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Studies on the ecology  
of the wood lemming,  
*Myopus schisticolor*

by  
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**Key words:** *Myopus schisticolor*, population fluctuations, sex ratio, body weight, litter size, migrations, genetic variation, diet, *Dicranum*, nitrogen content

The aim of this thesis was to study the habitat structure, diet, population structure, population fluctuations and genetic variability of the wood lemming (*Myopus schisticolor*), an inhabitant of mossy spruce forests in the northern taiga. The material was collected mainly by searching for field tracks and collecting dead animals under bridges and in canals in Heinävesi, eastern Finland, and in the Keuruu region, western Finland.

The wood lemming feeds mainly on moss, and the preferred moss species are *Dicranum* spp. One reason for this preference may be the higher nitrogen content of *Dicranum* compared with the more abundant *Pleurozium* and *Hylocomium* species.

In the wood lemming population, the sex ratio varies considerably, but the mean sex ratio in late summer and autumn is about 25% males. The mean body mass and litter size of the wood lemming were smaller in the declining phase than in the increasing population phase.

In Heinävesi the wood lemming population fluctuates regularly in three-year cycles and in synchrony with the field vole population. The synchrony between lemming, field vole and owl populations seems to support the predation hypothesis, specialist predators such as weasels and owls probably causing the cycles in lemming and vole populations. In the Keuruu region, however, no cycles were found probably due to more variable snow depth in winter and constant predation by several generalist predators. Wood lemmings migrate in August and September from densely populated sites to areas of lower population density.

Genetic variation in the wood lemming population in Heinävesi is greater than in the other wood lemming populations studied in Fennoscandia and Siberia. In a consensus tree the Heinävesi population is placed between the Siberian and Scandinavian groupings. This is in agreement with the postglacial recolonization of the wood lemming westward from its Siberian refugia.

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## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, referred to in the text by their Roman numerals I-IV:

- I Eskelinen, O. 2002. Diet of the wood lemming *Myopus schisticolor*. *Annales Zoologici Fennici* 39: 49-57.
- II Eskelinen, O. 1997. On the population fluctuations and structure of the wood lemming *Myopus schisticolor*. *Zeitschrift für Säugetierkunde* 62: 293-302.
- III Eskelinen, O., Sulkava, P. and Sulkava, R. 2004. Population fluctuations of the wood lemming, *Myopus schisticolor*, in eastern and western Finland. *Acta Theriologica*, in press.
- IV Vuorinen, J. A. and Eskelinen, O. Long-term stability of allozyme frequencies in a wood lemming, *Myopus schisticolor*, with a biased sex ratio and density fluctuations. Submitted for publication in *Heredity*.

Some unpublished results are also presented.

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## 1. INTRODUCTION

### 1.1. The wood lemming

The wood lemming (*Myopus schisticolor* Lilljeborg, 1844) is a small vole species belonging to the family Muridae, subfamily Arvicolinae, and is the only species in the genus *Myopus* (Jarrell and Fredga 1993). It has a wide distribution from southern Norway to Kamchatka in the taiga area of Eurasia (Siivonen and Sulkava 1994, Fedorov et al. 1995). The Siberian subspecies (*M. s. vinogradovi* Scalon and Rajevski, 1940) is bigger and has a larger brown patch on its back than the European subspecies (*M. s. schisticolor*) (Kratochvil et al. 1979, Niethammer and Henttonen 1982). Two subspecies (*M. s. taylori* and *M. s. sajanicus*) occur in eastern Siberia (Gromov and Polyakov 1992). The wood lemming recolonized Fennoscandia from the east after glaciation (Fedorov et al. 1996, Jaarola et al. 1999). The distribution of the wood lemming is tied to taiga-like habitats where its main food source, the mossy ground layer, occurs abundantly (Helminen and Valanne 1963, Kalela et al. 1963a, 1963b). The local distribution of the wood lemming is mosaic-like, being concentrated to patches of mossy spruce forests (Kratochvil et al. 1979). During population peaks, however, its local distribution may cover larger continuous areas (Ims et al. 1993).

The population density of the wood lemming periodically shows large oscillations, but the peaks are not as regular as in other microtines and between the peaks the population density is very low (Kalela et al. 1971). In peak years during late summer and autumn lemmings may migrate from overpopulated areas to areas of low population density (Kalela 1963, Uino 1963, Eskelinen et al. 1983, 1984). In spring they may move from dry winter habitats to moister summer habitats (Kalela et al. 1963a, 1963b). The size of home range of different wood lemmings varies greatly. Male home ranges are larger (mean ca 2000 m<sup>2</sup>) than those of females (mean ca 300 m<sup>2</sup>), and the ratio of female home range to male home range is smaller than in other small rodents (Andreassen and Bondrup-Nielsen 1991).

In wood lemming populations, females predominate with only about 25% being males.

However, the sex ratio changes in the course of a year and in early spring may be about 1:1 (Skarén 1963, Kalela and Oksala 1966, Fredga et al. 1993). The reason for the skewed sex ratio is a mutation in the X-chromosome (X\*) causing three types of females, XX, X\*X and X\*Y, the last one producing only daughters (Fredga et al. 1976, 1977, Stenseth and Ims 1993a). X\*Y females have higher reproduction potential and more clumped distribution than the other female types do (Bondrup-Nielsen et al. 1993). Litter size of the wood lemming varies from 3 to 7, being largest in overwintered females (Skarén 1963, Fedorov and Cheprakov 1990, Bondrup-Nielsen et al. 1993). Reproduction of the wood lemming often begins in winter (Mysterud et al. 1972), and each female usually has two litters per a year. A third litter is also possible, but lemmings born in winter or early spring usually have only one litter in late summer (Skarén 1963). Female wood lemmings reach sexual maturity at the age of 22–40 days, males at over 44 days (Ilmén and Lahti 1968). They do not become mature before reaching a body mass of 20 g; and if they do not reach that weight in the summer they are born, they stop growing over winter and become mature the following spring (Skarén 1963, Ilmén and Lahti 1968). The wood lemming does not usually live over one year (Skarén 1963).

### 1.2. Population fluctuations of voles

In the northern hemisphere many small mammal populations fluctuate periodically, and several species may fluctuate in synchrony (e.g. Krebs and Myers 1974). The regular fluctuations, called cycles, have long interested scientists, and many hypotheses on the causes of these cycles have been presented (e.g. Krebs 1996, Boonstra et al. 1998, Stenseth 1999). The cycles are known specifically in voles and lemmings, but mice and shrews and many other mammals also undergo similar fluctuations. The causes of the cycles are proposed to be common to several small mammal species but ecologists still do not agree on the reasons for these cycles (e.g. Sundell 2002). The mechanisms underlying cycles can be divided into two main categories, intrinsic and extrinsic factors (Stenseth and Ims 1993b). The extrinsic factor hypotheses are often divided into biotic and abiotic factor

hypotheses. The most important and most often cited to are the following hypotheses: 1) food supply, 2) predation, 3) food supply and predation, 4) self-regulation and 5) multiple factors (Krebs 1996).

The food supply hypothesis (e.g. Krebs and Myers 1974) proposes that changes in food quantity and quality cause the cycles. A dense rodent population may deplete its food resources, usually in wintertime, which may lead to increased mortality and lowered reproduction. In addition, plant secondary compounds, which may increase under heavy herbivore pressure, may further increase mortality in the dense rodent populations found for example in the Norwegian lemming (Seldal et al. 1994). According to food supply hypothesis, rodent populations increase again after recovery of the vegetation during low population density. Some rodents, such as the bank vole, are dependent on plant seeds, which vary greatly in abundance in different years. Good yield of seeds may increase the reproductive success of voles and affect the cycles (Hörnfeldt 1994, Jedrzejewski and Jedrzejewska 1996, Oksanen et al. 2000). The result of a recent study on the field vole did not support the food supply hypothesis (Klemola et al. 2000). In the absence of predation, however, shortage of winter food supply may limit growth of *Microtus* vole populations (Huitu et al. 2003). Some voles have salivary tannin-binding proteins that prevent the negative effect of plant secondary compounds (Juntheikki et al. 1996). It is possible that some rodent cycles, such as those of Norwegian lemmings in arctic areas, may be driven by their interaction with the food plants (Turchin et al. 2000, Turchin and Batzli 2001).

The predation hypothesis has been suggested in many of the recent studies (e.g. Andersson and Erlinge 1977, Henttonen et al. 1987, Hanski et al. 1991, 1993, Hanski and Henttonen 1996). According to this hypothesis the cycles are apparently caused by the interaction between small mammals and their specialist predators. In contrast, generalist predators, which can rapidly switch to a more abundant alternative prey, have a stabilising effect on prey population dynamics. In areas of long winter with thick snow cover like

northern Fennoscandia, the small mammal cycles are probably caused mainly by the interaction between voles and the least weasel (Hansson and Henttonen 1985, Henttonen 1987, Hansen et al. 1999), but specialist avian predators are also important (Korpimäki 1993, Norrdahl and Korpimäki 1995). However, according to Graham and Lambin (2002), in Scotland weasel predation alone cannot drive the cycles. The refined predation hypothesis of Norrdahl and Korpimäki (2002) states that small mustelids and other mammalian and avian predators dependent on rodents cause delayed density-dependent mortality, which drives the vole cycles. Predation also causes synchrony between voles and other small mammals (Henttonen 1985, Korpimäki 1986, Huitu 2003). Synchrony between different areas is probably caused by nomadic avian predators (Ims and Steen 1990, Norrdahl and Korpimäki 1996, Huitu 2003) and may also be affected by climatic patterns (Krebs et al. 2002, Sundell et al. 2002). At present, most ecologists support the predation hypothesis, at least in Fennoscandia (Hansen et al. 1999, Oksanen et al. 2000, Henttonen and Hanski 2000, Hanski and Henttonen 2002, Klemola et al. 2002b, Sundell 2002).

Self-regulation or the individual-difference hypothesis (Krebs 1978, 1996) suggests that phenotypic or genotypic changes in individuals are necessary for cycles (Chitty 1960). However, genetic changes in different phases of populations have not been found in any of several studies (Boonstra and Boag 1987, Ergon et al. 2001a, 2001b). Some studies still propose that genetic mechanisms may influence the vole cycles (Boonstra et al. 1998). For example, spacing behaviour, which may vary over time, is probably inherited, and may influence population density by affecting the birth, death and dispersal rates of small mammals (Krebs 1996). Another type of self-regulation hypothesis involving stress (Christian 1950) has been rejected because in natural conditions crowding was not found to cause hormonal changes in individuals (Krebs and Myers 1974). Also the maternal effects have been suggested to cause the low phase of population density (Boonstra et al. 1998, Inchausti and Ginsburg 1998). Similarly, mere

risk of predation may cause stress that leads to delayed reproduction in the low phase of populations (Ylönen 1989, Hansson 1995, Ylönen et al. 1995). However, the commonly found larger body size in the increasing phase of populations (Krebs and Myers 1974) may be due to extrinsic factors such as food quality (e.g. Henttonen et al. 1984, Agrell et al. 1991, Ergon et al. 2001a, 2001b) or size-selective predation by the least weasel (Sundell and Norrdahl 2002). In general, intrinsic factors probably do not play a major role in driving vole cycles (Klemola et al. 2002a).

To summarise, although predation alone (e.g. Norrdahl and Korpimäki 2002) may be able to cause the vole cycles, it is probable that many factors act together in causing the cycles (multiple factor hypotheses). According to Krebs (1996), several mechanisms, e.g. spacing behaviour and predation together, are sufficient to cause the cycles while some studies (e.g. Hansson et al. 2000, Stenseth et al. 2002) have suggested that weather conditions, by controlling the seed production of plants, and predation, may together drive the rodent cycles. The influence of diseases and parasites is poorly known, but they may have some role in population cycles (Krebs and Myers 1974, Krebs 1996, Boonstra et al. 1998, Feore et al. 1997, Soveri et al. 2000).

### 1.3. Aims of the study

The aims of the study were:

- 1) To study the habitat structure utilised by the wood lemming.
- 2) To ascertain the diet of this species.
- 3) To investigate the age structure, sex ratio and litter size of the wood lemming population.
- 4) To study the population fluctuations of the wood lemming in eastern and western Finland and to attempt to understand the causes of the population fluctuations.
- 5) To investigate the movements of the wood lemming and the reasons for these movements.
- 6) To analyse the long-term genetic structure of the Heinävesi population and to compare its genetic diversity with previously studied populations.

## 2. MATERIAL AND METHODS

### 2.1. Study areas

The main study area was Heinävesi commune and its surroundings in eastern Finland (about 1500 km<sup>2</sup>, centre of the area 62° 25' N, 28° 40' E, see Fig. 2 in II). The area is largely surrounded by lakes, and 20% is covered by lakes and water routes. The lakes are connected by several canals for boats, and several road and railway bridges cross the water routes (Fig. 2 in II). Forests make up 85% of the land area, 90% of them being fresh spruce-dominated forests and only 10% dryer pine-dominated forests. Ten per cent of the area is marshland, mainly small spruce swamps and fens. Forests and marshes are mainly managed, old natural forests being small fragments. High hills and cliffs are common in the area.

Another study area was Keuruu region in western Finland, (2500 km<sup>2</sup>, centre 62° 15' N, 24° 25' E, 200 km west from Heinävesi). Forests cover 70% of the area, marshland 10%. Original spruce-dominated forests have been largely converted to pine-dominated forests by intensive forest management. Old spruce forests presently occur as small fragments. Cultivated fields and settlements are larger than in Heinävesi. Water covers 10% of the area. The hills are smaller and fewer than in Heinävesi. In Keuruu there are also some railway bridges but no canals.

### 2.2. Study of habitat structure and diet

Habitat use by the wood lemming was studied in detail in Heinävesi in 1997 and 1998, when the lemming population density was low (I). Proportions of different plant species were estimated in winter and summer habitats (Fig. 1) at the sites where lemming tracks (Fig. 2) were found in the moss cover. The proportions of different moss species available and eaten by the wood lemming were estimated. Winter food stores were sought in autumn, and the proportions of different moss species in stores and in their surroundings were estimated. Different moss species and lemming faeces were collected at the feeding sites of lemmings. The mosses and faeces were dried, and their nitrogen and carbon contents were determined in the laboratory. To determine how mosses



differ in their quality as food for lemmings the nitrogen and carbon contents of different moss species and faeces were compared.

### **2.3. Collecting and handling of dead lemmings**

Many dead wood lemmings were found for the first time in August-October 1982 in Heinävesi under bridges (Fig. 3), in canals (Fig. 4) and on roads (Eskelinen et al. 1983, II). Thereafter the bridges and canals were checked several times every summer during 1982-2003. The dead lemmings were counted and the unspoiled ones collected for further study. After dead lemmings had been found, the most important sites were checked daily or at least every other day and other locations once a week until no more animals were found.

The collected lemmings were weighed and measured, and their sex was determined. The length of the testes or diameter of the uterus was measured, and birth scars in the uterus were checked. The males were considered to be mature when the length of the testes was at least 7 mm (Skarén 1963, Artimo 1969) and females when the diameter of the uterus was at least 1 mm or when birth scars or embryos were found.

### **2.4. Study of population density**

The population densities on both study areas, Heinävesi and Keuruu, were monitored yearly in 1982-2003 by inspecting lemming tracks (feeding patches in moss with an abundance of faeces, paths and corridors under moss and in decomposed stumps, and winter food stores, Fig 2) in late autumn at their preferred habitats (Fig. 1, I, II, III). The relative abundance of traces was estimated on a scale of 0-3 at 20-22 sites yearly, and the sum of the scores was used as the abundance index (III, Appendix 1). The movements of lemmings were monitored by searching for tracks at different sites throughout the year and inspecting sites where dead lemmings might be found. To search for the causes of the population fluctuations, the relative abundance of other voles and some predator species was estimated yearly both in Heinävesi and in Keuruu (III).

### **2.5. Study of genetic variation**

A total of 184 wood lemmings collected from

Heinävesi during 1982, 1996, 1999 and 2002 were stored in a freezer for genetic analysis (IV). Allozyme electrophoresis was used to study genetic variation at 20 enzyme-coding loci. The genetic relationship of the Heinävesi population to previously studied Scandinavian and Siberian populations was illustrated with a neighbour-joining dendrogram. Confidence in tree topology was evaluated by bootstrap analysis over loci.

## **3. RESULTS AND DISCUSSION**

### **3.1. Habitat**

The preferred habitat of the wood lemming is an old spruce-dominated forest with a thick moss cover containing many decomposed trees or stumps and holes between moss-covered stones (Fig. 1). The summer habitat is usually moister than the winter habitat. The study on habitat use of the wood lemming (I) gave results consistent with those of earlier studies in Finland (Helminen and Valanne 1963, Kaikusalo and Skarén 1963, Kalela et al. 1963a, 1963b, Sulkava et al. 1996) and in Norway (Ims et al. 1993). The winter habitat may also be a dryer, pine-dominated or clear-felled mossy forest area, often a northern slope that remains snow-covered late in spring (I, II). In winter, tracks were not found in dense spruce forests, where the snow cover is thin and packed and melts early in spring (I). During population lows, tracks were found only in some of the most preferred habitats, but during the population peaks the tracks were found nearly everywhere in mossy spruce forests. In dry summers during low population density, fresh tracks were found mainly in and around the edges of spruce swamps. In wet summers, tracks were also seen in drier mossy spruce forests, where the lemmings live year-round during high population density. In August and September, lemmings disperse to new areas and to typical winter habitats. The wood lemming drinks more water than other voles do (Iilmén and Lahti 1968), which may be why lemmings move to moister areas in spring or early summer. On the other hand, marshy areas are not suitable for wintering, and the lemmings move to drier sites in autumn.





*Figure 1.* Preferred habitat of the wood lemming.



*Figure 2.* Feeding patches of the wood lemming.





*Figure 3.* Dead wood lemmings and a field vole under a railway bridge.



*Figure 4.* Kerma canal in Heinävesi.

### 3.2. Diet

The wood lemming feeds mainly on the tops of different moss species, on some grasses, such as *Deschampsia* spp., and on the leaves and stems of *Vaccinium* spp. In all studies on the diet of wood lemming a strong preference for *Dicranum* spp. has been found (I, Helminen and Valanne 1963, Kalela et al. 1963a, 1963b, Bondrup-Nielsen 1993, Sulkava et al. 1996). *Polytrichum* spp., *Ptilium crista-castrensis* and *Pleurozium Schreberi* are the other commonly used moss species. According to all these studies, *Hylocomium splendens* was used marginally and *Sphagnum* spp. was mainly avoided. *Aulacomnium palustre* was greatly utilised at one site in the present study (I) but not at all in the other studies (Helminen and Valanne 1963, Kalela et al. 1963a, 1963b, Bondrup-Nielsen 1993). *Dicranum* was the most abundant moss species in the winter food stores of the wood lemming in Heinävesi (I) as well as in Keuruu (Sulkava et al. 1996). In northern Finland, however, *Pleurozium* was found to be the most abundant species in the stores; but compared to their availability, *Dicranum* and *Ptilium* were the preferred mosses (Sulkava et al. 1996).

Analysis of nitrogen and carbon content in mosses and faeces revealed that the nitrogen content is greatest and the C:N ratio lowest in *Polytrichum* and *Dicranum* and in faeces derived from these mosses. One reason for the preference for these moss species may be their greater protein content and usability compared to the less preferred but more common *Hylocomium* and *Pleurozium* species.

### 3.3. Population structure

In this study the sex ratio of the wood lemming varied from 15% to 29% males (II, Appendix 2). The mean sex ratio, 25.9% males (Table 1), however, was near the expected sex ratio. Among migrating animals, the sex ratio changes in the course of migration (Table 2, unpubl.). The mean percentage of males was highest (33.9%) in the first half of August and lowest (19.8%) in late September (Table 2). The low proportion of males in 1986 and 1995 is probably due to the exceptionally late migration of wood lemmings in these years (Fig. 3 in II). The number of mature males was very low except in

the high peak years 1989, 1992 and 2002 (Appendix 2). No mature males, however, were found in the high peak year 1982. The proportion of migrating mature males was highest in the first half of August and none were found after the middle of September (Table 2). The material analysed in 1982 was mainly from the latter half of September (Eskelinen et al. 1983) as was also the case in the study of Skarén et al. (1984); this was probably the reason why no mature males were found then. The higher proportion of males in August than in September is probably due to the fact that males searching for new territories begin migration earlier than females. In general, according to many studies (Skarén 1963, Kalela and Oksala 1966, Fedorov and Cheprakov 1990, Gileva and Fedorov 1991, Fredga et al. 1993), the proportion of males is highest in spring and lowest in autumn. The proportion of mature females who have not given birth was usually very low and they were not separated from young females in Table 3 in II and in Appendix 2. In 2002 the number of those females was greater than before, and in Table 2 they are separated from young females. Their proportion was highest at the beginning of August (8.5%) and lowest in late September (1.4%). The proportion of pregnant females was 9.0% at the beginning of August and only 0.5% in September (Table 2). The proportion of females that had bred was highest in the latter half of August and first half of September but was low in late September (Table 2).

The mean number of uterine scars (mean 4.6, Table 1) varied from 2.8 in 1983 to 5.8 in 1982 and 1989 (II) and was significantly smaller in 1983, 1996 (II) and 2003 (t-test,  $p < 0.02$ , Appendix 2), when the population was high for two successive years, than in the previous years 1982, 1995 and 2002, when the population was growing. The weight of immature and mature females and immature males was significantly lower in the declining populations in 1983, 1996 (II) and 2003 (t-test,  $p < 0.001$ , Appendix 2). In addition, the mean length of wood lemmings was significantly less in 2003 than in 2002 (t-test, immature males  $p < 0.02$ , immature females  $p < 0.001$ , mature females  $p < 0.05$ , Appendix 2). The smaller litter size and individual size in the declining phase of population density compared with the

*Table 1.* Sexual maturity, sex ratio and morphological characteristics of the wood lemmings found dead in the years 1982-2003 in Heinävesi. SD = standard deviation.

	N	%	Body mass		Body length		Testes length		Uterine scars	
			g	SD	mm	SD	mm	SD	N	SD
Immature males	584	23.7	17.2	1.7	85.4	4.3	3.7	0.7		
Mature males	55	2.2	23.1	3.8	98.7	5.1	8.5	1.1		
Immature females	1552	62.9	16.8	1.7	84.0	4.7				
Mature females	278	11.3	21.8	2.6	93.7	4.8			4.6	1.4

*Table 2.* Population structure of migrating lemmings in two-week periods in the years 1992, 1996, 1999, 2002 and 2003 in Heinävesi.

Time period	N	Total males		Mature males		Immature males		Mature females not given birth		Pregnant females		Females that had given birth		Immature females	
		n	% of total N	n	% of total N	n	% of total N	n	% of total N	n	% of total N	n	% of total N	n	% of total N
		-15.8.	177	60	33.9	17	9.6	43	24.3	15	8.5	16	9.0	16	9.0
16.-31.8.	490	141	28.8	12	2.4	129	26.3	16	3.3	15	3.1	45	9.2	273	55.7
1.-15.9.	385	92	24.0	8	2.1	84	21.8	5	1.3	2	0.5	41	10.6	245	63.6
16.9.-	207	41	19.8			41	19.8	3	1.4	1	0.5	13	6.3	149	72.0
Total	1259	334	26.5	37	2.9	297	23.6	39	3.1	34	2.7	115	9.1	737	58.5

increasing phase was also found in Norway (Bondrup-Nielsen and Ims 1988). The mean weight and length of young wood lemmings (Table 1) did not differ from those of young lemmings in Norway (Kratovich et al. 1979). The mean litter size was about the same as found in other studies in Finland (Skarén 1963, Ilmén and Lahti 1968), Norway (Bondrup-Nielsen and Ims 1988, Bondrup-Nielsen et al. 1993) and Russia (Fedorov and Cheprakov 1990).

### 3.4. Population fluctuations

The wood lemming population in Heinävesi fluctuated in three-year cycles throughout the 22-year study period (II, III, Appendix 1). In the Keuruu region, however, no regular cycles were found (III). Moreover, no regular three-year cycles have been found in any other wood lemming population in Finland (Kaikusalo 1982). Even though the population fluctuations were large, in the decline years populations also survived on many sites both in Heinävesi and in Keuruu. In Heinävesi, lemming and field vole

populations cycled in synchrony but in Keuruu no synchrony between lemmings and voles was found. Owl populations also fluctuated in synchrony with lemming and field vole populations in Heinävesi but not in Keuruu (III). In Heinävesi, the synchrony between lemming, field vole and owl populations seems to support the predation hypothesis, specialist predators such as weasels and owls probably causing the cycles in lemming and vole populations (e.g. Hanski and Henttonen 2002, Sundell 2002, Sundell et al. 2002). In Keuruu, more abundant generalist predators probably prevent the wood lemming population from increasing and cycling (e.g. Hanski et al. 2001). Furthermore, milder winters in Keuruu with frequent thawing and freezing of the thinner snow cover may have directly increased the mortality of voles or made them more susceptible to predators, thus hampering the buildup of peak rodent densities (Solonen 2001, Sundell et al. 2002, see also Korpimäki 1986). Interestingly, even in Heinävesi, in the latter half of 1990, which was

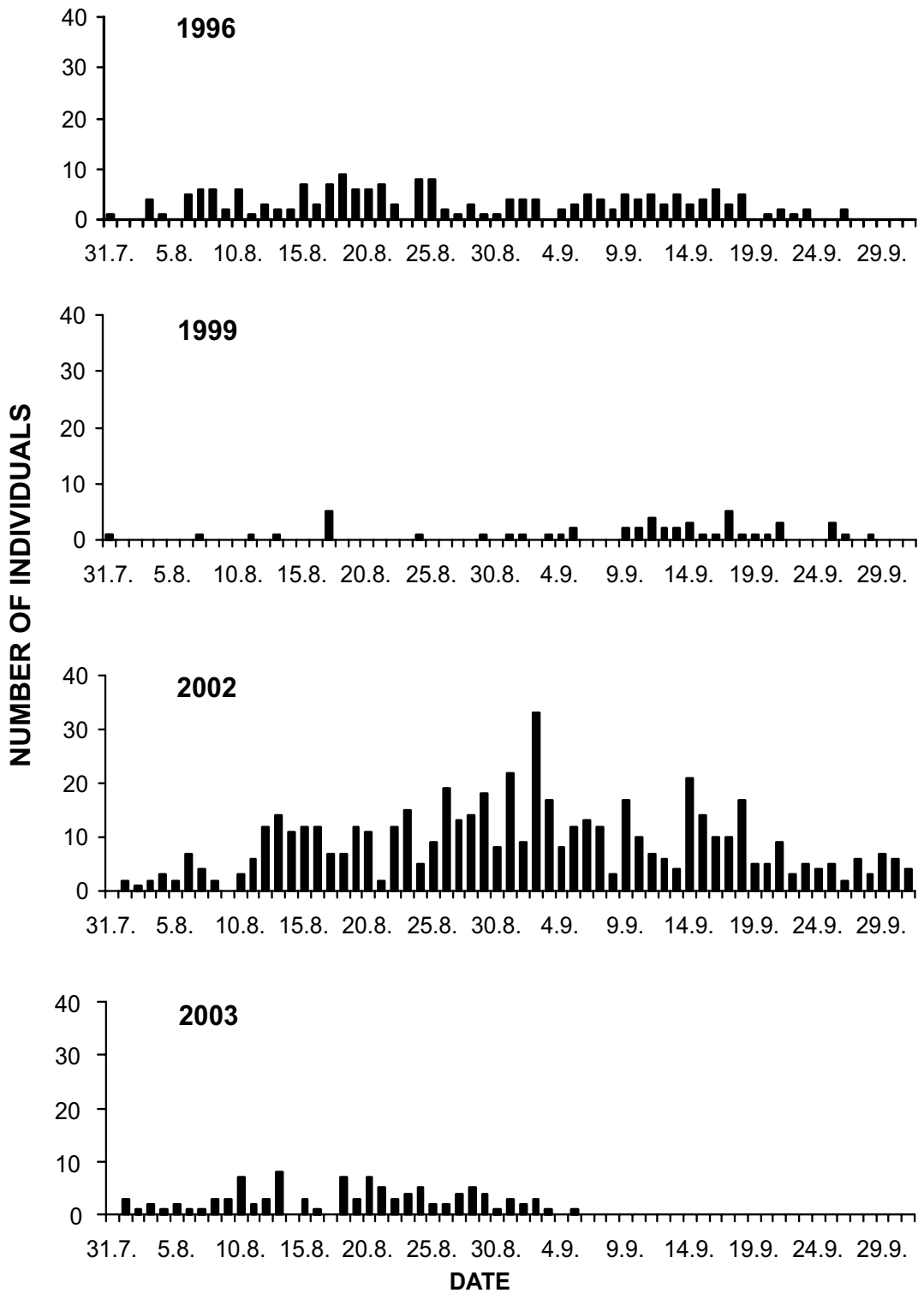


Figure 5. Number of dead wood lemmings found daily at the five most important collecting sites in Heinävesi.



characterised by very mild winters, population peaks of both field vole and wood lemming were only moderately high. At the same time during the decline phase of the cycles, the densities were not very low.

In general, food availability may not play an important role in wood lemming densities in the study areas. Decrease in the availability of preferred *Dicranum* moss, however, may have some effect in peak years (II). Mean individual size was smaller in the declining phase than in the increasing phase of the population (II, 3.3.), which may be a sign of food shortage (Ergon et al. 2001b). Spacing by increased dispersal may have been an important factor in decreasing local population densities. When the population density is very high, diseases may also cause a population crash (II, III). It is probable, however, that only interaction with predators can cause the type of regular three-year cycles in wood lemming found in the Heinävesi area.

### 3.5. Migrations

When wood lemming habitats become overpopulated, animals start to disperse to other areas. This mass movement of animals outside their normal habitats is called migration (Kalela 1963). In migrations, wood lemmings often go over and along roads and are killed by cars. When they reach a railway, they are forced to follow the rails; and they often fall from bridges and die (Fig. 3). Migrating lemmings also frequently follow lakeshores and readily begin to swim from a cape and many of them drown. Lemmings readily fall into canals (Fig. 4), where large numbers of dead animals can be found (II, III). They may also fall from precipices. Many predators, including cats and dogs, kill migrating lemmings. This kind of migration has occurred in all peak years in Heinävesi (II, III, Eskelinen et al. 1983, 1984). In other areas of Fennoscandia migrations of the wood lemming have been observed only irregularly (Kalela 1963, Skarén et al. 1984, Heinonen 1985, Haukkoara 1991, Fredga and Fedorov 1998). Usually the migration starts at the end of July, but in some years not until in September. Migrations have been most active at the end of August and the beginning of September, and

they have usually ended in the beginning of October (Fig. 3 in II, Fig. 5). In 1982 the migration lasted until the middle of October (Eskelinen et al. 1983) and in 2002 until the 9th of October. In 2003 the migration ended already at the beginning of September (Fig. 5). Usually freezing temperature and snow have stopped the migration in autumn.

Migrations are often local but may occur at the same time in several distant locations (II). The number of migrating animals differs greatly between sites even in peak years. In some peak years, such as 1989 and 1992, the number of lemmings found was great at all sites inspected, but in 2002 and 2003 most of the dead lemmings were found only at one site in Sappu, Heinävesi (Appendix 3). The lemmings move to the Sappu bridge from a forest area that is bounded by a lake and railway (see map in II). Cutting of the old forest in Kerma in the 1990's may explain the low number of lemmings on Vääräkoski bridge in 2002 and 2003.

The migrations of the wood lemming seem to be short, usually only a few kilometres at most; and they have no specific direction. Apparently wood lemmings always begin to move when the population density has become high in late summer. Wood lemmings disappear from many sites during low population density but reappear by migration from preferred high-density habitats. The spreading of a population during migration was seen clearly, for instance in 1983 when the population density was high during two successive years. Lemmings, which migrated in 1982, increased in new areas in 1983 and dispersed again before the population decline (Eskelinen et al. 1984).

Not only wood lemmings but also field voles and some other small mammals disperse at the same time and die at the same sites as the wood lemmings (II, III, Appendix 4). The number of other animals found at those sites is usually smaller than the number of wood lemmings. The reason why wood lemmings have been found migrating often and in great numbers in Heinävesi but not in other areas may be the fragmentation of forests by many lakes in Heinävesi. There dead animals can easily be found under railway bridges and in canals (see Fig. 3, Fig. 1 in II). In continuous forest areas, migrating lemmings cannot be found so easily.

### 3.5. Genetic variation

Three of the 20 loci were polymorphic at the 0.95 level (IV). *Gpi* “glucose-6-phosphate isomerase” had two alleles and *Idhp-2* “isocitrate dehydrogenase-2” and *Pgm* “phosphoglucomutase” three alleles. Furthermore, a single *Pgdh* “phosphogluconate dehydrogenase” heterozygote was observed. In Scandinavian populations and in a population in Sotkamo, 200 km N of Heinävesi, only *Gpi* and *Idhp-2* were variable and polymorphic (Fedorov et al. 1995). Within different sampling years no significant evidence of heterogeneity was observed since genotypic proportions conformed to Hardy-Weinberg expectations. The genotype frequencies between years were also homogenous. The proportion of polymorphic loci (P) was 15% for all years, and the observed heterozygosities (H) varied from 0.056 to 0.061. In Scandinavian populations the P-value was only 6.7% and the mean H-value was 0.031 (Fredga et al. 1993). In western Siberia the P-value was 11.5% and the H-value 0.031 (Fedorov 1993). Thus the variability in the Heinävesi population is clearly higher than that previously reported for the wood lemming. This difference is mainly due to the polymorphic *Pgm* locus, which has been invariant elsewhere. The genetic variation in the Heinävesi population is higher than the mean value (0,042) in rodent species (Nevo 1985). In the consensus tree the Heinävesi population is situated between the Siberian and Scandinavian populations. This corresponds to the presumed post-glacial colonisation route of the wood lemming westward from its Siberian refugium.

### 4. CONCLUSIONS

1. An old mossy spruce forest is the preferred habitat of the wood lemming. Occurrence of the preferred food plant, *Dicranum* moss, and plenty of holes for shelter from enemies may be the main factors for the habitat selection of the wood lemming.
2. Greater nitrogen content in *Dicranum* than in the more abundant *Pleurozium* and *Hylocomium* species may be the main reason why wood lemmings prefer *Dicranum* moss.
3. The sex ratio in the wood lemming

population varies, but the mean proportion of males in a migrating population in late summer and autumn is about 25%.

4. The individual size and litter size of the wood lemming have been found to be smaller in the declining phase than in the increasing phase of population.
5. The population fluctuations of the wood lemming are regular in three-year cycles in Heinävesi, but irregular in the Keuruu region. In Heinävesi the wood lemming population fluctuates in synchrony with the field vole population. The synchrony between lemming, field vole and owl populations seems to support the predation hypothesis, specialist predators probably causing the cycles in lemming and vole populations.
6. In Heinävesi the wood lemmings have always migrated when the population density has been high in August and September. Many dead lemmings have been found under bridges and in canals. The main reason for these short migrations is probably that the lemming population density becomes high in small areas of old spruce forest and the animals disperse to areas of lower population density.
7. Genetic variation in the wood lemming population in Heinävesi is greater than that in the other wood lemming populations studied in Fennoscandia and Siberia.

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Appendix 1. Abundance indices of lemmings at different sites in Heinävesi in spring (s) and autumn (a) of the study years (1 = few tracks, 2 = moderate number of tracks, 3 = large number of tracks).

Site no	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003																
	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a															
1	2	1			1			2	1		2			1	2			1	2	1	1	3	1	1														
2	3	1			1			3			3			1	2	2	2	2	3	2	2	3	2	2														
3	3	1			2			3			3	3	1		3	2	2	2	2	2	1	1	3	3	1													
4	3	1			2	1		3			3			1	2	1	2	2	2	2	1	2	2	3	3	1												
5	3	1			2			3			3			1	2	2	1	3	2	1	3	2	2	2	3	1												
6	3	1			2			3			3			1	1	2	2	1	2		1	2	2	2	3	1												
7	3	1			1			3	1		3			1	2	2		1			1	2	2	1	2	2	1											
8	2	1			3			2			2			1	1	1	1	1	1	1	1	1	3	2	2	2	1											
9	3	2			3	3	1	1	3	1	3			2	1	3	2	2	2	1	1	1	3	2	3	2	3											
10	3	3			2	1	1	3	1	1	3	3	1	2	3	2	2	2	1	1	1	1	1	3	2	2	2											
11	3	2			1	1		2	3		3	3		1	2	2	2	1	1	2		2	1	3	2	2	2											
12	3	3			1	1		3			3	3	1	1	2	1	1	1	1	1	1	1	1	3	1	1	1											
13	3	1	2		3	3	3	1	3	3	3	2		1	2	2	2	1	2	3	3	1	1	1	2	3	1											
14	3	1	1		1			3			3			2	2			1		1	3	3	1	1	3	3	1											
15	3	1			1			3			3			1	2			2	1		1	2	1	1	3	3	1											
16	3	1			2			1	3		3			2	2			2		1		2	1	1	2	1	1											
17	2				1	1		2			1	3		2	2			1		1	1	1	1	1	1	2	1											
18	3				1			3			2			2	2			2		2		2	1	3	3	2	2											
19	2	3			1			3			3	1		2	2	1	1	1	2		2	1	3	3	2	3	2											
20	3				1			3	1		1	3	2	1	2			1		2		1	1	2	2	3	2	3										
Total	48	4	34		4	8	30	8	7	1	6	57	4	5	1	2	11	57	7	5		19	13	40	16	19	10	16	17	32	13	11	6	15	24	47	43	21

Appendix 2. Body size, sex ratio, sexual maturity and reproduction marks of female wood lemmings found dead in Heinävesi (m=male, t=total, f=female, mat=mature, i=immature, scars=scars in uterus).

Sex	Year	N	%	Weight		Length		Testis		Scars	
				X g	SD	X mm	SD	X mm	SD	X	SD
m t	1982	40	21.8	17.7	1.8	86.0	4.2	3.7	0.5		
	1983	14	24.6	18.3	4.9	86.5	7.2	4.6	2.8		
	1986	4	14.8	15.3	2.0	80.3	3.3	5.1	1.3		
	1989	237	25.8	18.6	2.9	91.0	4.5	3.9	1.2		
	1992	129	28.8	18.5	2.2	89.7	5.6	4.2	1.7		
	1995	4	16.0	18.3	1.2	81.3	4.4	3.3	0.5		
	1996	27	20.8	17.9	3.5	87.3	8.2	3.9	1.6		
	1999	12	24.5	16.3	1.6	85.8	4.5	5.3	1.8		
	2002	151	28.4	17.9	1.9	87.3	5.1	4.4	1.1		
	2003	21	20.1	17.3	3.5	86.0	6.2	4.2	2.1		
m i	1982	40	21.8	17.7	1.8	86.0	4.2	3.7	0.5		
	1983	11	18.3	16.1	2.2			3.3	0.5		
	1986	3	11.1	15.2	2.4	80.3	4.0	3.9	0.8		
	1989	225	24.5	18.2	1.7	91.0	3.6	3.6	0.6		
	1992	117	26.1	18.1	1.4	89.0	5.2	3.7	0.9		
	1995	4	16.0	18.3	1.2	81.3	4.4	3.3	0.5		
	1996	25	19.2	17.1	1.6	85.3	3.7	3.5	0.6		
	1999	8	16.3	16.8	1.4	84.8	4.7	4.1	0.9		
	2002	132	24.9	17.7	1.5	86.8	4.9	3.9	0.7		
	2003	19	18.8	16.3	1.6	84.4	3.6	3.6	0.5		
m mat	1982	0									
	1983	3	5.3	26.3	3.8			9.7	1.2		
	1986	1	3.7	21.1		101		6.6			
	1989	12	1.3	25.4	8.3	101.0	7.4	8.2	1.3		
	1992	12	2.7	22.3	4.2	96.4	5.7	8.7	1.3		
	1995	0									
	1996	2	1.5	27.5	5.5	112.0	9.0	9.0	1.0		
	1999	4	8.2	15.5	1.7	88.0	3.4	7.5	0.9		
	2002	19	3.6	19.8	3.1	91.1	4.5	7.8	1.0		
	2003	2	2.0	27.0	0	101.5	0.7	10.5	0.7		
f i	1982	111	60.7	17.4	1.7	84.4	6.2				
	1983	39	68.4	15.5	2.0	79.9	5.0				
	1986	21	77.8	16.6	1.9	80.6	5.2				
	1989	603	65.7	18.1	1.7	90.0	3.5				
	1992	241	53.8	17.7	1.6	87.6	5.1				
	1995	19	76.0	17.7	1.4	82.6	4.3				
	1996	86	66.2	16.0	1.6	84.2	3.9				
	1999	31	63.3	16.7	1.9	83.9	5.7				
	2002	335	63.1	17.3	1.6	85.6	4.1				
	2003	68	67.3	15.1	1.5	81.0	4.2				
f mat	1982	32	17.5	22.9	3.0	94.6	4.7			5.8	2.3
	1983	4	7.0	19.8	3.7	84.0	6.1			2.8	1.0
	1986	2	7.4	22.2	0.2	95.0	1.4			5.0	0.0
	1989	78	8.5	23.3	4.0	99.0	5.6			5.8	2.6
	1992	78	17.4	22.1	3.9	94.0	7.8			4.8	2.0
	1995	2	8.0	25.0	0.0	101.0	1.4			7.0	1.4
	1996	17	13.1	19.1	2.2	89.9	5.6			3.4	1.5
	1999	6	12.2	20.3	3.1	92.8	6.3			3.2	1.2
	2002	45	8.5	23.2	3.3	94.9	4.9			4.4	1.1
	2003	14	14.0	20.4	2.7	92.0	4.4			3.6	1.2



Appendix 3. Number of dead wood lemmings found at different sites in Heinävesi in different study years (rail. br. = railway bridge).

Location	1982	1983	1986	1989	1992	1995	1996	1999	2002	2003
Vääräkoski rail. br.	50	28	7	234	121	3	42	8	18	2
Station rail. br.	350	2	8	224	176	1	29	2	2	
Vihovuonne canal	100	5	6	211	67	4	1	5	41	
Kerma canal	100		2	138	66		12	1	31	3
Sappu rail. br.	25	17	15	399	159	18	62	28	463	114
Sepänsalmi rail. br.	10	2		62	13	12	44	7	11	1
Koivumäki rail. br.	220	27		20	48		15		3	
Vaaluvirta road br.				54	17		3			
Karvio road br.	20		1	23	9		4			
Varistaival canal	10		2	17	9		4	1		
Taivallahti canal	10		1	14	9				3	
Pilppa canal				28	35		2			
Korpivaara rail. br.	3	46		8	33			4	6	
Others	100	61	6	61	80		7	9	8	1
Totals	998	188	48	1493	842	38	225	65	586	121
Analysed	183	57	27	918	448	25	130	49	531	101

Appendix 4. Number of dead individuals of other small mammal species found at the wood lemming study sites in Heinävesi.

Species	1986	1989	1992	1995	1996	1999	2002	2003
<i>Microtus agrestis</i>	22	109	132	27	30	11	317	4
<i>Clethrionomys glareolus</i>		13	7	5	2	7	34	
<i>Micromys minutus</i>	1	6	1			4	5	
<i>Rattus norvegicus</i>		1	1					
<i>Mus musculus</i>		1	1					
<i>Sorex araneus</i>		10	11	8	6	6	14	
<i>Sorex isodon</i>	1	2	1			3		
<i>Sorex minutus</i>	1			1				2
<i>Sorex caecutiens</i>					1		1	
<i>Mustela nivalis</i>					1			
Totals	25	142	154	41	40	31	371	6