

Reindeer in tundra ecosystems: the challenges of understanding system complexity

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The resilience of tundra ecosystems is limited, with relatively few key biotic components determining the general pattern of the dynamics of these systems. Sustainable use of reindeer pastures, which are natural tundra ecosystems, should take into account interactions within the whole complex of key components. Among the most important are the small herbivorous rodents. For example, during peak densities lemmings may reduce above-ground plant biomass by 50–70%. At the same time, rapid turnover of nutrients in the form of significant amounts of potassium, phosphorus and nitrogen that lemmings excrete in urine promotes vascular plant growth. It is concluded that these kinds of studies are essential for the sustainable management of Russia's grazing lands: 1) comparative studies of productivity, biological diversity and structure of plant communities under the different pressures exerted by the main groups of herbivorous animals (reindeer and small rodents), as well as under varying levels of industrial development; 2) studies of the direct and indirect effects of herbivorous mammals on biological turnover and energy flow within the system; 3) studies of the role of industrial contamination on the turnover of nutrients in tundra ecosystems.

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It is widely recognized that the resilience of tundra ecosystems is limited, resulting in low tolerance to many extrinsic pressures. This feature is a product of 1) low productivity of the dominant plant communities, and 2) the simple structure (including species composition, trophic chains and energy allocation pathways) of tundra ecosystems (Bolshakov et al. 1993). These characteristics are related to thermal instability of permafrost, the relatively short period of evolution of these ecosystems and severe climatic conditions. As a consequence, a relatively few key biotic components determine the general pattern of biological turnover and, consequently, the whole dynamics of tundra ecosystems.

Protection and sustainable use of reindeer pastures, which are in fact natural plant communities, should not ignore the effects caused by other components of tundra ecosystems in addition to reindeer. Moreover, interactions within the whole complex of key components of tundra ecosystems are essential for the long-term, sustained production of reindeer pastures. Among

these components, the most important for the vegetative cover are small herbivorous rodents. Lemming species (*Dicrostonyx torquatus* and *Lemmus sibiricus*) play the leading role within this group (Thompson 1955; Tikhomirov 1959; Pitelka 1964; Chernyavskii & Tkachev 1982; Tishkov 1985).

In this paper we take a brief look at this group to demonstrate the importance of examining reindeer habitats as natural ecosystems with complex networks of interrelations. Most data were collected on the Yamal Peninsula. We attempt to show the practical and theoretical importance of a complex approach to studying tundra ecosystems.

The modern state of reindeer pastures in Russia from the viewpoint of an ecologist

Reindeer herding, a traditional activity in Russia's northern regions, is one of the most important factors affecting the state of vegetative cover

(Andreev 1972; Polezhaev 1980; Stchelkunova 1992). Extensive studies of pastures aimed toward evaluating their foraging possibilities were started in Russia in the early 1930s (Andreev 1930; Sochava 1931; Gorodkov 1935; Igoshina 1937; Avramchik 1939). The research became focused on processes of pasture degradation and their restoration abilities (e.g. Andreev 1972; Utkin 1977; Polezhaev 1980; Karpov 1991; Dobrinskii 1995). Intensive herding of domestic reindeer leads to dramatic changes in the structure of vegetative cover, lowering its productivity and, consequently, the quality of pastures (Stchelkunova 1992; Polezhaev 1993; Magomedova 1994). In general, excessive grazing pressure suppresses valuable species of lichens, and results in the replacement of typical tundra plant communities by graminoid-dominated ones. On the other hand, since tundra ecosystems developed under some pressure from reindeer (Andreev 1972), complete cessation of grazing also results in changes in the vegetative complex, these changes being negative from the viewpoint of plant productivity and species richness (Karpov 1991). Apparently, both lack of grazing and overgrazing threaten to degrade the structure of tundra ecosystems as grazing lands for reindeer. Therefore, the responses of vegetation to grazing pressure are not linear. This non-linearity provides a basis for understanding what conditions are optimal for maintaining the productivity of tundra vegetation for sustainable reindeer grazing.

During the 20th century, grazing pressure of domestic reindeer on their pastures in Russia has increased significantly. For instance, in the Yamalo-Nenets Autonomous Region the numbers of reindeer have doubled since the beginning of the century (Fig. 1). Recently, rapid industrial devel-

Table 1. The ratio between fluxes of carbon dioxide from the soil and its intake by vegetation in southern Yamal $\text{g CO}_2/\text{m}^2$ (Dobrinskii et al. 1983).

Plant community	Intake of CO_2	CO_2 flux from the soil	Release/intake
Alluvial cereal-sedge meadow	25	15.7	0.63
Moss tundra with <i>Rubus chamaemorus</i> and <i>Carex</i> spp.	6.9	6.4	0.93
Sphagnum bog with dwarf shrubs and cottongrass	4.2	4.9	1.17

opment has added to the pressure generated by the increasing herds. In the Russian North a unique combination of factors, both natural and artificial, are affecting the natural ecosystems. These ecosystem level changes may have consequences at the global level through their alteration of atmospheric gas fluxes. For example, in situ studies of CO_2 fluxes in different types of plant communities in southern Yamal showed that in typical tundra communities the photosynthetic intake of carbon dioxide by vegetation in the peak of the growth season was practically equal to its release by soil respiration, while in meadows the uptake of CO_2 was significantly greater than its release (Table 1). These results suggest that if typical tundra communities are replaced by meadow-like ones, dominated by cereals and sedges, as a consequence of heavy grazing pressure, the general balance of carbon in Arctic and sub-Arctic regions may be altered.

The role of small rodents in tundra ecosystems

Among herbivorous animals, reindeer and small rodents have the most visible influence on the vegetation of tundra ecosystems. The role of small rodents in shaping the appearance of tundra ecosystems in Russia was first described by Tikhomirov (1959). Judging by rough estimations of the mass of dry matter removal by reindeer (Polezhaev 1993) and lemmings (Danilov 1995), their impact on the vegetation is quantitatively similar. However, the character of this influence is different in reindeer and rodents. In addition to the differences in the diet (small rodents make little use of lichens), the temporal and spatial character-

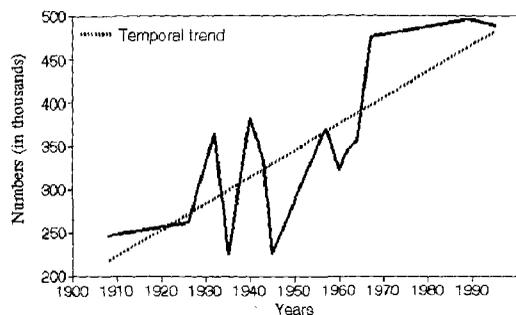


Fig. 1. Numbers of domestic reindeer in the Yamalo-Nenets Autonomous Region during the 20th century (Dobrinskii 1995).

istics of the impact differ between these two groups of mammals.

Lemming populations fluctuate, reaching high density at the peak phase (up to 200–300 individuals/ha), with a biomass of about 5–8 kg/ha. In years of peak density lemming may reduce above-ground plant biomass by 50–70% (Thompson 1955; Pitelka 1964; Batzly 1974). During periods of low density, when the impact of rodents on vegetation is practically absent, accumulation of dead parts of plants occurs. (Kiryustchenko 1979; Danilov 1995). The pressure of rodents on the vegetative cover, therefore, oscillates over time, in contrast to that of reindeer. This cyclic alteration of herbivore pressure was shown to be an important factor in the dynamics of tundra vegetation in the southern Yamal (Peshkova 1977).

Rodents also play an important role in the turnover of nutrients in the tundra. It is clear from Fig. 2 that significant amounts of potassium, phosphorus and nitrogen that lemmings consume in their food are rapidly released in their urine.

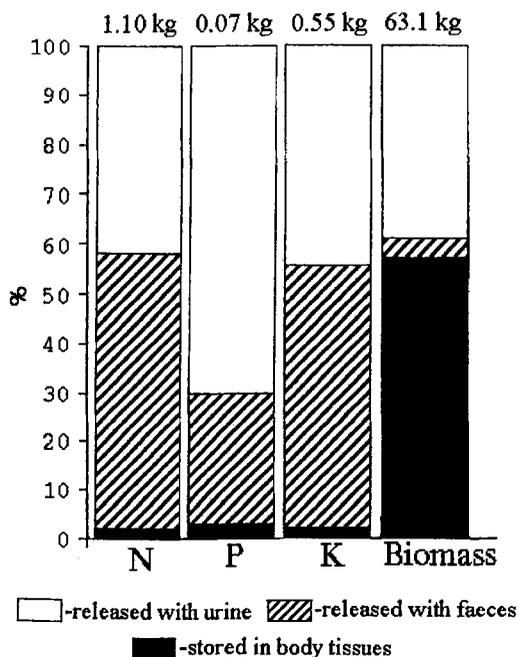


Fig. 2. Intake and release of nutrients (N, P and K) and plant biomass by lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) during a population cycle in southern Yamal (Danilov 1995). Kg values indicate the absolute value of nutrients involved in turnover, per ha. Column segments represent proportion (%) of different components of turnover for each nutrient.

This rapid turnover of nutrients can be viewed as natural fertilization, promoting vascular plant growth. The rate of decomposition of faeces of herbivorous mammals is, however, slow – usually not exceeding 2% of dry matter per year (Malafeev & Kryazhinskii 1990; Mukhin 1993). Thus utilization of faecal nutrients by plants is delayed. This temporal complexity of biotic turnover in tundra is not well known and should be carefully examined.

Prospects for further studies

It follows from the above that there is an urgent need to study tundra reindeer pastures as components of whole ecosystems. There is little hope that sustained production of reindeer pastures can be achieved with the aid of agricultural measures, such as fertilization, seeding etc., since economic justification for such measures is questionable.

Reindeer herding remains an important use of biological resources in the Russian North. The state and dynamics of the natural ecosystems upon which herding is based are dependent on a complex of interactions between a variety of extrinsic and intrinsic factors. However, since tundra ecosystems are relatively simple, it is possible to outline several key biotic components determine the general pattern of its dynamics (Schwarz 1971). Studying the responses of these components to changes (which are not simple and linear) in both intrinsic and extrinsic factors (including the inevitable continuation of industrial development) should provide information essential for the sustainable management of Russia's reindeer grazing systems. We recommend the following research emphases:

- 1) Comparative studies of productivity, biological diversity, and structure of plant communities under the different pressures exerted by the main groups of herbivorous animals (reindeer and small rodents), as well as under varying levels of industrial development.
- 2) Study of the direct and indirect effects of herbivorous mammals (both reindeer and rodents) on biological turnover and energy flow within the system.
- 3) Study of the role of industrial contamination on the turnover of nutrients in tundra ecosystems.

These studies should be based on the modern system approach, taking into account both tem-

poral and spatial dynamics of the subjects of the studies.

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