



# Cyclic small rodents in boreal forests and the effects of even-aged forest management: Patterns and predictions from a long-term study in southeastern Norway

Per Wegge<sup>a,\*</sup>, Jørund Rolstad<sup>b</sup>

<sup>a</sup> Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1432 Ås, Norway

<sup>b</sup> Department of Forest Genetics and Biodiversity, Norwegian Institute of Bioeconomy Research, 1431 Ås, Norway



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## ABSTRACT

Small mammals, especially microtine rodents, play an important role in the dynamics of boreal forest ecosystems. Even-aged forest management, in which old, semi-natural forests are converted to clear-cuts and culturally regenerated stands, is expected to have pronounced impact on the abundance and composition of this group of animals due to changes in the understory vegetation. During a 39 year-period we sampled autumn numbers of small mammals in uncut, semi-natural old forest and in recent clearcuts, supplemented by a 7-year sample from middle-aged plantations. Field voles *Microtus agrestis* were almost exclusively trapped in clearcuts. Bank voles *Myodes glareolus* dominated in the old forest, but reached equal or higher densities than field voles in clearcuts. Here, their combined abundance exceeded that of bank voles in old forest. Some years, wood lemmings *Myopus schisticolor* contributed significantly to vole abundance in old forest. Other rodents *Apodemus* spp. were rarely captured, mainly in clearcuts, and shrews *Sorex* spp. numbered < 15 percent of the total number of captured animals. Throughout the whole period we discerned 11 vole cycles, with highest peaks in bank voles in old forest. After high numbers during the 1980s, abundances of all species fell markedly during the 1990s, most distinctively in clearcuts, where the field vole almost totally disappeared. From the late 2000s, abundances of all species returned to pre-1990 levels and beyond. In the early and late periods, combined vole numbers were 26% higher in clearcuts compared to old forest, whereas the opposite was true in the middle period. In middle-aged plantations, bank voles numbered only one third of what it was in clearcuts and old forest, and other voles were rarely trapped. The results support the general notion that bank voles thrive in bilberry-rich, older forest and field voles in grass-dominated habitat. Contrary to general assertions, bank vole was abundant also in clearcuts, possibly due to invasion from surrounding old forest, but peak densities were lower than in old forest, possibly due to suppression by field voles. The variation of small mammals in forest age classes concurred closely with recent results reported from Finland. On a landscape scale, the results from these two and other studies predict that the total biomass of small rodents will be reduced by even-aged forest management, not because of conversion of older, semi-natural forest to clearcuts, but because of a decline in numbers in middle-aged and older, secondary forests.

## 1. Introduction

Small mammals are a key component of the boreal forest ecosystem. In Fennoscandia, this group consists of early-successional *Microtus* species and older forest *Myodes* species and wood lemmings *Myopus schisticolor*, besides wood mice *Apodemus* spp. and shrews *Sorex* spp. Microtine rodents are known to fluctuate in 3–5-year cycles with quite large amplitudes (e.g. Stenseth, 1999), thereby impacting small and medium-sized predators both numerically and functionally. For instance, ground-nesting forest grouse *Tetraoninae* suffer heavy mortality

from generalist predators when vole numbers decline after population peaks – a relationship referred to as the alternative prey hypothesis (Lack, 1954; Hagen, 1969; Angelstam et al., 1984). Similarly, both specialist mammalian predators like stoat *Mustela erminea* and least weasel *M. nivalis* and several species of raptors produce large litters and fledglings during “vole years”.

The *Myodes* and *Microtus* voles differ in habitat and diet as well as in morphology and social organization. Studies in the 1970s and 1980s (Hansson, 1971; Myllymäki, 1977) showed that the field vole *Microtus agrestis* subsists almost exclusively on graminoids; the species is

\* Corresponding author.

E-mail addresses: [per.wegge@nmbu.no](mailto:per.wegge@nmbu.no) (P. Wegge), [jorund.rolstad@nibio.no](mailto:jorund.rolstad@nibio.no) (J. Rolstad).

therefore restricted to grass-dominated habitats like old fields and clearcuts. The granivorous bank vole *Myodes glareolus* has a wider food niche and is distributed in forests with an understory of herbs and dwarf shrubs, especially bilberry *Vaccinium myrtillus*. Since field voles are larger than bank voles they are considered to be dominant over bank voles (Hansson, 1983; Henttonen and Hansson, 1984; Gurnell, 1985). Furthermore, their social structures differ; the field vole forms matrilineal clusters during the breeding season with territorial males living in large non-overlapping home ranges, whereas in bank vole, females are territorial with hierarchical, overlapping males inside their home ranges (Pusenius and Viitala, 1993; Ylönen et al., 1995; Pusenius et al., 1998). Presumably due to their different social structures, the field vole typically shows more pronounced annual fluctuations than the bank vole, with larger amplitudes between peak and low densities during the cycle (Hansson and Henttonen, 1985). The wood lemming may periodically contribute significantly to the overall biomass of microtine rodents in boreal forest. It belongs to the taiga fauna and mainly occurs in old spruce forests rich in mosses. In contrast to other boreal rodent species it is a specialized bryophagist with a diet consisting of 75–90% mosses (Eskelinen, 2002). The population density periodically shows large fluctuations, but the peaks may not be as regular as in other microtine rodents (Eskelinen et al., 2004; Bobretsov and Lukyanova, 2017). During population peaks, however, its local distribution may cover larger continuous areas (Ims et al., 1993).

In a historical perspective – before commercial forestry – natural forest fires created early successions and presumably favorable habitat for *Microtus*, with surrounding non-burnt forest probably constituting optimal habitat for *Myodes* and wood lemming. However, pine forests burnt more often than richer spruce forests. Hence, larger landscape sections on more productive soils consisted of bilberry-rich, old spruce forests (Rolstad et al., 2017). With the onset of commercial forestry 2–3 centuries ago, the conifer forests were for a rather long period harvested by high-grading and selection cuttings, combined with extensive control of forest fires. By late 1800s and early 1900s, this management regime had presumably reduced the areas of open, grass-rich fields and favored sparsely stocked coniferous forests with dense bilberry ground cover (Lie et al., 2012). *Microtus* was probably then less abundant than in earlier times. The present clearcutting harvesting method, with subsequent planting of Norway spruce *Picea abies* and natural regeneration of Scots pine *Pinus sylvestris* from retained seed trees – leading to even-aged forest management – started in Fennoscandia in the late 1940s and early 1950s. This recent increase in early successions from clearcuts presumably restored prime habitats for *Microtus*.

Despite the long-term pervasive transformation of the Fennoscandian boreal forest ecosystem, first by means of extensive high-grading and recently by clearcutting and even-aged plantations, surprisingly few studies have addressed how these changes in management regime might have affected the small rodents community and their dynamics (Bogdziewicz and Zwolak, 2014). In a comparative study in North America, Sullivan and Sullivan (2001) concluded that regeneration systems which leaves overstory trees either singly or in groups are less favorable for *Microtus* than treeless clearcuts. In another review article from the same continent, Kirkland (1990) found no consistent results on the effects of harvesting methods on small mammals, except that – in general – species richness was enhanced on clearfelled areas. In Fennoscandia, from early, general studies of diets and habitat use of small rodents (e.g. Hansson, 1971, 1983), some authors have predicted that clearcutting forestry will increase total vole abundances owing to the creation of prime *Microtus* habitat after clearfelling (Henttonen 1989; Rolstad and Wegge, 1989; Ims, 1991), and because this species has higher growth potential than *Myodes* (Henttonen and Hansson, 1984). Conversely, Gorini et al. (2011) predicted a decline in small rodents due to the harvesting of semi-natural old forest, since the loss of this prime *Myodes* habitat would not be compensated for by *Microtus* on the following grassy clearcuts. This view is partly supported by other Fennoscandian studies, which

recorded low abundances of bank voles in middle-aged and older regenerated plantations (Ecke et al., 2002; Panzacchi et al., 2010; Savola et al., 2013). However, these field studies suffer from short temporal duration (2–5 years), besides being conducted during a period of remarkably low numbers of field voles.

As part of a long-term field study of forest grouse in southeastern Norway (Wegge and Rolstad, 2011, 2017) we measured the abundance of small mammals in a coniferous forest subjected to industrial, clear-cutting forest management. Here, we report on their temporal variation pattern during 39 years (1979–2017), with particular focus on the two main vole species, i.e. the bank vole and the field vole. Besides contributing to the general understanding of small mammal dynamics in boreal Fennoscandia, we specifically address the above-mentioned predictions regarding the likely impacts of clearcutting and plantation forestry on this important animal group.

## 2. Study area

The study was carried out in Varald State Forest, located next to the Swedish border in southeast Norway (60°10'N, 12°30'E). The gently undulating terrain between 200 and 400 m a.s.l. consists of Norway spruce and Scots pine interspersed with scattered birch *Betula* spp. and aspen *Populus tremula*. Mixed pine and spruce forest – the *Vaccinio-Pinetum* vegetation type (Kielland-Lund, 1981) – covers > 50 percent. The remaining semi-natural forest of this type consists of an overstory dominated by pine, with spruce in the lower strata, and a dense field layer consisting of a mixture of bilberry, crowberry *Empetrum nigrum* and intermingling bog whortleberry *Vaccinium uliginosum* and cowberry *Vaccinium vitis-idaea*. These old forest stands originated after mixed-severity fires during the 18th and 19th centuries, of which the last fires occurred during the 1850–1870s (Bråthen, 2016). Thus, the age of the overstory pine trees today amounts to 150–200 years. Contiguous with other mixed conifer forests on all sides – only interspersed with small patches of small abandoned farmlands – the forest has been subjected to timber harvesting for several centuries. When clearcutting became the main harvesting regime in the early 1950s – replacing the selection method – cutting blocks were initially rather large (> 50 ha in the 1960–1970s), but have successively been reduced in size, today rarely exceeding 20 ha. During the last four decades, the coverage of semi-natural, old conifer forests has been more than halved from 50 to 20%, the remaining consisting of middle-aged (55%) and young (10%) silvicultural stands of pure and mixed plantations of spruce and pine. Today, clearcuts < 10 years of age cover 15%.

In addition to a dense population of moose *Alces alces*, fewer roe deer *Capreolus capreolus*, semi-resident wolves *Canis lupus* and lynx *Lynx lynx* and smaller herbivores, fluctuating numbers of stoat, least weasel and denser populations of red fox *Vulpes vulpes* and pine marten *Martes martes* are the main predators of small mammals, supplemented by different species of owls, goshawk *Accipiter gentilis* and common buzzard *Buteo buteo*. For more detail, see Wegge and Rolstad (2011, 2017).

## 3. Material and methods

### 3.1. Trapping

The small mammal guild consisted of bank voles *Myodes glareolus*, field voles *Microtus agrestis*, wood lemmings *Myopus schisticolor*, wood mice *Apodemus* spp., and shrews *Sorex* spp. We estimated the abundance of these species in the early successional stage after clearfelling (henceforth termed clearcuts) and in semi-natural old forest by the standardized snap trapping method (Hansson, 1967; Myllymäki et al., 1971). Baited with raw potato, the traps were placed along c. 250 m long transects for two days, spaced 5 paces apart and checked every day. The clearcuts were between 4 and 12 years old, dominated mainly by hairy wave-grass *Deschampsia flexuosa* and *Calamagrostis* spp. Other species – depending on site conditions – were various herbs like

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