Diet of the wood lemming Myopus schisticolor

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The diet of the wood lemming *Myopus schisticolor* (Lilljeborg) was studied in eastern Finland in 1997 and 1998. The most preferred habitat of the wood lemming is an old spruce dominated-forest with a thick moss cover. In winter, it prefers drier areas than in summer. The wood lemming feeds mainly on moss with *Dicranum* and *Polytrichum* as the most preferred species. Different moss species and faeces were collected at the feeding places and dried. The contents of nitrogen and carbon were determined both in the faeces and in the moss species most probably fed by lemmings at a particular place. The nitrogen and carbon contents in the moss species correlated significantly with their contents in faeces. The nitrogen content was highest in the *Dicranum* and *Polytrichum* species. This may be one reason for the preference of these moss species than more common *Pleurozium* and *Hylocomium* species.

Introduction

The most preferred habitat of the wood lemming *Myopus schisticolor* (Lilljeborg) is an old sprucedominated forest with a continuous thick moss cover and plenty of decomposed trees or stumps and holes between moss covered stones (Helminen & Valanne 1963, Kaikusalo & Skarén 1963, Kalela *et al.* 1963a, 1963b, Ims *et al.* 1993). The wood lemming feeds mainly on moss and only to a minor degree on grasses, mainly *Deschampsia*, and stems and leaves of *Vaccinium myrtillus* and *V. vitis-idaea* (Helminen & Valanne 1963, Kalela *et al.* 1963a, 1963b, Andreassen & Bondrup-Nielsen 1991, Bondrup-Nielsen 1993, Sulkava *et al.* 1996).

Besides lemmings, the bank vole (Clethrionomys glareolus), field vole (Microtus agrestis) and field-mouse (Apodemus flavicollis) feed on moss to a minor degree but their diet is much more diverse than that of lemmings (Hansson 1970, 1971). Mosses belong to the diet of only a few animal species, specifically ones living in cold climates (Prins 1981). Mosses do not differ from other plants in their nutrient content (Barkley et al. 1980, Prins 1981, Batzli & Pitelka 1983). However, they are rich in multiunsaturated fatty acids which possibly help animals and their young to survive in a cold climate (Prins 1981). Digestibility of mosses seems to be very poor for most animals. The main reason for this may be the presence of specific (phenolic) secondary compounds (Seigler 1998). Most secondary plant compounds are harmful for small rodents (Tahvanainen *et al.* 1991). The composition and dietary effects of the secondary compounds of mosses are, however, poorly known.

According to the general model of optimal foraging theory (Stephens & Krebs 1986, Belovsky & Schmitz 1991), animals have the following constraints to diet selection: nutritional requirements, time for feeding, and capacity to process food in the alimentary tract. Herbivores should optimize their diet by selecting plant species with high content of energy, nutrients (nitrogen) and certain minerals and low content of undigestable fibers and repellent or toxic secondary compounds. Those food items among the acceptable ones which are abundant should be eaten more than the items which are scarce (Belovsky & Schmitz 1991). The intake of proteins or amino acids is very important for many herbivores. Plants with high digestibility are often high in protein content and herbivores may favour these kind of plants (Stephens & Krebs 1986).

The density and structure of the wood lemming population has recently been studied in eastern Finland (Eskelinen 1997). The aim of this study is to examine the food plant composition and consumption of the same wood lemming population. The diet of the wood lemming is already quite well known, but in this work I try to study the palatability of different moss species and the role of the nitrogen content of the moss species on the selection of the species eaten.

Material and methods

The material was collected in Heinävesi, eastern Finland, in the years 1997 and 1998 when the wood lemming had a low population density and a highly patchy distribution (*see* Eskelinen 1997). Nine sites used by the wood lemming as wintering places were studied in 1997 and six summer habitats in 1998. The area of each site was about 0.5–1 hectares, and they were situated 1–15 kilometres apart from each other. All the sites were rich in mosses and there were holes in decomposed stumps or between mossy stones. For vegetation analyses, plots of four square meters were chosen from places where holes,

paths and feeding patches of the wood lemming had been found. Altogether 30 plots were studied in winter habitats, and 12 in summer habitats (Table 1). Twenty-one plots in the winter habitats were in old spruce-dominated forests (12 plots on shady northern slopes). Five plots were in poorer pine-dominated forests. Three plots were on a clear felled area and one on a sapling stand. Nine plots in the summer habitats were situated between a spruce forest and a spruce swamp, two in the spruce forest and one at the edge of the swamp.

The coverage of the plant species in the field and ground layer was estimated visually in each 4-m² plot, and the proportions of different tree species surrounding these plots within a 5-m radius were evaluated, too. The sample plots were also evaluated visually in order to find out the proportion of the eaten moss tops of the moss cover. At the same time, two moss species with highest percentage of their tops damaged were observed. Moreover, the proportion of the different moss species eaten by lemmings was evaluated on the summer feeding tracks.

The sample areas were mainly composed of spruce-dominated moss-rich forests (Table 1). Pine and birch were also abundant tree species. *Vaccinium myrtillus, V. vitis-idaea* and *Deschampsia flexuosa* were the most abundant plants in the field layer. The most abundant moss species were *Pleurozium Schreberi, Hylocomium splendens* and *Dicranum* spp.

Winter and summer habitats did not greatly differ from each other. They both represent mainly Myrtillus or Oxalis-Myrtillus forest site type (Cajander 1909). Among the winter habitats there were also some pine dominated Vaccinium type forests where Vaccinium vitis-idaea was more abundant than in the summer habitats and even Calluna vulgaris occurred. In summer, the wood lemming favours moister habitats, including even swampy forests where Rubus chamaemorus and Vaccinium oxycoccos occurred in some sample areas. The abundance of *Pleuro*zium and Hylocomium did not differ clearly between winter and summer habitats. Dicranum species were more abundant in summer, Ptilium in winter habitats. Polytrichum and Sphagnum species were more abundant in summer than in winter habitats.

Winter food stores were searched in the late autumn at the places where traces of wood lemming were found. The composition of the stores was analysed and the cover of different moss species was evaluated visually within a 1-m radius around the stores.

Faeces and moss samples were collected from the winter feeding patches in the dry period from 15 May to 15 June 1997, and fresh faeces and mosses were collected between the end of June and the beginning of August 1998.

The moss samples were taken from those moss species which had been grazed most by lemmings in a particular plot, and faeces were collected from the same plots. Judging from traces, the lemmings had often fed on the same moss species for a long time on the same patch where also their excrements had accumulated. Therefore, the faeces probably have come from the mosses that have been eaten at the same place. The samples (27 altogether) were dried first at room temperature, and later for 24 h at

Table 1. Mean coverage and a frequency (F, %) of plant species (D = dominance, %) on study plots in areas where the wood lemming was found (SD = standard deviation).

	Winter habitats $n = 30$ plots			Summer habitats n = 12 plots			Total $n = 42$ plots		
	D	SD	F	D	SD	F	D	SD	F
Picea abies	50.2	41.3	63.3	86.7	14.6	100.0	60.6	39.4	73.8
Pinus silvestris	20.8	33.8	33.3	5.8	13.2	16.7	16.5	30.2	28.8
Betula alba	6.0	8.1	56.7	4.4	4.8	50.0	5.5	7.3	54.8
Populus tremula	2.2	2.8	40.0	4.0	4.0	58.3	2.7	3.3	45.2
Sorbus aucubaria	0.8	2.6	6.7	0.3	0.7	16.7	0.7	2.3	11.9
Alnus incana	0.2	0.9	3.3	0.4	1.4	8.3	0.2	1.1	4.8
Vaccinium myrtillus	34.3	18.7	96.7	44.2	23.3	91.7	37.1	20.6	95.2
Vaccinium vitis-idaea	14.6	14.9	73.3	7.9	9.6	83.3	12.7	13.9	76.2
Deschampsia flexuosa	6.6	11.1	60.0	4.9	7.0	66.7	6.1	10.1	61.9
Maianthemum bifolium	5.3	6.3	60.0	4.9	5.7	66.7	5.2	6.1	61.9
Calamagrostis arundinacea	2.7	6.7	23.3	0.5	1.4	16.7	2.1	5.8	21.4
Dryopteris spinulosa	2.7	6.7	16.7	0.9	2.8	16.7	2.2	5.9	19.0
Calluna vulgaris	2.6	4.9	26.7	_	_	_	1.8	4.3	19.0
Gymnocarpium dryopteris	1.3	5.4	10.0	_	_	_	0.9	4.6	7.1
Oxalis acetocella	1.3	2.6	23.3	0.5	1.4	16.7	1.1	2.3	16.7
Trientalis europaea	1.2	1.9	36.7	0.6	1.4	25.0	1.0	1.8	33.3
Linnaea borealis	0.8	2.1	16.6	0.9	2.8	16.7	0.8	2.3	16.6
Luzula pilosa	0.4	8.0	26.7	0.2	0.6	8.3	0.4	1.8	21.4
Rubus chamaemorus	_	_	_	4.2	13.8	8.3	1.2	7.6	2.4
Empetrum nigrum	_	_	_	1.7	5.5	8.3	0.5	3.1	2.4
Vaccinium oxycoccos	_	_	_	8.0	2.8	8.3	0.2	1.5	2.4
Orthilia secunda	_	_	_	0.2	0.4	16.7	0.1	0.2	4.8
Pleurozium schreberi	25.1	20.3	86.7	26.7	16.5	100.0	25.5	19.3	92.9
Hylocomium splendens	26.0	16.0	3.3	22.9	10.5	91.7	25.1	14.7	92.9
Dicranum sp.	12.9	14.0	86.7	16.7	12.8	91.7	14.0	13.7	88.1
Ptilium crista-castrensis	6.5	14.0	30.0	1.9	5.5	25.0	5.2	12.9	28.6
Sphagnum sp.	6.4	12.1	36.6	17.5	14.5	83.3	9.6	13.8	50.0
Polytrichum sp.	6.0	7.8	56.7	10.7	16.0	50.0	7.3	11.0	54.8
Aulacomnium palustre	1.7	9.0	6.7	1.3	3.0	16.7	1.6	7.7	9.5
Rhytidiadelphus triquetrus	0.2	0.9	3.3	_	_	_	0.1	0.8	2.4
Cladonia sp.	0.4	1.3	10.0	0.2	0.6	8.3	0.4	1.2	9.5
Peltigera sp.	0.2	0.7	10.0	0.2	0.6	8.3	0.2	0.6	9.5
Eaten moss (%)	10.0	9.2		21.0	12.9		13.1	11.5	

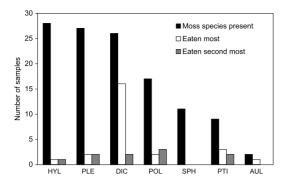


Fig. 1. The occurrence and feeding of lemmings on different moss species in winter biotopes in 30 sample plots. HYL = *Hylocomium*, PLE = *Pleurozium*, DIC = *Dicranum*, POL = *Polytrichum*, SPH = *Sphagnum*, PTI = *Ptilium*, AUL = *Aulacomnium*.

+105 °C. The content of nitrogen and carbon was determined in the laboratory by elemental analyser (Carlo Erba 1106). Three analyses were made of each moss and faeces sample and the mean value was taken for processing.

For the statistical analysis of summer food selection, the "palatability index" was estimated. The percentage cover of each moss species was visually estimated using 4 × 4-m plots. The proportion of each moss species eaten by lemmings within each plot was estimated visually. If all moss tops were eaten the proportion would be 100%. An index for palatability for a certain moss species was calculated as a ratio of proportion of tops eaten (estimated as a percentage of total cover of the particular species) and its proportion in total moss cover.

If there would not be any preference in the palatability (Ho) of certain moss species, the index would obtain a value of one, i.e. the proportion of moss species eaten would be the same as the proportion of moss species present in the study plot. This Ho is tested here with Wilcoxon's signed rank sum test, comparing the observed palatability index with the theoretical median of one, if a moss species was eaten less than its abundance in the plot, but the values can be much higher than one, if the species is highly palatable. The test is two-sided: significant *p*-values indicate a divergence from the Ho (no species preference).

The nitrogen and carbon contents and C:N relation between the faeces and moss species used as food were tested with Duncan, one-way ANOVA and Pearson Correlation (SPSS 1992).

Results

Diet

According to the field observations, the wood lemmings feed on the tops of different moss species, and the stems and leaves of *Vaccinium myrtillus* and *V. vitis-idaea*. Pieces of these plants were found on the paths and feeding patches of wood lemmings. Distinct marks of feeding on grasses were not found in the field. However, the tracks of moss feeding were clear. From the colour of faeces it is even possible to distinguish the different moss species eaten. Lemmings graze for a long time on the same

Table 2. The mean cover of the moss species, the mean percentage of moss species grazed by wood lemming and the ratio of percentage grazed and total cover of moss species in summer biotopes (n = 12). Preference of the moss species tested with Wilcoxon's W statistic.

	Dicranum		Polytrichum		Ptilium		Pleurozium		Hylocomium		Sphagnum	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
Cover (%) Grazed (%)	16.7 42.9	12.8 32.8	10.7 21.3	16.0 34.0	1.9 3.1	5.5 8.2	26.7 23.9	16.5 21.1	22.9 7.2	10.5 7.1	17.5 1.0	14.5 2.8
Grazed:cover	2.6		2.0		1.6		0.9		0.3		0.1	
W P	63.5 0.0049		8.5 0.3750		6 0.2500		21 0.5566		0 0.0010		0 0.0020	

moss species within the same plot. Lemmings that have eaten *Pleurozium* or *Hylocomium*, *Polytrichum*, *Dicranum* and *Ptilium* have light brown, dark brown, dark green, and light green faeces, respectively.

On average, 13% (2% to 30%) of the moss cover in the study plots had been eaten by lemmings (Table 1). A higher percentage of the moss cover had been eaten in the summer habitats (21%) than in the winter ones (10%).

The Dicranum species proved to be the most utilized moss species both in winter (Fig. 1) and in summer habitats (Table 2). Lemmings had eaten mostly Dicranum if it was available in the particular place. The moss species with the second highest percentage of damaged tops in the winter habitats was Ptilium crista-castrensis. It occurred, however, only in 30% of the sample plots and its cover was usually small. Some samples were rich in Ptilium and a great part of it had been eaten. Polytrichum was found in about 60% of the sample plots but its mean cover was smaller than that of Ptilium. Despite the relatively high abundance of the Polytrichum species they were not as favoured by lemmings as Ptilium in winter habitats. Pleurozium schreberi occurred in nearly every sample area and its cover was high but only in a few samples was it the most or second most eaten moss species. In those areas there was no Dicranum. However, in most samples at least a little of Pleurozium had been eaten. Besides Pleurozium, Hylocomium splendens is the most numerous species in the study area and occurs in nearly all the sample plots, but it had been severely damaged in only a few plots and usually it had been eaten very little. Aulacomnium palustre occurred in two plots in winter habitats, sparsely in one and quite abundantly in another. It proved to be very badly eaten in the latter plot; 30% of the cover of the species had been eaten. Other moss species had been eaten only very little. The Sphagnum species occurred commonly at the studied sites but they were untouched in winter habitats. They were eaten in very few places outside the studied areas. Rhytidiadelphus triquetrus occurred sparsely in the studied areas but it was totally untouched.

The most preferred mosses in summer habi-

tats were *Dicranum* and *Polytrichum* species (Table 2). *Ptilium* was preferred where it occurred. *Pleurozium* had been eaten nearly in the same proportion as it occurred, but *Hylocomium* had been eaten much less. *Sphagnum* had been eaten very little even though it occurred abundantly. The preference for *Dicranum* and the avoidance of *Hylocomium* and *Sphagnum* was statistically significant (Table 2).

Winter food stores

Winter food stores were searched just before the winter in the places where wood lemmings stayed in the autumn. Nine stores were found in three areas in 1998, and nine in five areas in 1999. One store was found already on 13 September, others at the end of October and in the beginning of November. They were situated in decomposed stumps or between stones in the openings of the wintering holes or under stones, and their sizes were mainly between 2 and 3 dl. Only one store was about two liters and one about one liter. The mosses were collected round the stores less than one meter from the holes, which was seen from the field tracks.

Nearly all the stores were mainly composed of *Dicranum* (Fig. 2), although its abundance was low (15%) in the vegetation around the stores. The proportion of *Pleurozium* in the stores was only 11% on average, although it consisted of nearly half of the moss cover in the surroundings. The proportion of *Hylocomium* was about 30% in the wintering areas but about 3% in the stores. The proportion of *Ptilium* was small both in the field and in the stores. There was very little *Polytrichum* and *Sphagnum* near the holes and they did not occur in the stores.

Proportion of nitrogen and carbon in mosses and faeces

The nitrogen content was highest in *Polytrichum* and second highest in *Dicranum* (Table 3 and Fig. 3). The difference in nitrogen content among species was significant (one-way ANOVA, df = 5, p = 0.018). The decrease of the N content in

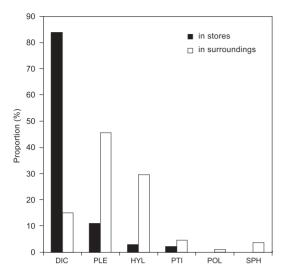


Fig. 2. The proportion of the different moss species in the lemming winter food stores (n = 18) and the proportion of the species of the moss in the surroundings. DIC = Dicranum, PLE = Pleurozium, HYL = Hylocomium, PTI = Ptilium, POL = Polytrichum, SPH = Sphagnum.

faeces, as compared with that in the moss species eaten, was greatest in *Polytrichum* and *Dicranum* (Table 3 and Fig. 3). A significant correlation between the mosses and faeces was found in nitrogen (n = 25, r = 0.541, p = 0.005) (Fig. 4a) as well as in carbon (n = 25, r = 0.528, p = 0.007) (Fig. 4b). The proportion of C was lower in *Aulacomnium*, *Ptilium* and *Dicranum* than in the other moss species (Table 3 and Fig. 3). The difference among species was significant (one-way ANOVA, df = 5, p = 0.001).

The increase of the carbon:nitrogen ratio

(C:N) in faeces as compared with that in mosses was highest in *Aulacomnium* faeces, second highest in *Dicranum* and *Polytrichum* faeces. It was lowest in *Pleurozium* faeces (Table 3 and Fig. 3).

Discussion

Habitat and food preference

The main result of this study is the preference of *Dicranum* and *Polytrichum* species in the diet of the wood lemming and nitrogen content of these moss species as one possible reason for this preference. The main reason for the habitat selection is probably the supply of high quality food.

The most preferred habitat of the wood lemming in this study, old spruce forest with a thick moss cover, does not evidently differ from those found in other studies (Kalela et al. 1963a, 1963b, Kaikusalo & Skarén 1963, Helminen & Valanne 1963, Kalela et al. 1971, Ims et al. 1993, Sulkava et al. 1996). In winter, the wood lemming occurs also in pine forests and even in clear cut areas if there is plenty of moss (Eskelinen 1997). Wintering tracks (grazing patches and faeces) were not seen at all in dense spruce forests. These kind of areas often lack snow cover that gives the wood lemming essential protection against the cold. The edge areas of spruce forests and clearings where snow cover is thick in winter, and open spruce forests were preferred by the lemmings. There is usually a thick moss cover and a thick and long lasting snow cover on northern slopes in winter which explains the occurence of most lemmings in

Table 3. The nitrogen (N) and carbon (C) content (%) and the ratio of nitrogen and carbon (C:N) in moss species and faeces of the wood lemming coming from the same moss. The means are compared with the Duncan test. Values with no common superscript letter differ at p < 0.05. (SD = standard deviation)

		N (mea	n ± SD)	C (mea	an ± SD)	C:N (mean ± SD)		
	n	Moss	Faeces	Moss	Faeces	Moss	Faeces	
Polytrichum	6	1.13 ± 0.33 ^a	0.92 ± 0.30	47.4 ± 0.89	46.4 ± 1.70	45.5 ± 12.5 ^a	53.5 ± 19.3	
Dicranum	11	0.92 ± 0.16^{ab}	0.71 ± 0.16	46.8 ± 0.97	44.5 ± 1.72	52.6 ± 9.97^{a}	66.8 ± 16.6	
Hylocomium	4	0.71 ± 0.08^{b}	0.61 ± 0.12	47.6 ± 0.81	44.3 ± 1.46	68.1 ± 9.03 ^b	74.9 ± 14.9	
Pleurozium	4	0.70 ± 0.12^{b}	0.60 ± 0.02	47.6 ± 0.64	45.5 ± 1.54	69.6 ± 11.5 ^b	75.5 ± 2.08	
Aulacomnium	1	0.74	0.57	42.0	43.8	56.8	76.9	
Ptilium	1	0.63	0.51	45.9	43.5	72.9	85.3	

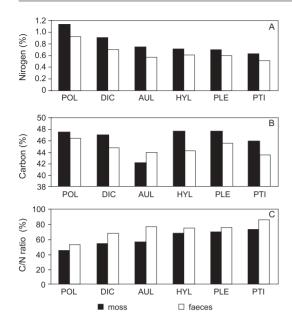


Fig. 3. The contents (%) of (**A**) nitrogen (N), (**B**) carbon (C), and (**C**) the carbon/nitrogen (C/N) ratio (%) in mosses and lemming faeces. POL = *Polytrichum*, DIC = *Dicranum*, AUL = *Aulacomnium*, HYL = *Hylocomium*, PLE = *Pleurozium*, PTI = *Ptilium*.

these areas. In summer, the wood lemming lives in a moister habitat (Helminen & Valanne 1963, Kalela *et al.* 1963a, 1963b).

The results of this study on the diet composition of the wood lemming mainly agree with the other studies (Helminen & Valanne 1963, Kalela et al. 1963a, 1963b, Bondrup-Nielsen 1993). The *Dicranum* species are the most preferred moss species in all the studies and the supply of Dicranum seems to be one of the main factors in habitat selection. Polytrichum spp, Ptilium cristacastrensis and Pleurozium Schreberi are the other preferred moss species. Hylocomium splendens was found not to be considerably utilised in any of these studies. Sphagnum spp. are usually avoided by the wood lemmings (Kalela et al. 1963b, Bondrup-Nielsen 1993). Aulacomnium palustre was greatly utilized in one area in this study, but it did not occur at all in the diet of the wood lemming in the other studies. The composition of the winter food stores studied here differed to some extent from the study of Sulkava et al. (1996) in which Pleurozium was the most abundant species in stores.

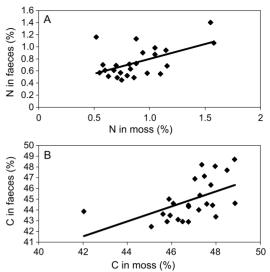


Fig. 4. The correlations of (**A**) the nitrogen (N) content (%) in mosses and faeces (n = 25, r = 541, p = 0,005), (**B**) carbon (C) content (%) in mosses and faeces (n = 25, r = 0,528, p = 0,007) (the single dot on the left indicates *Aulacomnium*).

Factors affecting the palatability of different moss species

Herbivores ought to select the plant species that are rich in nutrients and energy, easily digestable and do not contain plenty of toxins. If the amount of toxins in the plants increases above the critical level animals ought to change the diet (*see* Hughes 1993). The wood lemming has only a few possibilities for diet change if the toxicity of a few potential food plant species increases.

Mosses probably contain substances that are not easily digestable. For instance the brown lemming, which also feeds largely on mosses, digests grass better than moss (Batzli & Cole 1979). The wood lemming can survive on a diet of moss alone but young wood lemmings supplementing their diet with other plants grow faster (Andreassen & Bondrup-Nielsen 1991). Mosses contain much more long-chain fatty acids, especially arachidonic acid, than other plants (Prins 1981). Intake of arachidonic acid can increase heat production. That might be a primary reason for the common utilisation of moss by arctic animals (Prins 1981) and the wood lemming in winter. The arachidonic acid

content of mosses is higher in wet than in dry areas and the highest under snow (Aro & Karunen 1979) which may also affect habitat selection of the wood lemming.

The reason for favouring some moss species over others can be explained by different digestibility, nutrient content and taste. The nitrogen content of moss species indicates that protein content and the usability of proteins in food is of crucial importance. The increase of the C:N relation in faeces as compared to mosses themselves may show to some degree the relative efficiency of the nitrogen consumption.

The efficiency of nitrogen uptake seems to be best on a diet of Dicranum, Polytrichum, Aulacomnium and Ptilium. The highest nitrogen content and the lowest C:N ratio is in Polytrichum. However, Dicranum is the most preferred moss. The reason for this differential preference is probably that *Dicranum* is more abundant than Polytrichum in the habitats of the wood lemming, and *Dicranum* may be more easily digested. The high protein content of Dicranum and Polytrichum explains quite well the preferrence for these moss species. It does not, however, explain the low feeding on Hylocomium as compared with that on Pleurozium. Different secondary compound constitutions (see Seigler 1998) may explain part of the differences in the palatability of different moss species. Detailed information on differences in concentrations of different secondary compounds in moss species is not available, however. The nitrogen content of Sphagnum was not analysed because the Sphagnum species do not largely belong to the diet of the wood lemming. According to Prins (1981), the nitrogen content in *Sphagnum* is the same but the contents of phosphorus, calcium and magnesium are much lower than those in the other mosses, and perhaps also acidity limits the usability of Sphagnum as food (Bondrup-Nielsen 1993). The reason for the correlation of nitrogen and carbon contents between mosses and faeces is that the greater the intake of nitrogen or carbon, the greater its amount in faeces. Thus, only a part of the nutrients are absorbed in digestion.

The significant correlation between nutrient contents in the main moss species eaten and in the faeces at the same sample areas supports the assumption that the lemmings are staying at the same feeding place for extended periods. These results of the nutrient analyses, however, are preliminary ones, and require further more complex studies on the subject.

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