Table of Contents

Mammalian Herbivores in the Boreal Forests: Their Numerical Fluctuations and Use by Man

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ABSTRACT

Within the boreal zone, there are about 50 native mammalian herbivore species that belong to the orders Artiodactyla, Rodentia, and Lagomorpha. Of these species, 31 occur in the Nearctic and 24 in the Palaearctic. Only six species occur in both regions. Species of the family Cervidae have probably been, and still are, the most important group for man, as they provide both meat and hides. Pelts from squirrels, muskrats, and hares were commercially harvested at the beginning of the century, but have less value today. The semi−domestic reindeer in the Palaearctic produces meat and hides on a commercial basis. It is also used for milking, to a limited extent, as is the semi−domestic moose in Russia. The Siberian musk deer is used for its musk and is raised in captivity in China. All species heavier than 1 kg are utilized by man, those with a body mass in the range 1 kg − 1 hg are sometimes used, and species lighter than 1 hg are rarely used. Here, we review the numerical fluctuations in terms of periodicity and amplitude, based on an extensive data set found in the literature, especially from the former Soviet Union. Current understanding of the underlying factors behind the population fluctuations is briefly reviewed. Management and conservation aspects of the mammalian herbivores in the boreal zone are also discussed. We conclude that there is a challenge to manage the forests for the mammalian herbivores, but there is also a challenge to manage the populations of mammalian herbivores for the forests.

KEY WORDS: boreal forests; conservation; fluctuations; herbivores; human use; mammals; management; populations; variability.

INTRODUCTION

Within the boreal forest, the mammalian herbivores constitute a valuable natural resource for man because of their meat, skin, pelts and antlers. They are also vectors for diseases transmitted to man, e.g., Lyme diseases, tularemia, and nephropathia (e.g., Vikoren 1966, Sato et al. 1996, Stewart 1996, Ahlm et al. 1997), and under high densities they can cause significant damage to commercial forest regeneration (e.g., Rousi 1983, Lavsund 1987).

The mammalian herbivores are also an important food source for many avian and mammalian predators in the boreal forest. Because of their high abundance during some years, they have the potential to influence the structure and function of the boreal ecosystems. Some of the mammalian herbivores, such as the hares and the microtine rodents, show regular and sometimes dramatic fluctuations between years. The population "peaks" of these dominant herbivores are often seen as "signals" in patterns and processes occurring on different trophic levels. In Fennoscandia, the vole density changes are strongly correlated with variation in density of a wide range of other species, but in the Canadian boreal forest, fewer species are correlated with the dominant herbivore, the snowshoe hare (Boutin et al. 1995).

Even less abundant species, e.g., moose, can act as keystone species by their influence on plant succession (e.g., Bryant and Chapin 1986), rate of organic matter turnover, and element cycling (Pastor et al. 1993, Kielland et al. 1997). The impact of beaver on boreal forest landscapes by increasing the wetland mosaic and altering the hydrology is also significant (e.g., Naiman et al. 1988).

The aim of this paper is to give a global perspective on the numerical fluctuations and the interrelationships with humans of mammalian hebivores occurring in the boreal forests of the Nearctic and Palaearctic.

THE MAMMALIAN HERBIVORE SPECIES

Mammalian herbivores are here defined as species feeding mainly on plant matter. The native species inhabiting forest landscapes of the boreal zone in the Nearctic and Palaearctic are listed in Table 1. The definition of the boreal zone follows Hämet–Ahti (1981), and refers to the northern, middle, and southern boreal zone, including the arctic and complex mountain oroarctic areas.

Table 1. List of native mammalian herbivore species inhabiting forest landscapes of the boreal zone (sensu Hämet–Ahti 1981) of the Nearctic and Palaearctic. Taxonomy and nomenclature follow Wilson and Reeder (1993); common names are according to Corbet and Hill (1991). Recent human use (in the last 20 yr) of the different species is indicated: Ab, abomasum (for cheese production); A, antlers; VA, velvet antlers; G, glands; M, meat; Mi, milk (only from semidomesticated animals); S, skin/pelts; *, their food storage collected and consumed by man; and **, their food storage collected and given as food to domestic animals.

Species	Nearctic	Palaearctic	Human use of animals
Family Moschidae			
Siberian musk deer (*Moschus moschiferus*)		x	G, M, S
Family Cervidae			
Wapiti, red deer (*Cervus elaphus*)	x	x	A, VA, M, S

Moose, elk (*Alces alces*)	x	x	A, M, (Mi), S
Western roe deer (*Capreolus capreolus*)		x	A, M, S
Eastern roe deer (*C. pygargus*)		x	A, M, S
Mule deer (*Odocoileus hemionus*)	x		A, M, S
White−tailed deer (*O. virginianus*)	x		A, M, S
Caribou, reindeer (*Rangifer tarandus*)	x	x	Ab, A, VA, M, Mi, S
Family Bovidae			
Bison (*Bison bison*)	x		A, M, S
Family Sciuridae			
Woodchuck (*Marmota monax*)	x		M
Eurasian red squirrel (*Sciurusvulgaris*)		x	S
Least chipmunk (*Tamias minimus*)	x		
Siberian chipmunk (*T. sibiricus*)		x	S
Eastern chipmunk (*T. striatus*)	x		
American red squirrel (*Tamiasciurus hudsonicus*)	x		
American flying squirrel (*Glaucomys sabrinus*)	x		
Siberian flying squirrel (*Pteromys volans*)		x	S
Family Castoridae			
American beaver (*Castor canadensis*)	x		G, M, S
Eurasian beaver (*C. fiber*)		x	G, M, S
Family Dipodidae			
Northern birch mouse (*Sicista betulina*)		x	
Woodland jumping mouse (*Napaeozapus insignis*)	x		
Meadow jumping mouse (*Zapus hudsonicus*)	x		
Western jumping mouse (*Z. principes*)	x		
Family Muridae			
European water vole (*Arvicola terrestris*)		x	S
Gapper's red−backed vole (*Clethrionomys gapperi*)	x		
Bank vole (*C. glareolus*)		x	
Grey red−backed vole (*C. rufocanus*)		x	
Northern red−backed vole (*C. rutilus*)	x	x	
Amur lemming (*Lemmus amurensis*)		x	
Field vole (*Microtus agrestis*)		x	
Rock vole (*M. crotorrhinus*)	x		

Long–tailed vole (*M. longicaudus*)	x		
Root vole (*M. oeconomus*)	x	x	S *
Meadow vole *(M. pennsylvanicus)*	x		*
Yellow–cheeked vole (*M. xanthognathus*)	x		
Wood lemming (*Myopus schisticolor*)		x	
Muskrat (*Ondatra zibethicus*)	x		M, S
Heather vole (*Phenacomys intermedius*)	x		
Northern bog lemming (*Synaptomys borealis*)	x		
Yellow–necked mouse (*Apodemus flavicollis*)		x	
Korean field mouse (*A. peninsulae*)		x	
Harvest mouse (*Micromys minutus*)		x	
Bushy–tailed woodrat (*Neotoma cinerea*)	x		
Deer mouse (*Peromyscus maniculatus*)	x		
Family Erethizontidae			
North American porcupine (*Erethizon dorsatum*)	x		M, S
Family Leporidae			
Northern pika (*Ochotona alpina*)		x	**
Collared pika (*Ochotona collaris*)	x		
Snowshoe hare (*Lepus americanus*)	x		M, S
Arctic hare, mountain hare (*L. timidus*)	x	x	M, S

The 49 species listed belong to the orders Artiodactyla, Rodentia, and Lagomorpha. In the Nearctic, there are 31 species of mammalian herbivores distributed among eight families, and in the Palaearctic, the corresponding figures are 24 species and seven families. Of the 49 species, only 6 species occur in both regions (Table 1). In this count, we have excluded a few species that have their main distribution outside the boreal zone, but marginally and temporally occur within it. Examples of such species are the striped field mouse (*Apodemus agraricus*), with a more southern distribution, and the Norway lemming (*Lemmus lemmus*), which mainly occurs on the tundra, but penetrates into the boreal forest during peak years. Introduced species are excluded. White–tailed deer, American beaver, and muskrat have been introduced into the Palaearctic from the Nearctic, but we are not aware of any mammalian herbivore species being successfully transferred in the opposite direction.

THEIR USE BY MAN

Most of the animals in this review are harvested for their meat and skin (Table 1). The antlers of species belonging to the family Cervidae are used for various purposes. Cervid species have probably been, and still are, the most important group for humans, as they provide both meat and hides (e.g., for clothes). In Scandinavia, the amount of moose meat harvested by sport hunters is now larger than it ever has been, because the moose population has increased greatly during the last 30 years. A similar expansion has also occurred for white–tailed deer in North America. The harvest of animals for their pelts has decreased in both the Nearctic and the Palaearctic, probably due to declining prices. Pelts from squirrels, muskrats, and hares were commercially harvested at the beginning of the century, but have little value today. Semi–domesticated reindeer in the Palaearctic produce meat and hides on a commercial basis, and are also used to a limited extent for milking, as are semi–domesticated moose in Russia. The Siberian musk deer is used for its musk and is raised in captivity in China.

In addition to these direct uses, some species have a more indirect and beneficial interrelationship with humans. Before the arrival of the Europeans, meadow voles served the Mandan Indians of the Great Plains in North America well: their autumn caches of ground beans and "artichokes" provided the Indians with vital food, which was collected by Indian women (Banfield 1974). Alaskan Eskimos trained special dogs to locate the autumnal caches of liquorice roots collected by root voles, which the Eskimos would then add to their own winter larders (Banfield 1974). Hay collected and piled by pikas is harvested by farmers and given to sheep and cattle in Siberia.

Body mass values for the mammalian herbivore species used by man for meat, skin, pelts, and antlers are given in Table 2. Species with a body mass < 1 hg are rarely used; within the range of 1 hg – 1 kg, they are sometimes used. Species heavier than 1 kg are always regarded as useful to man. This overall pattern seems to hold for both the Nearctic and the Palaearctic.

Table 2. Percentage of the mammalian herbivore species used by humans (for meat, skin/pelts, and antlers) for different classes of body mass. Information refers to recent use (in the past 20 yr) in the Nearctic, Palaearctic, and both regions combined.

Body mass (kg)	Percentage of the species used by man		
	Nearctic (31 spp.)	Palaearctic (24 spp.)	Nearctic + Palaearctic (49 spp.)
<0.1	0	17	8
0.1 – 0.9	20	75	44
1 – 999	100	100	100

Skins or pelts are collected from species smaller than those that are harvested for meat. One explanation might be that it is more profitable to extract the skin than the meat from small animals. The really small animals might be avoided because it is not profitable to extract the skin, which is often of low quality. Another explanation for the low interest in the smallest animals is that they may be regarded as vectors for diseases and, therefore, are not handled.

NUMERICAL PATTERNS OF THEIR POPULATIONS

In [Appendices 1](#) and [2](#), we have gathered information on the numerical fluctuations of the mammalian herbivores in the Nearctic and Palaearctic, respectively. [Appendix 2](#) contains a large number of data sets from the former Soviet Union, many of which, until now, have been more or less unknown to western scientists. For each study, the species, study area, period of study, and periodicity and amplitude of population changes, as well as methods used to collect the information, are included.

For the boreal forest of the Nearctic, there is information on population changes over time for about half of the species. For the Palaearctic, there is a substantial amount of information for about two–thirds of the species. Even if the mammalian herbivores are among the most studied taxa in the northern hemisphere, there are large gaps in our knowledge about several species.

By considering the information in the appendices, it is clear that the different species cannot easily be classified according to the characteristics of their population fluctuations. There is a large component of spatial and temporal variation. For example, the pattern shown by one species in one area may not be present in the same area at another time, or in another area at the same time.

Here, we recognize three types of fluctuation patterns, but are fully aware that attempts to make simple classifications are justified only for pedagogical reasons. The first two groups contain species with regular fluctuations and the third group contains species with irregular fluctuations. We placed species that show high predictability in their fluctuation pattern in the first group, and species with regular fluctuations, but with variation in periodicity, in the second group.

Many of the species with regular fluctuations (with high predictability) include the Muridae and the snowshoe hare. They either fluctuate in regular "cycles" with a specific periodicity, or do not fluctuate at all. Many of the voles fluctuate with a 3–4 yr cyclic pattern in large parts of their distribution, both in the Nearctic and Palaearctic. There are numerous data sets of either a 3–4 yr fluctuation pattern or mostly seasonal changes, although with a possible long–term trend. Even for these species with highly predictable patterns, the fluctuations can disappear over time and space. The microtine "cycles" have recently "disappeared" for some of the vole species (especially *Clethrionomys* species) in northern Fennoscandia during the last decade (Hanski and Henttonen 1996, Klemola et al. 1997). The snowshoe hare, only present in the Nearctic, is another example of a species that either fluctuates in a "typical" "cyclic" pattern (about 10 yr), or does not show any "cyclic" pattern at all (Keith 1990). The hare fluctuations are more or less spatially correlated over the whole North American continent, and occur strongly within the core distribution area. At the edges of the distribution, where the hare populations are fragmented or in low numbers, the "cycles" disappear.

We put muskrat, mountain hare, and the red squirrels in the second group (regular fluctuations with low predictability). The muskrat fluctuates with different periodicities over its vast distribution in North America ([Appendix 1](#)), where it is native. In Canada, it lost its "cycling" in the middle of this century (Bulmer 1974, Boutin and Birkenholz 1987), as seen from fur harvests. Even earlier, there were periods without any statistically significant 10–yr "cycle" for the muskrat ([Appendix 1](#)). When the species was introduced into Fennoscandia, it fluctuated with an even shorter periodicity (Danell 1978). Variations in periodicity of the fluctuations are also present at smaller geographical scales. For example, mountain hares in Finland showed period lengths of 9–11 yr in nine provinces, but periods of 4 yr in two of the provinces (Ranta et al. 1997). A 3–4 yr "cyclic" pattern is common in Sweden and Norway, whereas both 5–6 and 9–10 yr periodicities can be found in the former Soviet Union. The shorter "cycle" is mostly found in the European part; the longer "cycle" is present in the taiga zone and the west Siberian steppe. The Eurasian red squirrel shows both 5–7 and 9–10 yr fluctuation patterns. However, the regularity found in the numerical fluctuations of squirrels is weak.

The third group (irregular fluctuations) contains species that rarely show any regular fluctuations, e.g., the

families Cervidae, Bovidae, and Castoridae. Only a few studies have shown periodic fluctuations in ungulates (Appendices 1 and 2). One reason may be the lack of long–term studies of ungulate populations that are not exposed to human interference through hunting, predator control, large–scale habitat change, or introductions. Very little empirical evidence supports the idea that variation in one (e.g., food) or a combination of extrinsic factors can generate "cyclic" variation in the population sizes of large ungulates (Saether 1997). Both long delays and overcompensation in the density–dependent feedback and stochastic variation in climate can easily generate large fluctuations in population sizes of large ungulates, often of a "cyclic" nature. Thus, an eruption–like pattern of variation in population size, with a lack of stable resource–dependent equilibrium, seems to be characteristic for population fluctuations of many large ungulates, at least in the absence of large carnivores (Keith 1974, Saether 1997).

The amplitude of the fluctuations over time is also an important characteristic of the numerical fluctuations. This variation in animal numbers over time can be described in different ways. Here, we have chosen to simply give the ratio between the highest and the lowest values reported during each observation period. We feel that it gives a good description of the potential changes that a species will show from the perspective of harvesting. However, a weakness in the estimate of the amplitude is the difficulty of estimating low densities in the field; often no animals are caught during such a situation. It is a common procedure to set the lowest value slightly greater than zero (e.g., 0.1), even if no animals were caught. The estimated amplitude will, of course, be dependent upon the value chosen.

The amplitude of the fluctuation also seems to depend upon the area sampled and the time period. Great fluctuations may be "smoothed out" over large areas because some of the populations can be in slightly different phases. For example, the amplitude of changes in the beaver harvests in the whole of Canada during 1919–1984 was about sixfold, but when considering Ontario alone, the amplitude was about 100–fold. At even smaller spatial scales, the local amplitudes might be even larger.

Mammalian herbivores of the boreal forest show a wide range in their amplitude of population fluctuation, i.e., from 2 to about 1000 (Appendices 1 and 2). Squirrels and beavers show amplitudes around 10 or some 10s. Many of the murid species and the hares show even larger amplitudes of variation, i.e., about 100 or more. From a harvesting perspective, the periodicity and amplitude of fluctuation of a population might have been important factors for the development of harvesting traditions and strategies. These activities often need investments in knowledge and, to some extent, equipment. These investments are probably related to fluctuation patterns of the target species. It would be an interesting to explore how the patterns in animal populations affect the behavior of hunters.

HOW CAN THESE PATTERNS BE EXPLAINED?

Calder (1983) proposed that herbivore populations should fluctuate at periods proportional to the fourth root of the body mass $M^{1/4}$), a basic allometric relationship linking physiological cycles to population processes. Supportive empirical data including 41 species of birds and mammals were presented by Peterson et al. (1984), but the relationship has been questioned by Krukonis and Schaffer (1991). For example, they claimed that the explanatory power of the proposed scaling law depends critically on whether or not populations are treated individually or are averaged by species. Further, adding new herbivore species to the Peterson data sets decreased the fit and changed the scaling exponent. Berryman (1995) also criticized the approach of explaining the periodicity of "cycles" by body mass or intrinsic growth rate.

An overlooked difficulty with such general analyses is the exclusion of species that show "pseudocycles." Such species show "cycles" when they are tightly linked to a "cyclic" community driven by species having an innate "cyclic" pattern, whereas they will not show "cycles" in other situations.

The question of population regulation has been much debated in population dynamics, and populations with

strong numerical fluctuations have attracted the interests of many researchers. Much effort has focused on dichotomous factors, extrinsic vs. intrinsic, density–dependent vs. density–independent. The vole "cycle" has been intensively studied and several hypotheses have been put forward (see Krebs and Myers 1974, Taitt and Krebs 1985, Norrdahl 1995). The causitive factors have been sought in food, predation, weather, social stress, behavior, and genetics. Although it is difficult to find any consensus among scientists as to the explanation of the vole "cycle," many of them now seem to favor a multifactor approach.

Recent experimental evidence on the showshoe hare "cycle" shows that predator exclosures doubled hare density and food addition tripled hare density during the "cyclic" peak and decline. Predator exclosure combined with food addition increased density 11–fold (Krebs et al. 1995). These results support the general ideas of Keith (1983) and Wolff (1980) that both predation and food play a role in generating hare cycles, but do not necessarily support Keith's proposed sequential two–level interaction, which assumes food shortage to be temporarily followed by predation.

For the microtine rodents, Stenseth (1995) suggests a simpler, two–trophic–level hypothesis (instead of the three–trophic–level in snowshoe hares), based on the estimated dimension of the time series for small rodents. Such a hypothesis could involve predators or food, but empirical tests are lacking.

Sinclair et al. (1993) showed that hare numbers, scars made by hares on trees, and sunspots were correlated, and argued that the snowshoe hare cycle is modulated indirectly by solar activity through an amplified climate cycle that affects the whole boreal forest ecosystem. If the sunspots synchronize the hare cycles, they should be seen on a larger scale. However, the Nearctic and Palaearctic hare populations do not fluctuate in phase (Ranta et al. 1997). Still, it is too early to rule out the role of sunspots for snowshoe hares, because mountain hare populations do not fluctuate in phase with the snowshoe hare populations. They are two different species, with great differences in many characters, e.g., body mass and fluctuation pattern.

The 3–4 yr fluctuation of small game in Norway and Sweden has been attributed to predators switching between voles when they are abundant to small game during periods of low abundance (Hagen 1952, Hörnfeldt 1978). The alternative prey hypothesis was tested in an island experiment (Marcström et al. 1988, 1989), and gained further support during the outbreak of sarcoptic mange, which dramatically reduced the fox population (Lindström et al. 1994).

The seed supply seems to be an important factor regulating population size of squirrels. Both Pulliainen (1984) and Andrén and Lemnell (1992) found a time lag of 1 yr between a rich food supply and high squirrel density for Fennoscandia. For the American red squirrel, Sullivan (1987) reported a 1–yr time lag between lodgepole pine (*Pinus contorta*) and squirrel density. Several squirrel species appear to be connected to the fluctuation in cone production of different conifers, and any "cyclic" fluctuation will thus be determined by a "cyclic" production of cones.

Keith (1974) suggested that large predators prevent ungulates from reaching densities limited by food supply. Removing the large predators would open the possibility for unchecked growth, followed by overgrazing and starvation. Delays and overcompensation in the density–dependent processes are an important part of the explanation of this fluctuation pattern (Grenfell et al. 1992, Clutton–Brock et al. 1997, Saether 1997).

MANAGEMENT AND CONSERVATION ASPECTS

Boreal forests have been inhabited by sparse human populations, which have used plants as well as animals in various ways almost since the end of the last glaciation period. During the last two centuries, exploitation of the forest has increased. From the perspective of the mammalian herbivores, two main categories of human activities are going on. The first concerns loss of habitats and changes in the remaining habitats of the animals, and the second is direct actions on the animal populations.

Boreal forest habitats are mainly affected by forest management that reduces the structural and spatial diversity at the stand, as well as the landscape, level (Hansson 1997). The prevailing silvicultural methods favor monocultures of a similar age, increase the proportion of younger stands, and reduce the amount of dying and dead wood. Overall, this will improve conditions for species that favor young forest stands, e.g., moose, but it will make the situation worse for species that depend on old–growth forests with abundant lichens on tree branches and trunks, and on the forest floor, e.g.. reindeer.

At present, we do not know to what extent the changes induced by forestry will affect one of the important characteristics of the boreal forests, i.e., the periodic fluctuations ("cycles") of some mammalian herbivores. We only have limited sets of observations around which we can speculate. In the boreal forests of northern Fennoscandia, there have been distinct 3–4 yr "cycles" since more general monitoring started (around 1970). During the last decade, however, these "cycles" have been less dramatic and have even faded away. "Modern forestry" started after World War II and has gradually converted most of the forest land in Fennoscandia into managed forests. Clear–cutting of forest stands, which has been the predominant regeneration method, creates areas with grasses and herbs that become excellent habitats for microtine rodents during the first few years. From this perspective, we can ask if the 3–4 yr "cycles" were amplified during 1960–1985 by these ongoing habitat changes, or if these changes caused a gradual disappearance of the "cycles" after 1985.

Actions directed at the management of some herbivores, especially the larger species, often aim to increase the harvestable population by changing the population sex and age ratios. Losses due to predation can be reduced by predator control, and winter losses due to starvation can be reduced by supplemental feeding. All of these measures aim to increase population size and to keep the population at a high and stable level. In the past, population sizes of the largest species, e.g., moose, most likely changed dramatically over time, even before man started to significantly influence them. In Fennoscandia, management efforts have been successful at increasing the population sizes of moose. However, keeping the population at a high–yield level also implies that one can more easily obtain highly precise information from the population. Otherwise, the population might be out of control, becoming destabilized and starting to show large fluctuations (Ferguson and Messier 1996, Saether 1997). In Fennoscandia, we have also experienced heavy moose damages, and the impact of overgrazing by reindeer is under debate.

What is the long–term impact of high and stable populations of large herbivores? How will "biodiversity" and ecosystem processes be influenced? Are we reducing important processes in the boreal forests by managing the herbivore populations at a constant and high level? Should management plans include actions to keep the populations moving from low to high densities?

We have to realize that large animals, in particular, are more than passive components of ecological systems, and that the implications of this for wildlife management are substantial and long lasting (Naiman 1988). Management of boreal forest ecosystems has implications that are both substantial and long lasting. There is a challenge to manage the forests for the mammalian herbivores, but there is also a challenge to manage the populations of mammalian herbivores for the forests.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a comment, follow this link. To read comments already accepted, follow this link.

Acknowledgments:

LITERATURE CITED

Ahlm, C., O. A. Alexeyev, F. Elgh, B. Aava, G. Wadell, A. Tärnvik, P. Juto, and T. Palo. 1997. High prevalence of hantavirus antibodies in bank voles (*Clethrionomys glareolus*) captured in the vicinity of households afflicted with *Nephropathia epidemica. American Journal of Tropical Medicine and Hygiene***56**:674–678.

Andrén, H., and P.–A. Lemnell. 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris. Ecography***15**:303–307.

Banfield, A. W. F. 1974. *The mammals of Canada.* University of Toronto Press, Toronto, Canada.

Bashenina, N. V. 1981. *Bank vole.* Nauka, Moscow, Russia. (In Russian.)

Bernstein, A. D., N. S. Apekina, L. F. Kopilova, J. A. Mjasnikov, and I. N. Gavrilovskaja. 1987. Comparative ecological and epizootological characteristics of forest voles (*Clethrionomys*) of Middle Urals. *Zoologicheskii Zhurnal* **66**:1397–1407. (In Russian.)

Berryman, A. A. 1995. Population cycles: a critique of the maternal and allometric hypotheses. *Journal of Animal Ecology***64**:290–293.

Bobretsov, A. V. 1986. Dynamics of numbers of forest voles in the upper part of Pechora River taiga. Pages 167–168 *in* V. E. Sokolov, editor. *IV c'ed Vsesojuznogo Teriologicheskogo Obschestva, Moscow.* Institut problem ekologii i evolutsii, Moscow, Russia.

Boutin, S., and D. E. Birkenholz. 1987. Muskrat and round–tailed muskrat. Pages 314–325 *in* M. Nowak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America.* Ontario Ministry of Natural Resources, Toronto, Canada.

Boutin, S., et al. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos***74**:69–80.

Bryant, J. P., and F. S. Chapin, III. 1986. Browsing – woody plant interactions during boreal forest plant successions. Pages 213–225 *in* K. Van Cleve, F. S. Chapin, III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, editors. *Forest ecosystems in the Alaskan taiga.* Springer–Verlag, New York, New York, USA.

Bulmer, M. G. 1974. A statistical analysis of the 10–year cycle in Canada. *Journal of Animal Ecology***43**:701–718.

Butler, L. 1962. Periodicities in the annual muskrat population figures for the province of Saskatchewan. *Canadian Journal of Zoology***40**:1277–1286.

Calder, W. A. III. 1983. An allometric approach to population cycles of mammals. *Journal of Theoretical Biology***100**:275–282.

Clutton–Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. *American Naturalist***149**:195–219.

Corbet, G. B., and J. E. Hill. 1991. *A world list of mammalian species.* Natural History Museum Publications and Oxford University Press, London, UK.

Danell, K. 1978. Population dynamics of the muskrat in a shallow Swedish lake. *Journal of Animal Ecology***47**:697–709.

Dvornikova, N. P. 1987. *Dynamics of populations and biocenotic role of beaver in southern Urals.* Dissertation. Sverdlovsk, Russia. (In Russian.)

D'yachkov, V. S. 1988. *Dynamics of numbers of squirrels in central Kamchatka.* Vladivostok, Russia. (In Russian.)

Egorov, O. V. 1961. *Ecology and hunting of Yakutian squirrel.* Izdatel'stvo Akademii Nauk, Moscow, Russia. (In Russian.)

Elton, C., and M. Nicholson. 1942. Fluctuations in numbers of the muskrat (*Ondatra zibethica*) in Canada. *Journal of Animal Ecology***11**:96–126.

Erlien, D. A., and J. R. Tester. 1984. Population ecology of sciurids in northwestern Minnesota. *Canadian Field–Naturalist***98**:1–6.

Ferguson, S. H., and F. Messier. 1996. Can human predation of moose cause population cycles? *Alces***32**:149–161.

Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white–tailed deer. *Journal of Wildlife Management* **55**:377–385.

Fuller, W. A. 1977. Demography of a subarctic population of *Clethrionomys gapperi:* numbers and survival. *Canadian Journal of Zoology***55**:42–51.

Galaktionov, Ju. K. and V. M. Efimov. 1988. *Abiotic factors in dynamics of numbers of water vole.* Sverdlovsk, Russia. (In Russian.)

Gilbert, B. S., and C. J. Krebs. 1991. Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973–1989. *Holarctic Ecology* **14**:250–259.

Grenfell, B. T., O. F. Price, S. D. Albon, and T. H. Clutton–Brock. 1992. Overcompensation and population cycle in an ungulate. *Nature***355**:823–826.

Hagen, Y. 1952. *Rovfuglene og viltpleien.* Gyldendal, Oslo. Norway. (In Norwegian.)

Hanski, I., and H. Henttonen. 1996. Predation on competing rodent species: a simple explanation of complex patterns. *Journal of Animal Ecology***65**:220–232.

Hansson, L., editor. 1997. Boreal ecosystems and landscapes: structures, processes and conservation of biodiversity. *Ecological Bulletin***46**.

Hjeljord, O. 1980. *Viltbiologi.* Landbruksforlaget, Oslo, Norway.

Hämet−Ahti, L. 1981. The boreal zone and its biotic subdivision. *Fennia* **159**:69−75.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia* **32**:141−152.

Hörnfeldt, B. 1994. Delayed density dependence as a determinant of vole cycles. *Ecology* **75**:791−806.

Ivanter, E. V. 1975. Population ecology of small mammals of taiga north−west of USSR. Nauka, Leningrad, Russia. (In Russian.)

Keith, L. B. 1974. Some features of population dynamics in mammals. *International Congress of Game Biologists* **2**:17−58.

_____ . 1983. Role of food in hare population cycles. *Oikos* **40:**385−395.

_____ . 1990. Dynamics of snowshoe hare populations. *Current Mammalogy* **2**:119−195.

Keith, L. B., and J. R. Cary. 1991. Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. *Journal of Mammalogy* **72**:373−378.

Kielland, K., J. P. Bryant, and R. W. Ruess. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos* **80**:25−30.

Kiris, I. D. 1973. *Squirrel.* Volgo−Vjatskoe knizhnoe izdanie, Kirov, Russia. (In Russian.)

Klemola, T., M. Koivula, E. Korpimäki, and K. Norrdahl. 1997. Size of internal organs and forage quality of herbivores: are there differences between cycle phases in *Microtus* voles? *Oikos* **80**:61−66.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* **269**:1112−1115.

Krebs, C. J., and J. M. Myers. 1974. Population cycles in small mammals. *Advances in Ecological Research* **8**:267−399.

Krivosheev, V. G., and M. V. Krivosheeva. 1991. Problems of ecology of *Ochotona hyperborea*. Nauka, Moscow, Russia. (In Russian.)

Krukonis, G., and W. M. Schaffer. 1991. Population cycles in mammals and birds: does periodicity scale with body size? *Journal of Theoretical Biology* **148**:469−493.

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. *Swedish Wildlife Research, Supplement* **1**:229−244.

Lindén, H. 1988. Latitudinal gradients in predator−prey interactions, cyclicity and synchronism in voles and small game populations in Finland. *Oikos* **52**:341−349.

Lindström, E. R., H. Andrén, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P.−A. Lemnell, B. Martinsson, K. Sköld, and J. E. Swenson. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology* **75**:1042−1049.

Lubetskaja, E. V. 1976. Analysis of dynamics of numbers of a squirrel population of eastern Sayan by a method of mathematical modelling. Dissertation. Moscow, Russia. (In Russian.)

Marcström, V., N. Höglund, and C. J. Krebs. 1990. Periodic fluctuations in small mammals at Boda, Sweden

from 1961 to 1988. *Journal of Animal Ecology* **59**:753–761.

Marcström, V., L. B. Keith, E. Engren, and J. R. Cary. 1989. Demographic responses of arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). *Canadian Journal of Zoology* **67**:658–668.

Marcström, V., R. E. Kenward, and E. Engren. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology* **57**:859–872.

McLeod, J. A. 1950. A consideration of muskrat populations and population trends in Manitoba. *Transactions of the Royal Society of Canada (Section 5)* **44**:69–79.

Mihok, S., B. N. Turner, and S. L. Iverson. 1985. The characterization of vole population dynamics. *Ecological Monographs* **55**:399–420.

Mikheeva, K. V. 1975. *Dynamics of numbers and structure of populations of squirrel of Middle Urals.* Dissertation. Sverdlovsk, Russia. (In Russian.)

Moksnes, A. 1972. Bestandsvingninger hos småviltarter i Trollheimsområdet. *Naturen* **5**:315–319. (In Norwegian.)

Mordosov, I. I. 1988. Forest lemming of western Yakutiya. Moscow, Russia. (In Russian.)

Myllymäki, A. 1977. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis. Oikos* **29**:468–493.

Naiman, R. J. 1988. Animal influences on ecosystem dynamics. *BioScience* **38**:750–752.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* **38**:753–762.

Naumov, S. P. 1960. Investigations of reasons and regularities of number dynamics of *Lepus timidus* in Yakutia. Nauka, Moscow, Russia. (In Russian.)

Norrdahl, L. 1995. Population cycles in northern small mammals. *Biological Review* **70**:621–637.

Novak, M. 1987. Beaver. Pages 282–312 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America.* Ontario Ministry of Natural Resources, Toronto, Canada.

Obbard, M. E. 1987. Red squirrel. Pages 264–281 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America.* Ontario Ministry of Natural Resources, Toronto, Canada.

Panteleev, P. A. 1968. Population ecology of water vole and measures of its extermination. Nauka, Moscow, Russian. (In Russian.)

Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* **74**:467–480.

Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. *Science* **224**:1350–1352.

Pullianen, E. 1984. The predation system seed – squirrel – marten under subarctic conditions. *Zeitschrift fur*

*Säugetierkunde***49**:121–126.

Ranta, E., J. Lindström, V. Kaitala, H. Kokko, H. Lindén, and E. Helle. 1997. Solar activity and hare dynamics: a cross–continental comparison. *American Naturalist***149**:765–775.

Rousi, M. 1983. Susceptibility of pine to mammalian herbivores in northern Finland. *Silva Fennica***17**:301–312.

Ryabov, S. V. 1982. Peculiarities of multi–annual fluctuations of numbers of small forest rodents in Sakhalin, Vladivostok, Russia. (In Russian.)

Sato, Y., K. Miyamoto, A. Iwaki, T. Masuzawa, Y. Yanagihara, E. I. Korenberg, N. B. Gorelova, V. I. Volkov, L. I. Ivanov, and R. N. Liberova. 1996. Prevalence of Lyme disease spirochetes in *Ixodes persulcatus* and wild rodents in far Eastern Russia. *Applied and Environmental Microbiology***62**:3887–3889.

Saether, B.–E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology and Evolution* **12**:143–149.

Shvetsov, Yu. G., M. N. Smirnov, and G. I. Monakhov. 1984. Mammals of the Baikal basin. Nauka, Moscow, Russia. (In Russian.)

Siivonen, L. 1948. Structure of short–cyclic fluctuations in numbers of mammals and birds in the northern parts of the northern hemisphere. *Riistatieteellisiä Julkaisuja***1**:1–166.

Sinclair, A. R .E., J. M. Gosline, G. Holdsworth, C. J. Krebs, S. Boutin, J. N. N. Smith, R. Boonstra, and M. Dale. 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist* **141**:173–198.

Skarén, U. 1972. Fluctuations in small mammal populations in mossy forests of Kuhmo, eastern Finland, during eleven years. *Annales Zoologici Fennici***9**:147–151.

Stenseth, N. C. 1995. Snowshoe hare populations: squeezed from below and above. *Science***269**:1061–1062.

Stewart, S. J. 1996. Tularemia: association with hunting and farming. *FEMS Immunology and Medical Microbiology***13**:197–199.

Sullivan, T. P. 1987. Red squirrel population dynamics and feeding damage in juvenile stands of lodgepole pine. Research Branch, Minististry of Forestry, Victoria, British Columbia, *Forestry Research Development Agreement Report***19**:1–20.

Taitt, M. J., and C. J. Krebs. 1985. Population dynamics and cycles. Pages 567–620 *in* R. H. Tamarin, editor. *Biology of New World Microtus.* American Society of Mammalogists, Special Publication Number 8.

Tavrowskii, V. A., O. V. Egorov, and V. G. Krivosheev. 1971. Mammals of Yakutiya. Nauka, Moscow, Russia. (In Russian.)

Telegin, V. I. 1980. Chipmunk of Western Siberia. Nauka, Novosibirsk, Russia. (In Russian.)

Tomilova, T. P. 1981. Peculiarities of distribution of *Lepus timidus* in subzone of southern taiga of the European part of the USSR. Moscow, Russia. (In Russian.)

Tugutov, L. D., V. F. Chernjavskii, and A. F. Tupitsina. 1985. Dynamics of numbers of small rodents in central Yakutiya. Vladivostok, Russia. (In Russian.)

Vikoren, T. 1966. Wild animals as sources of infections in humans. *Norsk Veterinaertidskrift***108**:467–473. (In

Norwegian with English abstract.)

Wilson, D. E., and D. M. Reeder, editors. 1993. Mammal species of the world. A taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C., USA.

Wolff, J. O. 1980. The role of habitat patchiness in population dynamics of snowshoe hares. *Ecological Monographs* **50**:111–130.

APPENDICES

Appendix 1. Summary of information on characteristics of the numerical fluctuations of mammalian herbivores in Nearctic boreal forests. The amplitude is given as the ratio between the highest and lowest values in the data set. Abbreviations are: np, not periodic; trc, countings of tracks, signs of feedings or houses/push–ups; trp, trapping in order to estimate population density; har, harvest of animals for nonscientific purpose; cnt, counting of animals.

Species	Region and period	Periodicity (yr)	Amplitude	Type of information	Reference
Moose	Isle Royale, 1960–1983	about 30	2	cnt	Peterson et al. (1984)
White–tailed deer	Ontario, Canonto, 1953–1986	24	11	har	Fryxell et al. (1991)
Least chipmunk	Minnesota, 1954–1975	7	10	trp	Erlien and Tester (1984)
Eastern chipmunk	Minnesota, 1954–1975	9	10	trp	Erlien and Tester (1984)
American red squirrel	Canada, 1926–1984	np	about 10	har	Obbard (1987)
Alberta, 1965–1975	np	6	trp	Keith and Cary (1991)	
Yukon, 1987–1994	np	2–5	trp	Boutin et al. (1995)	
Minnesota, 1954–1975	11	10	trp	Erlien and Tester (1984)	
American flying squirrel	Alberta, 1965–1975	np	about 50	trp	Keith and Cary (1991)
American beaver	Canada, 1919–1984	np	6	har	Novak (1987)
Ontario, 1919–1984	np	about 100	har	Novak (1987)	
Meadow jumping mouse	Manitoba, 1969–1982	4?	about 90	trp	Mihok et al. (1985)
Gapper's red–backed vole	N.W.T. , 1961–1975	3–4?	about 100	trp	Fuller (1977)
Manitoba, 1969–1982	np	about 10	trp	Mihok et al. (1985)	
Northern red–backed vole	Yukon, 1976–1989	3–4?	47	trp	Gilbert and Krebs (1991)
Yukon, 1976–1994	3–4?	10–50	trp	Boutin et al. (1995)	

Species	Region and period	Periodicity	Amplitude	Type of information	
Meadow vole	Manitoba, 1968–1983	4?	200	trp	Mihok et al. (1985)
Muskrat	Hudson Bay Co., 1821–1913	10	14	har	Elton and Nicholson (1942)
Manitoba, 1920–1948	4–5	4	har	McLeod (1950)	
Saskatchewan, 1915–1960	6	15	har	Butler (1962)	
Canada, 1751–1847	not 10		har	Bulmer (1974)	
Canada, 1848–1909	10		har	Bulmer (1974)	
Canada, 1920–1944	10		har	Bulmer (1974)	
Canada, 1945–1969	not 10		har	Bulmer (1974)	
Canada, 1919–1984		5	har	Boutin and Birhenholz (1987)	
Yukon, 1988–1994		9	trc	Boutin et al. (1995)	
Deer mouse	Manitoba, 1969–1982	np	3–10	trp	Mihok et al. (1985)
Yukon, 1976–1989	np	12	trp	Gilbert and Krebs (1991)	
North American porcupine	Alberta, 1965–1975	np	7	trp	Keith and Cary (1991)
Snowshoe hare	Canada, 1848–1909	10		har	Bulmer (1974)
Alberta, 1961–1977	9–10	about 100	trp	Keith (1983)	
Yukon, 1977–1994	about 9	26–44	trp	Boutin et al. (1995)	

Appendix 2. Summarized information on characteristics of the numerical fluctuations of mammalian herbivores in boreal forests of the Palaearctic. Amplitude is given as the ratio between the highest and the lowest values in the data set. Abbreviations are: np, not periodic; que, questionable on population size; trc, countings of tracks, signs of feedings or houses/push–ups; trp, trapping in order to estimate population density; har, harvest of animals for nonscientific purpose; cnt, counting of animals; sd, semidomestic. For data marked with an asterisk, the regularity of fluctuation disappeared around 1985.

Species	Region and period	Periodicity	Amplitude	Type of information	

		(yr)			Reference
Moose	European Russia, 1650–1995	100–200?	100	har	L. Baskin (*unpubl. data*)
Reindeer (sd)	Sweden, 1910–1996	25–35?	2	cnt	Ö. K. Danell (*unpubl. data*)
Eurasian red squirrel	Sweden, 1978–1988	np	15	trc	Andrén and Lemnell (1992)
Finland, 1964–1983	8		que	Lindén (1988)	
Arkangelsk, 1909–1971	5	25	har	Kiris (1973)	
Kola, 1909–1971	5	8	har	Kiris (1973)	
M. Russia, 1909–1971	5	40	har	Kiris (1973)	
M. Urals, 1940–1970	11	7	cnt	Mikheeva (1975)	
W. Siberia, 1909–1971	5–9	6	har	Kiris (1973)	
E. Sayan, 1932–1972	9	80	cnt	Lubetskaja (1976)	
Krasnoyarsk, 1909–1971		10	har	Kiris (1973)	
Yakutiya, 1909–1971	5–7	5	har	Kiris (1973)	
Yakutiya, 1933–1957	6	2		Egorov (1961)	
Kamchatcka, 1960–1986	2–4 and 7–9	14		D'yachkov (1988)	
Siberian chipmunk	W. Siberia	np		cnt	Telegin (1980)
Yakutiya, 1933–1957	np	2	cnt	Egorov (1961)	
Eurasian beaver	S. Urals, 1949–1979	30?	28	cnt	Dvornikova (1987)
Northern birch mouse					

Species	Location, period	Cycle	N	Method	Reference
	Karelia, 1959–1972	np	10	trp	Ivanter (1975)
European water vole					
	Karelia, 1932–1972	np	22	har	Ivanter (1975)
	W. Siberia, 1898–1961		10	har	Panteleev (1968)
Bank vole	Sweden, 1961–1988	4	55	trp	Marcström et al. (1990)
	Sweden, 1971–1988	3–4	216	trp	Hörnfeldt (1994)
	Sweden, 1976–1986	3–4	350–1600	trp	Marcström (1989)
	Finland, 1957–1968	4–5	22	trp	Skarén (1972)
	Finland, 1970–1993	3–4 *	100	trp	Hanski and Henttonen (1996)
	Lapl. Res., 1935–1972	5	100	trp	Bashenina (1981)
	Karelia, 1944–1972	4	80	trp	Ivanter (1975)
	Komi, 1935–1972?	3	100	trp	Bashenina (1981)
	Moscow, 1948–1975	3	15	trp	Bashenina (1981)
	Ryazan, 1951–1973	4	12	trp	Bashenina (1981)
	Novgorod, 1949–1970	5	6	trp	Bashenina (1981)
	Tatar, 1936–1959	3–5	10	trp	Bashenina (1981)
Grey red–backed vole	Sweden, 1971–1988	3–4	248	trp	Hörnfeldt (1994)
	Finland, 1970–1993	3–4 *	100	trp	Hanski and Henttonen (1996)
	Sakhalin, 1957–1981	4?	15	trp	Ryabov (1982)
Northern red–backed vole	Finland, 1970–1993	3–4 *	100	trp	Hanski and Henttonen (1996)
	Karelia, 1958–1972	4?	26	trp	Ivanter (1975)

Upper Pechora, 1950–1984	4	30	trp	Bobretsov (1986)	
M. Urals, 1973–1985	3	100	trp	Bernstein et al. (1987)	
Yakutiya, 1960–1984	4?	230	trp	Tugutov et al. (1985)	
Field vole	Sweden, 1961–1988	4		trp	Marcström et al. (1990)
Sweden, 1971–1988	3–4	177	trp	Hörnfeldt (1994)	
Finland, 1969–1976	3	15	trp	Myllymäki (1977)	
Finland, 1970–1993	3–4	100	trp	Hanski and Henttonen (1996)	
Karelia, 1948–1972	5	20	trp	Ivanter (1975)	
Root vole	Finland, 1970–1993	3–4	100	trp	Hanski and Henttonen (1996)
Karelia, 1958–1972	np	36	trp	Ivanter (1975)	
Omsk, 1948–1982	7–10		har	Galaktionov and Efimov (1988)	
Novosibirsk, 1948–1982	5–12		har	Galaktionov and Efimov (1988)	
Tyumen, 1948–1982	5–6		har	Galaktionov and Efimov (1988)	
Yakutiya, 1960–1984	3	220	trp	Tugutov et al. (1985)	
Wood lemming	Karelia, 1957–1971	6	25	trp	Ivanter (1975)
Yakutiya, 1966–1984	11	260	trp	Mordosov (1988)	
Yellow–necked mouse	Sweden, 1961–1988	4	15	trp	Marcström et al. (1990)
Harvest mouse	Karelia, 1957–1971	np	25	trp	Ivanter (1975)
Northern pika	Baikal, 1961–1984		20		Shvetsov et al. (1984)
Yakutiya,	np			Krivosheev and	

1962–1984					Krivosheeva (1991)	
Mountain hare	Norway, 1945–1966	3–4	65	har		Moksnes (1972)
Norway, 1963–1976		3–5	8	har	Hjeljord (1980)	
Sweden, 1963–1980		3–4	6	har	Hörnfeldt et al. (1986)	
Finland, 1836–1976			100	har	Siivonen (1948)	
Finland, 1849–1934			12	har	Siivonen (1948)	
Finland, 1946–1984		9–11 and 4		que	Ranta et al. (1997)	
Russia, 1909–1981		9– 15			Tomilova (1981)	
Siberia		10	65		Naumov (1960)	
Yakutiya Verchoyansk		12	350		Tavrowskii et al. (1971)	

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