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Clethrionomys food: generic, specific and regional characteristics

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Clethrionomys voles are in the middle of a small rodent gradient from the folivorous, partly bryophagous, lemmings and *Microtus* to the granivorous, and even insectivorous, mice. Also within the *Clethrionomys* genus there is a similar but less diverse gradient from the partly folivorous *Clethrionomys rufocanus* to the partly granivorous *Clethrionomys rutilus*. Both *Clethrionomys gapperi* and *Clethrionomys glareolus* show regional differences in diet, with emphasis on, respectively, seeds and fungal tissues in deciduous and coniferous forests. Fungi are important in decomposition in taiga forests and may constitute a rich source of food.

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Small rodents show a gradient from folivorous to granivorous modes of feeding. At the extreme ends there are further adaptations: Lemmings usually consume large quantities of moss — an item eaten by few other animals — besides other green vegetation, and certain granivorous mice species are temporarily insectivorous. *Clethrionomys* are in the middle of this gradient but show fairly great variability in their food habits.

Lemmus and *Myopus* eat moss to a large extent during the winter part of the year but supplement this diet to a considerable degree by graminids during summer (Hansson 1969, unpubl., Kalela & Koponen 1971, Batzli & Pitelka 1983). Instead, *Dicrostonyx* is closer to *Microtus* and even *Clethrionomys* in their food habits (Batzli & Pitelka 1983). The diet of *Microtus* species is generally dominated by graminids but forbs are preferred and eaten in large amounts in summer (Zimmerman 1965, Gebczynska 1970, Stenseth et al. 1977). In winter, food even rougher than grass is taken, for example, bark, especially at high vole densities (Hansson & Larsson 1978). Seeds are eaten in small quantities during late summer and to a larger extent in, for example, *Microtus arvalis* (Holisova 1959), than in *Microtus agrestis* (Hansson 1971a). *Arvicola* is fairly similar to *Microtus* as regards food composition (Holisova 1976). The *Clethrionomys* species show certain interspecific differences, described below, but generally they do not eat grass. Forbs and forb-like green vegetation is the main food and seeds are often consumed in large quantities. Fungi function as a substitute for seeds. In winter some *Clethrionomys* species also consume considerable amounts of bark. The European *Apodemus* species are pronounced granivores and seeds dominate the food all year round (Hansson 1985a). In some areas or habitats animal food, mainly insects, is an important food component in spring and early summer. Bark and grass are almost never eaten and forbs are taken in only minute quantities. The American *Peromyscus* species have food habits (Baker 1968) very similar to the European *Apodemus* species. The cosmopolitan wild-living *Mus* compete with both the latter genera for seed and animal food (Whitaker 1966, Berry & Tricker 1969).

Clethrionomys rufocanus is a specialist of *Vaccinium* dwarf-shrubs. *Vaccinium myrtillus* stems dominate the food in winter while forbs are eaten in largest amounts in summer (Kalela 1957, Hansson & Larsson 1978). Moss and grass are also taken to some extent in summer and bark of, for example, *Betula nana*, in winter. In Japan, *C. rufocanus* is regarded as an important pest of forest seedlings (Nishiguchi et al. 1977) and this species may in places consume considerable

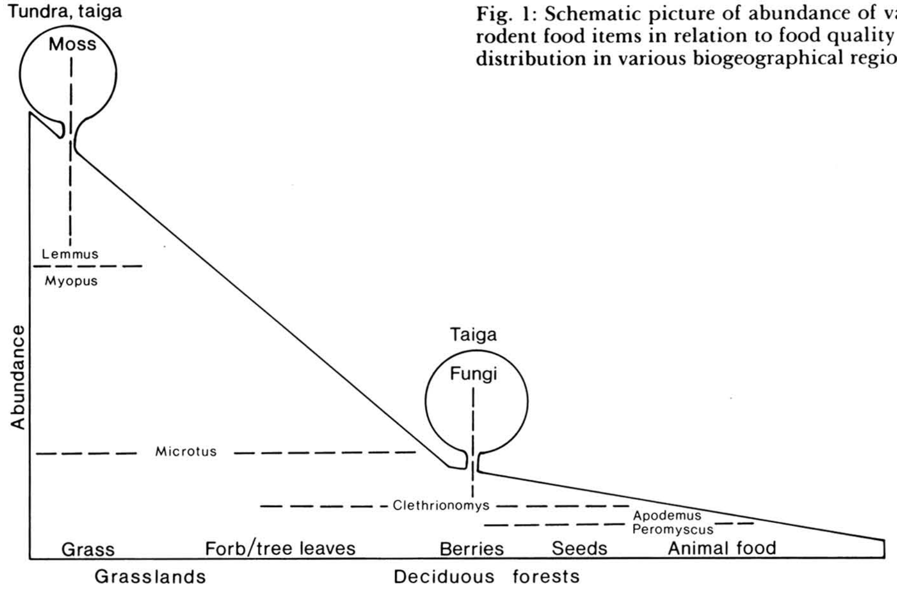

Fig. 1: Schematic picture of abundance of various small rodent food items in relation to food quality and of their distribution in various biogeographical regions.

amounts of bark in winter. It is obviously a more folivorous species than the other common *Clethrionomys* voles.

Clethrionomys rutilus appears at the other end of the spectrum. It prefers seeds and berries while few green vegetables are accepted (Grodzinski 1971). Fungi and chordate tree lichens are eaten in considerable quantities (Koshkina 1957). Insects are taken in summer (Grodzinski 1971). The granivorous habits of *C. rutilus* are also indicated by their low relative water consumption (Hansson 1971b), which was similar to that of the *Apodemus* species. *Clethrionomys glareolus* and especially *C. rufocanus* had much higher relative water consumption but still considerably lower than *M. agrestis*.

Clethrionomys gapperi and *C. glareolus* take an intermediate position in the *Clethrionomys* food habit gradient: *C. gapperi* eats much fungi, including hypogeous species, during summer and autumn in the western North America (including Rocky Mountains), while seeds are taken in larger amounts in winter (Merritt & Merritt 1978). Few insects are eaten. Maser et al. (1978) stress the mycophagous habits of West American *C. gapperi* and indicate a coevolution between these voles (and also *C. rutilus* and *C. californicus*), the hypogeous fungi and the coniferous tree species (the latter of which rely on mycorrhizal symbiosis). However, *C. gapperi* in South Manitoba at the southern limit of coniferous forests ate hardly any fungi at all (Perrin 1979) and there forbs and seeds dominated the diet. Voles from West Virginia and elsewhere in eastern United States had an intermediate diet (Schloyer 1979).

The diet of central European *C. glareolus* from deciduous forests is dominated by forbs, tree leaves and large tree seeds (e.g., Holisova 1971, for a general survey see Hansson 1985a). Some insects are eaten in spring. In planted spruce forests in central Europe *C. glareolus* eats far less seeds while fungi are more frequently consumed (Holisova & Orbtel 1979). In taiga coniferous forests in Scandinavia hardly any seeds or insects are taken (Hansson & Larsson 1978, Hansson 1979), while berries are eaten in late summer, fungi in summer-autumn and chordate lichens at least in winter-spring. The summer forb food is partly replaced by a dwarf-shrub (*Vaccinium*) diet in autumn-winter. However, the main change from central Europe is from easily digested and nutritious seeds to hard-digested and nutritionally diluted fungi and lichens. Bark is eaten in winter in both central and northern Europe (Holisova 1971, Hansson & Larsson 1978).

Within the *Clethrionomys* genus there is thus also a gradient from folivorous to granivorous animals, viz. from *C. rufocanus* to *C. rutilus*. These differences are most probably genetic. Many other species attributes correlate with the degree of granivory or folivory (Vorontsov 1962, see also Hansson 1985b). Thus different morphological, behavioural and population characteristics of the various *Clethrionomys* species may basically be related to food (and habitat) adaptations. The sluggish and clumsy behaviour and the large size of *C. rufocanus* and the alertness of the slender *C. rutilus* are certainly related to the different ways of feeding but there might be many other much more subtle differences caused primarily by the nutritive adaptations. However, within the distributions of at least the two species *C. gapperi* and *C. glareolus* there are regions where the food is dominated by fungi (including lichens) and by seeds, respectively. Generally, feeding on fungal tissues is much more common in coniferous than in deciduous forests. Such specializations may also cause differences in other characteristics, regardless of whether the different food habits are maintained environmentally or genetically.

How the diet depends on the availability of various food items is poorly known for *Clethrionomys* species. There have been several calculations of energy consumed in relation to energy available, for example, by Gorecki & Gebczynska (1962) for *C. glareolus* in central European deciduous forests and by Grodzinski (1971) for *C. rutilus* in an Alaskan taiga forest. Such estimates usually demonstrate a large energy surplus but the "available" energy is seldom broken down into more and less important components. However, Hansson (1971b) and Jensen (1982) pointed out that seeds may be a limiting food resource in at least beech forests in low beechmast years and Drozdz (1966) demonstrated a change in *C. glareolus* diet in such a forest from beechmast to especially fungi when the seeds were sparse. Jensen (1982) estimated the total small rodent consumption of beechmast to 1-10% in mast years but 30-100% in non-mast years. The consumption in relation to available energy was lower in South Polish coniferous than deciduous forests (Grodzinski, pers. comm.), but then "available" was at least partly determined from the food habits of the rodents in the deciduous forest. However, fungi play a more important role in coniferous than in deciduous forests, especially as regards decomposition where they at least partly replace bacteria. Food abundances decline abruptly from grass and forbs to seeds and insects (Fig. 1), but an exploitation of fungal tissues in taiga forests (as well as moss in both taiga and tundra) opens up a new abundant source of energy.

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