ecological groups of species of approximately the same size. It can be useful for many ecological studies, e. g. for the evaluation of dominance, degree of community similarity, biomass, food relations, etc.

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