

Diet differentiation between European arvicoline and murine rodents

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Abstract Small European muroid rodents are generally divided into species which feed on seeds and/or invertebrates and species which feed on green plant material; however, there is considerable plasticity in feeding behavior among species. Here, we analyze diets of 14 low-latitude rodent species from Western Europe based on published studies. The 77 studies were submitted to principal component analysis in order to compare diet plasticity within and between the 14 species. We observed variations in food composition of arvicoline and murine rodents which are associated with differences in morphology and habitat use. Most arvicoline rodents eat mainly green matter of the herbaceous layers of open habitats whereas most murine species are able to use a greater diversity of high energetic plant tissues from denser habitats, where they can exploit the different vegetation layers. Despite its phylogenetic position among arvicoline rodents, the bank vole (*Myodes glareolus*) shows morpho-physiological and ecological traits which tend to be more similar to murine species. These intermediate evolutionary characters seem consistent with the fact that bank voles are able to exploit a wide spectrum of trophic resources from low energetic lignified tissues to high calorific invertebrate prey. This results in a very diverse diet, which is intermediate between true herbivorous arvicolines and typical seed- and invertebrate-

eating murine species. More investigations on genetic affiliation and ecological driving forces will help understand this intermediate position of bank vole diet, and further investigations among other arvicoline species will help determine if bank voles and other *Myodes* species are unique.

Keywords Muroid rodents · Diet · Food diversity · Meta-analysis · Europe

Introduction

Rodents have long been regarded as largely herbivorous animals (Romer 1966; Anderson and Jones 1967) with a dental system adapted to gnawing and grinding vegetable food (Luckett et al. 1985). However, the most comprehensive review of rodent feeding habits to date was done by Landry (1970) who cited many authors that consider the primitive dentition of rodents to be also adapted to an omnivorous diet. Landry (1970) shows, in all major evolutionary lines, that many species can survive using only animal food resources. Evans et al. (2007) also pointed out that some rodents can periodically use animal foods. Moreover, in addition to their small size and short breeding cycle, the versatility of feeding adaptations of rodents has often been considered as the main factor responsible for their highly successful adaptive radiation (Landry 1970).

European muroid rodents are generally divided into seed/invertebrate-eating species and species feeding almost exclusively on green plant material (Hansson 1971a, 1985b). Many European Murinae species prefer invertebrate tissues and parts of plants with low-cellulose contents which need little mastication and bacterial digestion. On the other hand, as in North America, European arvicoline species such as

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Microtus are adapted to live on a low-energy diet of green vegetation, which contains a large amount of cellulose (Zemanek 1972; Holisova 1975). This difference between a high-caloric, but harder-to-get diet (seeds and invertebrates) and a lower caloric but easy-to-get diet (vegetative parts of plants) allows these two groups of rodents to live together while greatly reducing competition between them (Holisova and Obrtel 1980b). Significant differences in morphological and ecological life traits have evolved along with dietary differentiation of these small muroid rodents (Vorontsov 1962, 1979).

Within muroid rodents, Arvicolinae and Murinae are two well-discriminated subfamilies (Martin et al. 2000; Galewski et al. 2006). Muroid rodents contain 1,326 species, which are divided into 17 subfamilies (Musser and Carleton 2005) from which Arvicolinae and Murinae are the most often studied. These two subfamilies are represented in Europe by 11 and five genera, respectively. Studies on small rodents have been carried out in various ecosystems (Odum et al. 1962; Grodzinski 1971) but have often been limited by the general scarcity of detailed data on species-feeding habits (Obrtel and Holisova 1974).

In this review, we focused on some European muroid rodent species as data on their diets are abundant (e.g., Drozd 1966; Holisova and Obrtel 1977, 1980b; Hansson 1985a). Among muroid rodents of northern and central Europe, the most abundant/wide-ranging ones (e.g., *Apodemus* spp., *Myodes* (*Clethrionomys*) *glareolus*, *Microtus* spp.) have often been compared with regard to food requirements and their effects on behavior and population dynamics. Our main objective in this review was to provide a detailed analysis of diet composition and plasticity of 14 common European species and to discuss them in the light of their ecological and morphological life traits as well as their phylogenetic relationships.

Materials and methods

We performed a bibliographic survey in the Thomson-ISI Web of Knowledge/Web of Science data bank to find articles about diet of European rodent species published between 1975 and 2009. Keywords used were as follows: (diet or food or trophic) and (rodent* or *Apodemus* or *Micromys* or *Mus* or *Clethrionomys* or *Myodes* or *Microtus* or *Arvicola*). Some older papers were found by other ways. Herein, we use the denomination *Myodes* as the valid name for the genus of red-backed voles instead of the older moniker *Clethrionomys*, although we did searches for both (Musser and Carleton 2005).

In this review, we focused on European muroid rodent species whose data on diet are abundant (Holisova and Obrtel 1977, 1980b; Hansson 1985a). Sciuridae and

Gliridae were excluded to limit the review to small terrestrial species feeding mainly on ground and low vegetation layers. We also excluded European rats and hamsters (genus *Rattus* and *Cricetus*) because few detailed diet studies were available. Most retained studies concerned species living at low latitudes.

Among the available studies, we selected only those for which food data were sufficiently detailed to allow a comparative analysis. We included only publications in which relative amounts of the various food components ingested over a whole year were provided. Thus, we selected 77 studies that contained quantitative data that could be directly used or easily reworked from graphs or tables presented in these articles. The 77 studies (see Appendix) were published between 1965 and 2005 and concerned 14 species from six genera and two subfamilies). The total number of individuals and the number of seasonal surveys varied considerably between studies. Sometimes, only a yearly mean composition of the diet was available. More often, feeding habits were based on several seasonal replicates (2–20) along 1 or 2-year cycles. As our aim was to compare diet structure of the different species, we considered only the mean yearly food composition (percent volume), computed from the available seasonal data. Studies were performed in different habitats (e.g., farmland, forests, wetlands, grasslands), and food items consumed by the same species varied from one habitat to another. In the same way, different species studied in the same habitat had a great probability of feeding on the same food resources. In order to lessen this habitat effect, we did not consider specific composition of diets but only the type of food resource to which they belonged (e.g., green materials, seeds). Therefore, for all studies, we retained ten food items (see Supplementary Materials for details) as general diet structure: fungi (Fg), mosses and lichens (ML), underground vegetative parts of plants (UVP), aerial vegetative parts of plants (AVP), bark, flowers (Fl), and seeds and fruits (S-F). For animal resources, we distinguished: invertebrate tissues (Inv.) and vertebrate tissues (Vert.). The tenth category “unidentified material” (Un.), often mentioned in studies, concerns all components that did not belong to a specific plant or animal material.

A principal component analysis (PCA), carried out on correlation matrices, was used to discriminate the 77 studies (see Appendix). This PCA was performed by using the ADE-4 software™ (Thioulouse et al. 1997). As proportional data (%), relative abundances of food items were normalized by arcsine transformation (Sokal and Rohlf 1995). We generated four biplots where studies were clustered successively according to species, family, genera, and food components. This PCA was then followed by four between-groups analyses to check the effects of species, family, genera, and main food components. The statistical

significance of the dispersion of centroids on the factorial plane was tested by Monte-Carlo permutation tests ($n=1,000$ iterations).

We used Shannon's diversity index (H') (Magurran 1988) to evaluate the mean food diversity of the 14 species. Variations in H' values were tested by Hutcheson's t test (Hutcheson 1970; Heip and Engels 1974; Lande 1996). This test, based on the variance of H' and related to a Student's t test was computed using R software (R-Development-Core-team 2008). We carried out Hutcheson's t test for multiple comparisons on a 13×13 species matrix. *Arvicola sapidus* was excluded as its diet contained only one food category (aerial vegetative part of plants) and could not be submitted to food diversity computation.

Results

Diet composition according to taxonomic and ecological status

The first factorial plane (PC1 \times PC2) accounted for 42.5% of the total variance of data extracted from the 77 studies (Fig. 1e). The four analyses (Fig. 1 a–d) showed that dispersion of centroids on the PCA factorial plane was statistically significant (Table 1) indicating that centroids are significantly different from one another. However, variability occurred within each group which was probably dependent on habitat, season, and sample size effects. It explains the partial overlap of the different groups.

Variables AVP, ML, and S-F showed the greatest absolute contribution to PC1 axis (Table 2) indicating this first principal component discriminated diets of high caloric value (right part of PC1 axis) which are dominated by important amounts of seeds, fruits, and some animal food (Fig. 1e) from diets of low energetic value (left part of PC1 axis) consisting of mostly diversified green vegetation food (e.g., leaves, stems, mosses, lichens). The variables Fg, Bark, Un. and Inv. had the greatest absolute contribution to PC2 axis (Table 2) which tended to discriminate studies of species feeding mainly on plants to those feeding on bark, fungi, invertebrates, and some other unidentified material. Fl, Vért., and UVP were poor discriminating factors of the studies (Table 2).

The PC1 axis allows the discrimination of diets according to species (Fig. 1a), subfamilies (b), main food components (c), and genera (d). On Fig. 1c, the three main food components were constructed as follows: herbivorous (green vegetable material covering more than 50% of the diet), granivorous–insectivorous (animal with seeds and floral parts covering more than 50% of the diet), and mixed food (diet more balanced with no component exceeding 50%). Centroids of the various clusters (Fig. 1a–c) offer good

discrimination. *Arvicola* species are situated in the top left part of the factorial plane in Fig. 1a indicating a diet almost strictly based on aerial vegetative parts of plants. *Microtus* species had more food items in their diet. The bank vole, *M. glareolus*, was in an intermediate position between the herbivorous species and the insectivorous/granivorous species (*Apodemus* spp., *Mus musculus*, *Micromys minutus*) that feed mostly on invertebrates and higher energetic plant organs. PC1 illustrated the shift from herbivorous to granivorous–insectivorous diets (illustrated by the double-arrow on Fig. 1a).

Cluster analysis according to subfamilies (Fig. 1b) showed that Murinae was well distinguished from Arvicolinae along this gradient, although some studies on *Apodemus* and *Myodes* species diverged from the centroid of their taxonomic group (see Fig. 1a for details). This result can be better highlighted by clustering the studies according to main food components (Fig. 1c). In this case, all studies on *M. glareolus* were considered of mixed structure (see Fig. 1d for comparison). We observed a clear segregation of the three groups with most of *Microtus* and *Arvicola* studies in one part and most studies on *Mus*, *Apodemus*, and *Micromys* species in another part, all of which were well differentiated from studies on *M. glareolus* (Fig. 1d).

Species food diversity

We computed mean diet composition and diversity indices for the different species (except *A. sapidus*, see [Materials and method](#); Fig. 2) by averaging data from each study. The diet structure of herbivorous species (*Arvicola* and *Microtus* spp.) was generally less diverse ($0.74 < H' < 1.74$) than diet structure of murine species ($1 < H' < 2.01$) which fed both on plants and animals and always selected highly concentrated plant organs. *Microtus arvalis* was the only species showing diet diversity not significantly different from six out of the seven murine species. Among all species, *M. glareolus* showed the most diverse diet ($H'=2.25$), reflecting the fact that this species ingests significant amounts of fungi, invertebrates, and diverse plant organs. Hutcheson's t test indicated that bank vole was the only species whose diet diversity was not significantly different from that of most murine species (*Apodemus sylvaticus*, *Apodemus flavicollis*, *Apodemus alpicola*, *M. minutus*) but was always significantly more diversified ($P < 0.02$) than all the other arvicoline species (*Microtus* spp. and *Arvicola terrestris*).

Low versus high energetic food intake

All studies were finally grouped into a three-dimensional graphical representation according to dietary energetic value of food items (Fig. 3). For that, food items were distributed in three main components following groupings

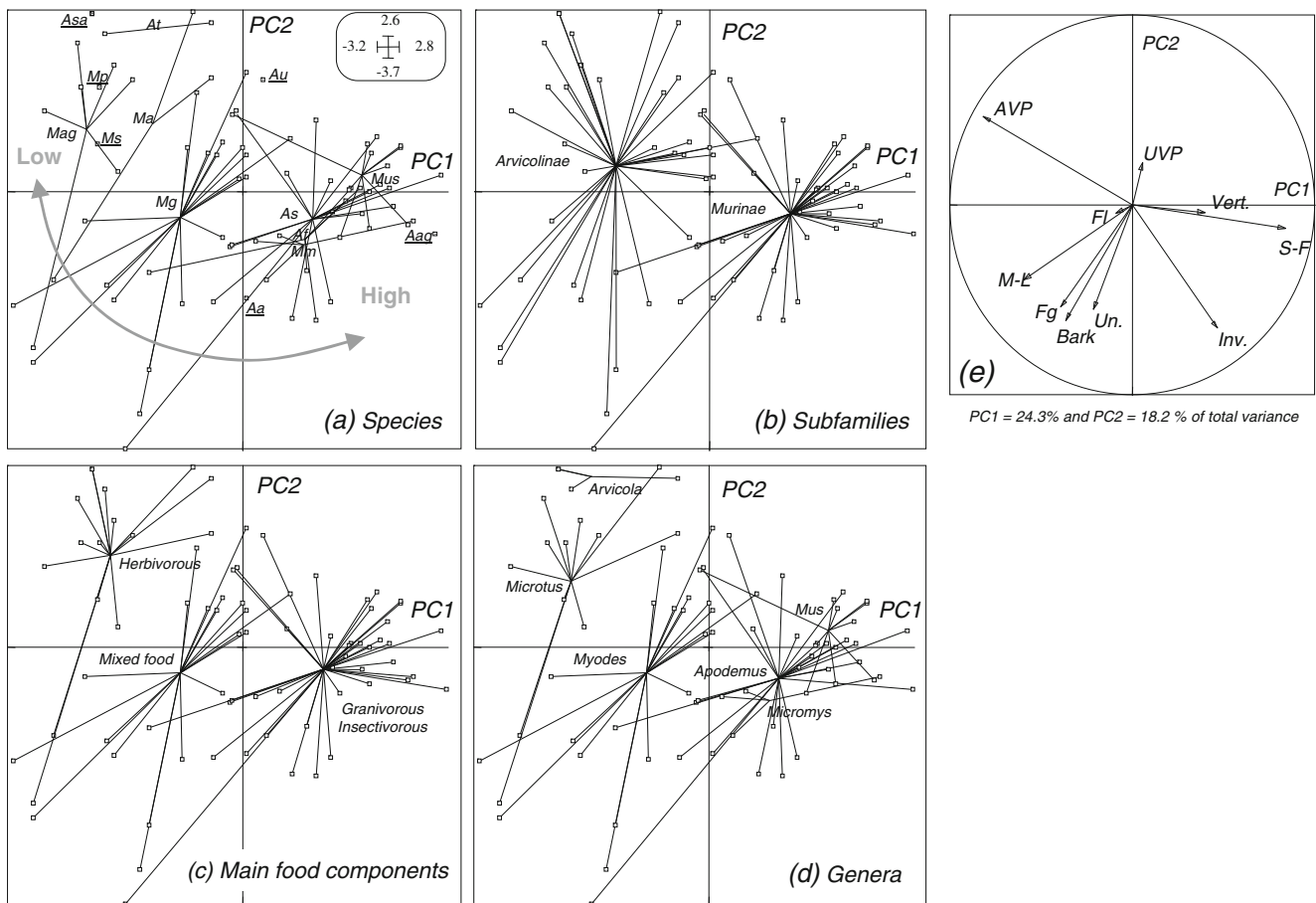


Fig. 1 Graphical interpretation of the principal components analysis (14 species, 77 studies). Positions of each study (*squares*) result from proportions of the ten food categories (see *Appendix* for details). PC1–PC2 factorial maps of studies are shown according to four different groupings: species **(a)**, subfamilies **(b)**, main food components **(c)**, and genera **(d)**. Fig. 1e is the correlation circle of the PCA representing the contribution of the different diet components to PC1–PC2 factorial maps (see *Table 2* for food components abbreviations). *Lines* represent connections to centroids of the different diet studies

according to these different groups. When only one diet study was available, species have been *underlined*. The *double arrow* indicates the shift from low energetic herbivorous diets to more concentrated energetic plant and animal diets. Species abbreviations: Asa (*A. sapidus*), At (*Arvicola terrestris*), Mp (*Microtus pyrenaicus*), Ma (*M. arvalis*), Mag (*Microtus agrestis*), Ms (*Microtus subterraneus*), Mg (*M. glareolus*), Au (*Apodemus uralensis*), As (*A. sylvaticus*), Af (*A. flavicollis*), Aa (*Apodemus alpicola*), Aag (*Apodemus agrarius*), Mm (*M. minutus*), Mus (*M. musculus*)

generally observed in published studies: animal food, concentrated plant food (flowers, seeds and fruits), and low energetic plant food (fungi, mosses, lichens, roots, bulbs, buds, stems, leaves, barks). Flowers can be of low

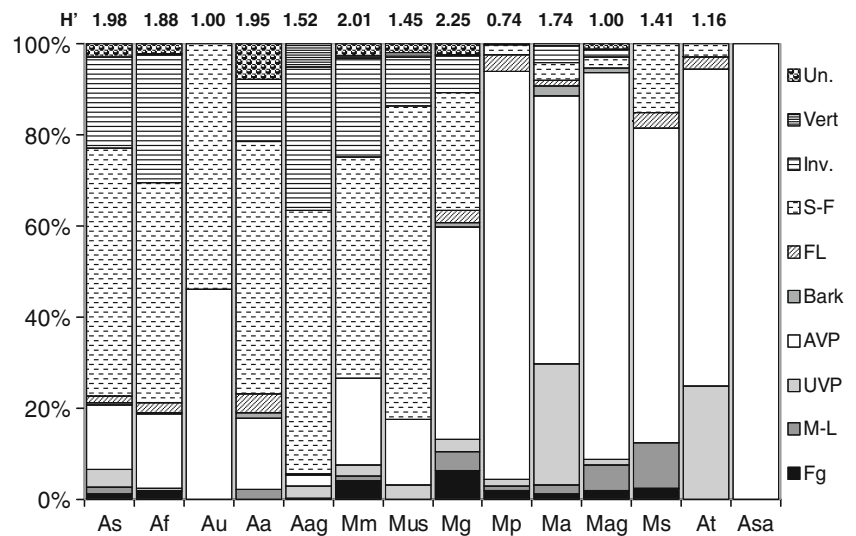
Table 1 Relative proportions of between-groups variance and *P* values of the Monte-Carlo permutation test for between-groups significance in the PCA dataset according to sub-families, genera, species, and main food components

	Between-groups variance (%)	Between-groups significance
Sub-families	16.53%	<i>P</i> <0.001
Genera	26.39%	<i>P</i> <0.001
Species	35.64%	<i>P</i> <0.001
Main food components	21.85%	<i>P</i> <0.001

Table 2 Absolute contributions of the ten food items to the two first principal components of the PCA analyses

	PC1	PC2
Fungal tissues (Fg.)	629	1,595
Mosses and lichens (M-L)	1,442	855
Underground vegetative part of plants (UVP)	13	269
Aerial vegetative part of plants (AVP)	2,724	1,169
Bark	543	2,025
Flower tissues (FI)	32	11
Seeds and fruits (S-F)	2,881	86
Invertebrate tissues (Inv.)	892	2,319
Vertebrate tissues (Vert.)	651	9
Unidentified materials (Un.)	187	1,658

Fig. 2 Mean diet structure of the 14 European small rodent species computed from 77 studies. For each species (except *A. sapidus*) the Shannon diversity index (H') was computed on the basis of the ten food items listed in Table 2 and detailed in Supplementary Materials

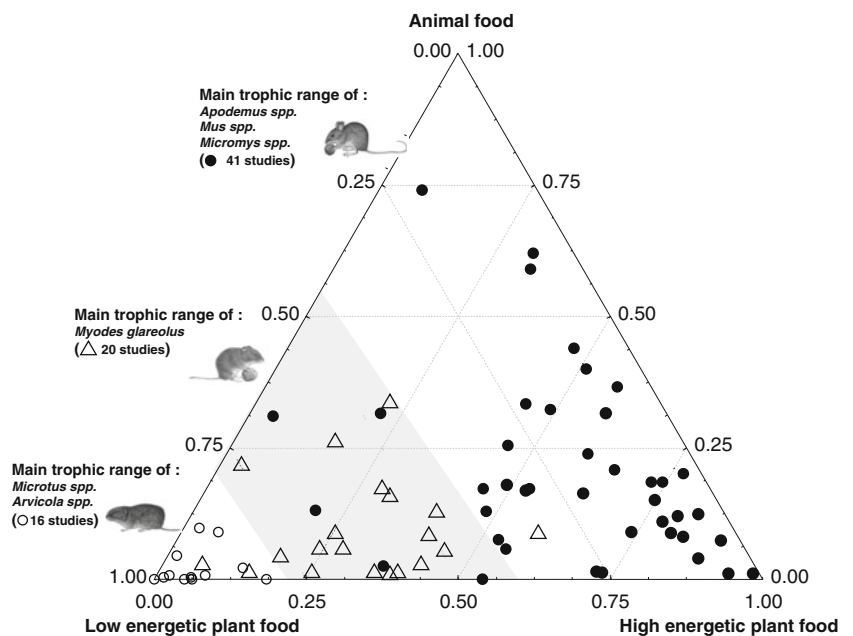


energetic content but are generally grouped with seed and fruits in published studies. Moreover, they generally represented low amounts in the diet and appeared as an unimportant factor in our study (see Fig. 1e). *Microtus* and *Arvicola* species were similar with no or very low proportions of animal or high energetic plant resources in their diet. Conversely, studies on *Apodemus*, *Mus*, and *Micromys* species showed more variable diets most often based on concentrated plant organs although there are some rare studies with occasional high proportions of animal food or important ratio of low energetic resources (Fig. 3). Most studies on *M. glareolus* appear in intermediate position (gray area on Fig. 3).

Discussion

There are lot of studies dealing with diet composition of small European rodent species, but most often only few species are involved in comparative syntheses (Hansson 1971a; Holisova and Obrtel 1977, 1980b; Canova and Fasola 1993). Our analysis based on 77 studies clearly discriminated the diets of 14 species whatever the clustering method used (species, families, main food components, and genera). Of course, we observed an important amount of variability within each grouping resulting probably from a habitat or a season effect depending on studies. For a given species, living in different habitats at different latitudes, the

Fig. 3 Three-dimensional graph of 77 European small rodent diet analyses. Food categories are grouped as animal food, low energetic, and high energetic plant resources (see Supplementary Materials for details). Main trophic ranges of each species group are delimited (gray area for *M. glareolus* alone)



available resources as well as the energy needs are variable and may strongly influence food choices. This is why, in our study, we considered only mean diet structure rather than diet composition or quantity. Based on these data, our results demonstrated more clearly that diet structure remained unchanged along these gradients. This was still the case when considering food diversity and food energetic level of species. For example, we showed that microtine species remain grass-eaters regardless of the climatic conditions they experience, corroborating some previous reports of Hansson (1971a) and Wheeler (2005). Similarly, based on 41 studies from different countries and habitats, we found mice species (*Apodemus*, *Mus*, and *Micromys* spp.) to be fundamentally seed-eaters from south to north Europe. Up to now, seeking high-energy resources (invertebrates, seeds) has mainly been reported only for *Apodemus* species (Hansson 1971a; Canova 1993).

Following our results, we think that latitude and body size influence mainly the amount of food ingested rather than diet structure of species and that various phylogenetic and anatomical constraints can be linked to our observations resulting from our discriminating analysis. Vorontsov (1962, 1979) gave a general account of the morpho-physiological changes which appeared during the shift from albuminous to cellular types of food, linked to the Miocene transition of the landscape towards steppes. He also mentioned some ecological traits connected with these nutritional and anatomical differences. For example, arvicoline species have reduced home ranges, low mobility, and more diurnal activity. They ingest greater amounts of food, generally do not provision food, and show a digestive physiology better adapted to low energy food, e.g., a longer digestive tract, larger cecum, and important intestinal microbial activity (Kellner 1956). Ever-growing molars, teeth structure, and development of masticatory musculature are also characters differentiating arvicoline from murine species. Reduced length of extremities (mainly hind legs and tail) is generally observed (Hansson 1971a), and smell, sight, and taste are also reduced (Martin et al. 2000). These characteristics are generally associated with a shift from closed to open habitats (Grodzinski 1962; Hansson 1971a). For example, voles are mainly associated with grassland habitats. They also show less complex social organization and mating systems, but are generally more prolific than murine species. Conversely, Murinae generally have long tails, large eyes and ears, are often habitat-generalist species, and show some specializations in their social structures and mating systems (Martin et al. 2000). They also have morphological traits, such as long hind legs that are characteristic of highly mobile species with large home ranges, and their activity is essentially nocturnal. They are known to select concentrated food resources and store foods (Hansson 1971a). They also have typical brachyodont

molars and their digestive tract (mainly the cecum) is reduced compared with arvicoline species. All these differences are consistent with our findings discriminating clearly diet structure of Murine and arvicoline species.

Variability of morpho-physiological life traits of rodents is often interpreted in the light of their genetic relationships (Robinson et al. 1997). According to many authors (Steppan et al. 2004; Jansa and Weksler 2004), the murine lineage split from the arvicoline lineage ca. 20 million years ago. Among Arvicolinae, there are many morphological and genetic studies (Catzeflis et al. 1987; Bonhomme et al. 1985; Michaux et al. 2001; Steppan et al. 2004) suggesting that *Microtus* and *Arvicola* species are more closely related to one another than to *Myodes* species but Niethammer and Krapp (1982) considered the genera *Microtus* and *Myodes* to be more closely related to each other. Although some controversial opinions still remain, these phylogenetic results offer a good basis to discuss the evolution of feeding life traits within muroid species.

An important result emerging from our study is the singular intermediate position of *M. glareolus* among all other rodent species. This intermediate position was confirmed whatever the diet clustering method (species, main components, genera) or the diet characteristics (diversity, energetic level) used. This intermediate phylogenetic position of *M. glareolus* and its specific feeding and morphological characteristics was already pointed 20–30 years ago by Hansson (1971a) but comparisons were done only with two other species (*A. sylvaticus* and *Microtus agrestis*). Hansson (1971a) suggested this intermediate position can be related to corresponding differences in the intestinal microbial composition (Kellner 1956). It has also been reported that bank voles store food during winter, but in lower quantity than *Apodemus* species. Food storage has rarely been reported for most other arvicoline species (Gebczynska 1983). It is also interesting to note the intermediate specificity of ear and tail sizes as well as teeth morphology of *Myodes* species (Raczynski 1983; Chaline et al. 1999).

Hansson (1985b) pointed out that while the phylogenetic position of *M. glareolus* was much the same as that of other *Myodes* species (*Myodes rutilus*, *Myodes rufocanus*), the diets of these two other vole species are more like those of other arvicolinae. This indicates that more investigation is needed to clarify the intermediate trophic position of the bank vole. Galewski et al. (2006) have pointed a possible closer relationship between *Microtus* and *Myodes* as suggested by Martin et al. (2000). So, other phylogenetic placements of bank voles cannot be rejected, and such alternative placement would make interpretation more complex. In this way, dietary data may help to confirm or reject alternative phylogenies.

While phylogeny likely influences the diet of most species, variation in diet characteristics may also be

connected to habitat preferences. Many rodents colonized the primeval forests of Europe, and today, the geographic range of many species is determined by the extent of forest habitats (Raczynski 1983). Many reports on habitat affinities of the bank vole (Corbet and Southern 1977; Wrangel 1940; Mazurkiewicz 1991) appear very similar to those of most murine species (Dickman 1986; Angelstam et al. 1987). Most studies consider typical habitat of bank vole to be forest with dense understory which is very different from grass-dominated habitats of most other arvicoline species (Hansson 1971a,b). Consequently, it is not surprising that *Apodemus* species (upper Miocene lineages) show diets partly similar to the much younger lineage of *Myodes* species because they both live in the same habitats. We may suppose that these habitat affinities together with morphological constraints dependent on phylogenetic affiliation are all factors leading to the intermediate characteristics of the diet of bank vole revealed by our analysis.

Moreover, as in murine rodents like *Apodemus* and *Micromys* species, bank voles are able to use arboreal vegetation (Montgomery 1980; Tattersall and Whitebread 1994) which has rarely been reported in *Microtus* or *Arvicola* species. Many authors have often pointed out the overlapping use of space by both *Apodemus* and *Myodes* species that dominate the rodent communities in the forested biotopes of central Europe and their possible interspecific competition (Geuse and Bauchau 1985; Fasola and Canova 2000). Inversely, there are few reports of competition between bank voles and other arvicoline species, while *Microtus* and *Myodes* voles are reported to co-exist (Eccard and Ylönen 2003).

To conclude, our study based on an important data bank showed that diet structure of most European rodent species can be differentiated according to different structural characteristics. These differences can be linked to phylogenetical and morphological constraints as well as habitat affinities. Nevertheless, further investigations on diets among arvicoline species would be useful to determine if bank voles, and more generally *Myodes* species, are unique among the other European small rodent species.

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