

On the population fluctuations and structure of the Wood lemming *Myopus schisticolor*

By O. ESKELINEN

Department of Biology, University of Joensuu, Joensuu, Finland

*Receipt of Ms. 01. 09. 1995
Acceptance of Ms. 13. 11. 1996*

Abstract

A population of the wood lemming *Myopus schisticolor* Lilljeborg has been studied in Heinävesi, Finland, for over a period of 15 years from 1982 to 1996 on animals which died during migration. The fluctuations of the population were regular with three year intervals. Migration took place in all peak years. During migration dead animals were collected and measured. Animal size and the number of offspring was greater in the years of growing population density than in the years with decreasing density. The sex ratio changed from 15% to 29% males in different years but there was no correlation between the proportion of males and the population density.

Introduction

The wood lemming *Myopus schisticolor* Lilljeborg occurs sporadically in the coniferous forests of Fennoscandia and Russia (see e. g. ERKINARO 1972; HEINONEN 1985; FEDOROV et al. 1994). The population density of the wood lemming fluctuates irregularly (e. g. KALELA 1963). When the population becomes very dense the lemmings begin to migrate, but the migrations are short. The migration may occur in a large area at the same time (KALELA 1963; UINO 1963) or in a small area (SKARÉN 1963; ALAJA 1983; ESKELINEN et al. 1983, 1984; SKARÉN et al. 1984). The wood lemming has an exceptionally large majority of females which is thought to cause the population explosion of the species (e. g. HENTTONEN 1983); the sex ratio is usually 3:1 (KALELA and OKSALA 1966). The reason for this exceptional sex ratio is considered to be the unusual sex determination of the species (FREDGA et al. 1977), a mutation in the X chromosome causing about half of the XY animals to be females.

Although there are numerous publications concerned with the migration of the wood lemming, only a few investigations have been devoted to a long-term observation of the same population.

The aim of the present study is to clarify the changes in the abundance, migration and the structure of the wood lemming population in Heinävesi, in southeastern Finland, during the years 1982–96. The population is the same as in the earlier publications concerning the years 1982 and 1983 (ESKELINEN et al. 1983, 1984).

Material and methods

The abundance of the wood lemming population has been studied by observing the traces (tunnels, faeces and feeding places) of the animals and in the late summer searching for dead animals especially under bridges and precipices and in canals (see ESKELINEN et al. 1983).

The railway bridges have proved to be the most effective "traps" (Fig. 1) because when migrating lemmings coming to the railway are forced to follow it. Not being able to go under or over the rails, they come to bridges and many of them fall down several meters and die. There are also several canals in Heinävesi (Fig. 2); when lemmings follow the shores, many of them fall into the canals and die. Traps have not been used except in 1982 (73 trap nights, see ESKELINEN et al. 1983) because numerous animals die anyway at the above-mentioned places.



Fig. 1. Dead wood lemmings on the roadside under the railway bridge in Koivumäki in autumn 1982.

The most advantageous places for collecting were checked daily or at least every two days during migration in August and September. Animals in good condition were stored in deep freeze for later study. Decomposed animals were only counted and not kept for later study.

The most important sites for collecting in 1982 were the railway bridges near Heinävesi station and Koivumäki. These bridges were subsequently repaired and the lemmings could no longer fall between the sleepers onto the road. However, the station bridge continued to be one of the best places for collecting. Other important places were Sappu and Vääräkoski railway bridges and the canals in Kerma and Vihovuonne. The Vaaluvirta bridge was built in 1987 and was one of the sites for future collecting.

The collected animals were measured, weighed, sex-determined, the length of the testes or the diameter of the uterus were measured, and the birth scars of the uterus were checked. The males were considered to be mature when the length of testes was over 6.5 mm (see SKARÉN 1963) and females when birth scars were evident in uterus.

In statistics t-test have been used.

The methods have been similar all through the study period.

Results

Occurrence, changes in abundance and migration

Surrounded by waters and field, the area of occurrence of the present population of lemmings has been the same every year when the population density has been high (ESKELINEN et al. 1983, 1984; SKARÉN et al. 1984).

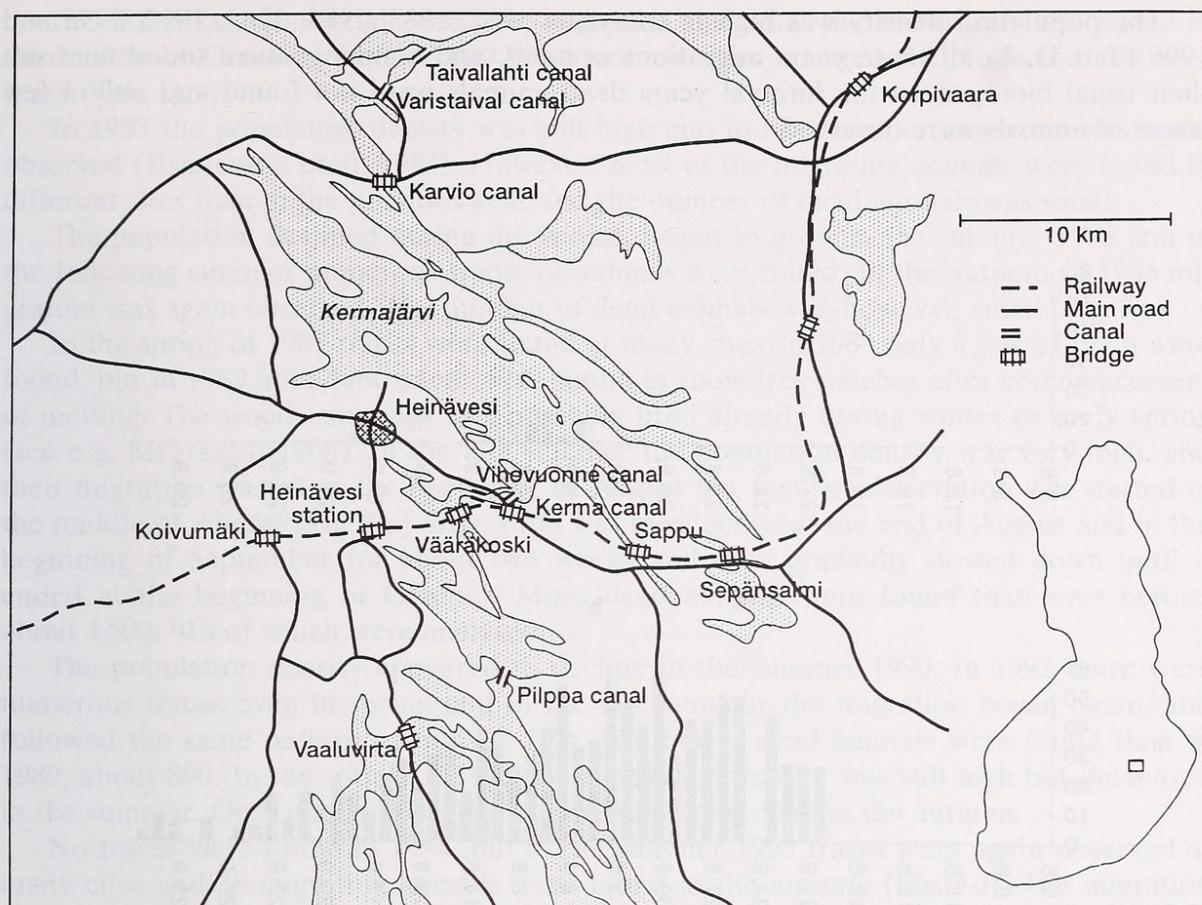


Fig. 2. Map of the study area in Heinävesi showing main waters, roads and collecting sites.

Traces of animals were found in all the observation years except in 1994. When the population density was low only a few traces of animals were found in old spruce forests and swamps where the moss cover is thick. In peak years there were numerous traces in optimal biotopes in summer, in late summer also in pine forests and even in mossy clear-felled areas.

Table 1. The number of wood lemmings found at different sites in different years (rail.br. = railway bridge).

		1982	1983	1986	1989	1992	1995	1996
Vääräkoski	rail.br.	50	28	7	234	121	3	42
Station	rail.br.	350	2	8	224	176	1	29
Vihovuonne	canal	100	5	6	211	67	4	1
Kerma	canal	100		2	138	66		12
Sappu	rail.br.	25	17	15	399	159	18	62
Sepänsalmi	rail.br.	10	2		62	13	12	44
Koivumäki	rail.br.	220	27		20	48		15
Vaaluvirta	road br.				54	17		3
Karvio	canal	20		1	23	9		4
Varistaival	canal	10		2	17	9		4
Taivallahti	canal	10		1	14	9		
Pilppa	canal				28	35		2
Korpivaara	rail.br.	3	46		8	33		
Others		100	61	6	61	80		7
Totals		998	188	48	1 493	842	38	225
Analysed		183	57	27	918	448	25	130

The population density was high in the years 1982, 1983, 1986, 1989, 1992, 1995 and 1996 (Tab. 1). In all these years migrations occurred, and lemmings were found far from their usual biotopes. In the interval years dead animals were not found and only a few traces of animals were observed.

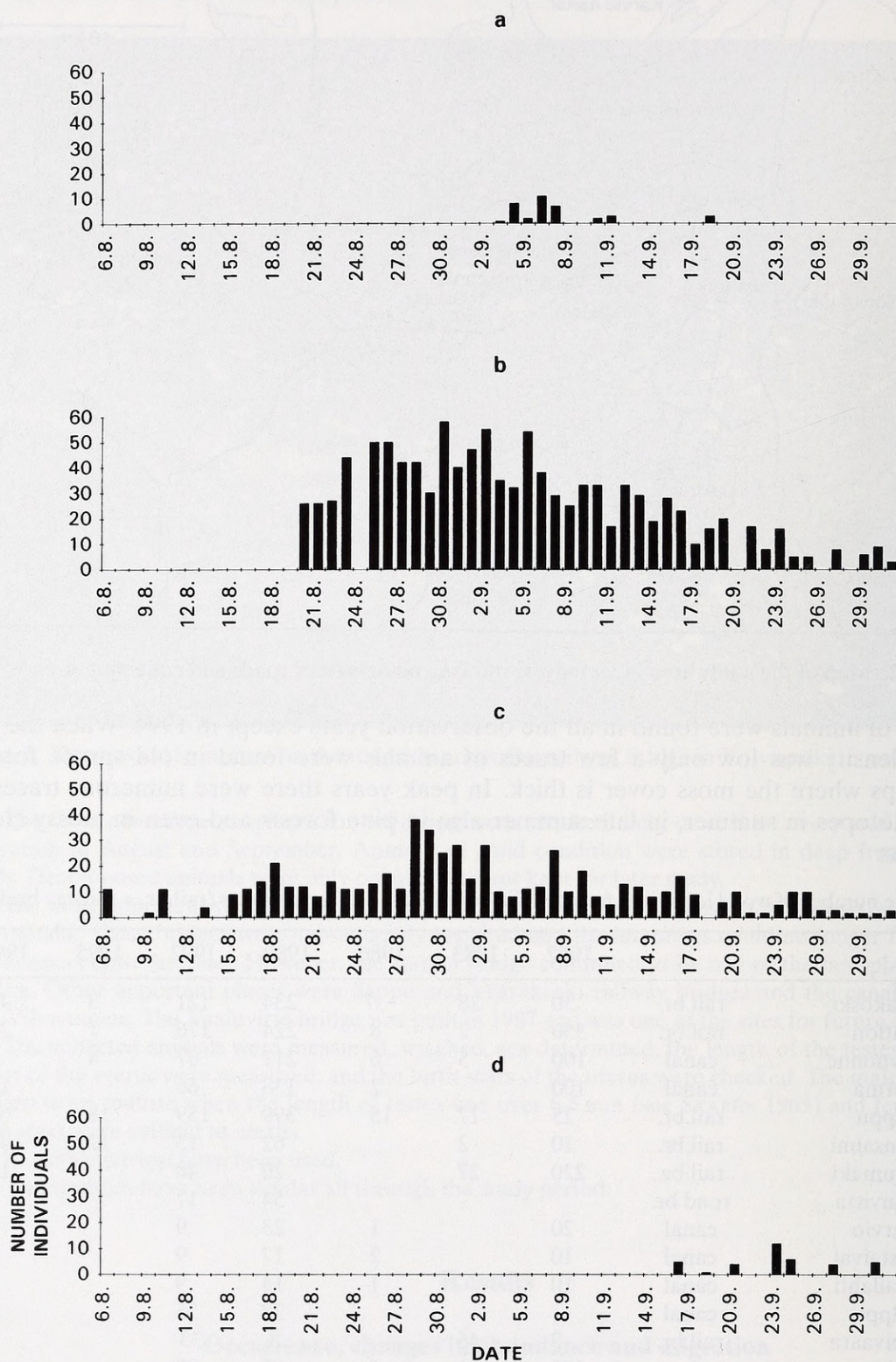


Fig. 3. Number of dead wood lemmings found daily in the 5 most important collecting sites (see Tab. 1) a-1986, b-1989, c-1992, d-1995. In 1989 the daily checking started 20. 8. but the total number of animals in 10. 8.–20. 8. was 100. 25. 8. and 21. 9. the sites were not inspected.

In 1982 (ESKELINEN et al. 1983) the migration started at the end of July and ended in the middle of October. About 1 000 dead animals were counted, 183 collected and analysed (Tab. 1).

In 1983 the population density was still high and in late summer migration was again observed (ESKELINEN et al. 1984). However, most of the migrating animals were found in different sites than in the previous year and the number of dead animals was small.

The population declined during the winter, began to grow in the summer 1985 and in the following summer numerous traces of animals were found. In the autumn of 1986 migration was again observed. The number of dead animals was, however, small (Fig. 3 a).

In the spring of 1987 traces were found at many sites, in 1988 only a few of them were found, but in 1989 abundant traces were found in snow-free patches after commencement of melting. The wood lemmings had probably bred already during winter or early spring (see e.g. MYSTERUD 1966). In the late summer the population density was very high, and their migration started at the beginning of August but regular observation was started in the middle of August (Fig. 3 b). Migration was most active at the end of August and in the beginning of September for about two weeks and then gradually slowed down until it ended at the beginning of October. More dead animals were found than ever before, about 1 500, 918 of which were analysed.

The population density appeared to decline in the summer 1990. In 1992 there were numerous traces even in spring and in the late summer the migration began again, and followed the same pattern as in 1989 (Fig. 3 c). Fewer dead animals were found than in 1989, about 800. In the spring of 1993 the population density was still high but decreased in the summer. Only one migrating lemming was found dead in the autumn.

No traces were found in 1994, but in the summer 1995 traces were again observed at many sites and 38 migrating animals were found in the autumn (Fig. 3 d). The migration time was later than in the other years. In the summer 1996 more traces were observed than in the previous year and 225 dead animals were found in August and September.

There was one albino among the small number of dead wood lemmings collected in 1986, and also one in 1992 amongst a large number of 800 animals. In 1989 there were no albinos found amongst 1 500 wood lemmings.

Other animals

There were many short-tailed voles *Microtus agrestis* in the study area in 1982 and 1983 but the dead animals were not counted. From the year 1986 other animal species that were found in the same sites as the wood lemmings were also noted (Tab. 2). The most

Table 2. Number of dead individuals of other small mammal species found at the same sites.

	1986	1989	1992	1995	1996
Short-tailed vole <i>Microtus agrestis</i>	22	109	132	27	30
Bank vole <i>Clethrionomys glareolus</i>		13	7	5	2
Harvest mouse <i>Micromys minutus</i>	1	6	1		
Brown rat <i>Rattus norvegicus</i>		1	1		
House mouse <i>Mus musculus</i>		1	1		
Common shrew <i>Sorex araneus</i>		10	11	8	6
Graves shrew <i>Sorex isodon</i>			1	2	1
Pygmy shrew <i>Sorex minutus</i>	1			1	
Masked shrew <i>Sorex caecutiens</i>					1
Pygmy weasel <i>Mustela nivalis</i>					1
Totals	25	142	154	41	41

abundant species is the short-tailed vole. The number of other animals is small. The fluctuation of the short-tailed vole population is similar to that of the wood lemming and a small migration was also found. Quite a large number of dead short-tailed voles were found in the same years as the wood lemmings, but the number of animals was much smaller than that of the wood lemming.

Population structure

There are distinct annual variations in sex ratio, body weight and body length in the population of wood lemmings (Tab. 3). The sex ratio (the proportion of males) was 22% in 1982, 25% in 1983, 15% in 1986, 26% in 1989, 29% in 1992, 16% in 1995 and 21% in 1996, the mean proportion of males being 25%. The low number of males in the small number of animals collected in 1986 and 1995 differs clearly from that of the other years.

Table 3. Body size, sex ratio, sexual maturity and reproduction marks of females (m = male, t = total, f = female, mat = mature, i = immature, scars = scars in uterus).

Sex	Year	N	%	Weight X̄ g	SD	Length X̄ mm	SD	Testis X̄ mm	SD	Scars X̄	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		
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		
mmat	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		
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				
fmat	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

The differences in the mean sex ratio (25) are not, however, statistically significant. The greatest proportion of males in 1992 (29%) differs only slightly ($p = 0.1$) from that of 1982 (22%).

The mean body weight of young females in 1983 was significantly smaller ($p < 0.001$) than in 1982 (Tab. 3). The difference in the body weight of males is not statistically significant. In 1986 the young females were significantly smaller ($p < 0.05$) than in 1982. In 1989 the young females were significantly larger ($p < 0.01$) than in 1982, but the weights of young males do not differ significantly. In 1992 the young females and males were about the same weight as in 1982 but the young females in 1992 were significantly smaller ($p < 0.001$) than in 1989. In 1995 the young females were of the same weight as in 1982 and 1992. In 1996 the young females were significantly smaller ($p < 0.001$) than in the other years except in 1983 and 1986 and also the young males were significantly smaller ($p < 0.001$) than in 1989 and 1992.

The mean body weight of mature females (Tab. 3) was in 1992 significantly lower ($p < 0.05$) than in 1989 and in 1996 it was significantly lower ($p < 0.001$) than in 1982, 1989 and 1992.

The differences in the body length were quite similar to those in weight (Tab. 3). In 1989 young males and young and mature females were significantly bigger ($p < 0.001$) than in 1982 and 1992.

The mean size of testes of mature males was largest in 1992 when the proportion of mature males was also largest. In the material from 1989 the size of testes was slightly smaller. There are no yearly differences in the mean size of the testes of young males.

There is a clear positive correlation between body weight and maturity both in males and females (Tab. 3).

The proportion of mature females that have produced young was the same, 17.5% in the peak years 1982 and 1992, in 1996 13.1% but in the peak year 1989 only 8.5%, in 1995 8% and in 1983 and 1986 still smaller.

The mean number of the scars of the uterus was 5.8 in 1982 ($n = 32$) and 1989 ($n = 78$), but in 1992 it was 4.8 ($n = 78$). Also more females had embryos in 1992 than in the other years (embryos have also been counted as scars of the uterus in Tab. 3). In 1983 and 1996 the number of scars was significantly ($p < 0.001$) smaller than in the other years.

Discussion

Changes in the abundance and migration in different areas

Unlike other voles, the population fluctuations in the wood lemming are known to be irregular (e.g. KALELA 1963). There are no observations of wood lemmings in many areas between the years of population explosion. In the population at Heinävesi the change in abundance, however, forms a regular cycle with three-year intervals at least during the study period. Moreover, the peak occurrences coincides with that of the short-tailed vole. There are also many observations in the interval years. Also in Kuhmo (SKARÉN 1972) the change in abundance has been regular with 4–5 year intervals.

The population explosion and related migration of the wood lemming may happen in different areas at the same time as in 1982 (SAVOLAINEN et al. 1982; SKARÉN et al. 1984) or only locally in a small area. In 1989 migration was also observed, for instance, in Rautjärvi, 100 km southeast of Heinävesi (S. PASANEN unpubl.). In Kontiolahti, 100 km north-east of Heinävesi, there was a migration in 1991 (T. TAST unpubl.), when the population density was low in Heinävesi, but there was a population explosion in the following year, as well as in Ilomantsi, 50 km NE of Kontiolahti (H. HYVÄRINEN unpubl.). The interval of the two large population explosions and migrations (1989 and 1992) in Heinävesi was only three years, which might be unusual.

Population density mostly declines after migration and is very low thereafter (e.g. KALELA 1963). The population density in Heinävesi has often been high over the winter following a migration but has declined during the following spring or summer. In 1983 the population density was, however, high after migration and a small migration was observed in the year thereafter (ESKELINEN et al. 1984). The population peak had moved a little to the east of the main area of the previous year. In 1995 a small migration was observed in the growing phase of the population density and a larger migration in the following year while the population was declining. In the district of Rovaniemi UINO (1963) has also observed migrations in two successive years (1957 and 1958).

The course of the migration was much the same in all the years. It started in the first half of August, being most active at the end of August or at the beginning of September and ceased at the end of September or the beginning of October. In 1995, however, the migration time occurred in late September, but the number of animals was small. Elsewhere, e.g. in Rovaniemi (UINO 1963), the time of the migration has been similar.

Comparison of population structure

The mean body weight and length of young males and females does not differ from corresponding material in south Norway (KRATOCHVIL et al. 1979). Judging from the literature (ILMÉN and LAHTI 1968; KRATOCHVIL et al. 1979), the largest males (46 g) and females (32 g) are born in the previous autumn, the others in the same year. The mean weight of mature females is 4–6 g greater than that of immature ones, but there is a great difference between individuals, while the lightest mature (produced young) female weighed only 15.5 g. According to SKARÉN (1963) a female is able to breed when its weight reaches 15 g.

The largest males whose testes measured 9–11 mm are born early in the spring or in the previous autumn. The medium-sized animals whose testes are 6.5–8 mm have apparently just become mature or are close to reaching maturity. The small male lemmings are young and immature.

There were no mature males in my material from 1982, the same being true in the material of SKARÉN et al. (1984) collected partly from the same area at the same time in Heinävesi and Vesanto. However, there were three mature males in the small material from 1983 and one in 1986. In 1992 the proportion of mature males was larger than in the previous peak year 1989, but the difference is not statistically significant.

There are only very few old males in my large collection, similar to the material collected in Rovaniemi in 1957 (KALELA 1963). According to SKARÉN et al. (1984) the old males obviously die before autumn. Less than 4% of the migrating females were born before summer in the material of SKARÉN et al. (1984).

The positive correlation between body weight and maturity is similar to that found by ILMÉN and LAHTI (1986) among female wood lemmings and by HEIKURA and LINDGREN (1977) among male short-tailed voles.

Breeding effectiveness becomes evident from the number of young animals per female that has been greater in the years of growing population density than in the phase of decreasing density. The mean litter size was slightly larger (5.2) in the peak years than according to KALELA and OKSALA (1966) in northern Finland (4.5). According to SKARÉN (1963) the females born in the previous year have 4.6 and the females born in the same year 3.5 young, on average.

The size of animals appears to be related to their breeding effectiveness because the size of the lemmings was larger in the growing than in the decreasing population. In 1982, 1989, 1992, and 1995 while the population was growing in the autumn the size of the lemmings was greater than while the population was decreasing in 1983 and 1996. According to HYVÄRINEN (1984) the size of animals affects their ability to take care of their young.

Sex ratio

It appears that the purpose of the female majority especially in the growing phase of the population is to produce a great number of offspring quickly (HENTTONEN 1983). The sex ratio has changed greatly in different years but the mean proportion of males does not differ from the expected value of 25% males. According to many studies (SKARÉN 1963; KALELA and OKSALA 1966; FRANK 1966; GILEVA and FEDOROV 1990) the sex ratio changes greatly in the course of a year and the proportion of males is usually smaller in the autumn than in the summer.

Reasons for the fluctuations and migrations of the population

Some observations confirm the known opinions concerning the reasons for fluctuation and migration of population. Some refer to the role of disease in taxing the population. In the late summer 1983 many wood lemmings were seen moving slowly in the daytime and obviously ill. The animals that were caught alive usually died within a few days. Listeriosis was found to be the cause of death for the wood lemmings caught alive by SKARÉN (1981).

Over 90% of the food of the wood lemming is moss (ANDREASSEN and BONDRUP-NIELSEN 1991 a), the sufficiency of which in the wintering areas is important for the lemming to be able to breed during the winter (MYSTERUD et al. 1972). The scarcity of moss is supported by field observations especially from 1983 when the population density was high during two successive years. SKARÉN's (1971) observations also agree with this.

The main reason for regular migration in an area divided by waters like Heinävesi is obviously the scarcity of living space. Although the home ranges of wood lemmings are small (ANDREASSEN and BONDRUP-NIELSEN 1991 b), the living space may still become overcrowded when the population density is high. Animals were clearly observed to settle down in new areas and breed there in 1983 (ESKELINEN et al. 1984). Another reason for a migration is thought to be lemmings search for new wintering areas. According to many observations, popular wintering areas were mossy northern slopes even in pine forests where the lemmings were not observed in the summer before migration.

Acknowledgements

I am grateful to Prof. HEIKKI HYVÄRINEN who gave me valuable advice on writing this study, to TIMO HOKKANEN who participated in the handling of the material, to SEPPO KOTILAINEN who helped in computer processing and to many others who helped in collecting the material. Mr. EDWARD ABRAHAM checked the English manuscript.

Zusammenfassung

*Über Populationsfluktuationen und -struktur des Waldlemmings *Myopus schisticolor**

Die Population des Waldlemmings ist in der Region von Heinävesi seit 15 Jahren untersucht worden. Fluktuationen der Populationsdichte erfolgten regelmässig in Perioden von drei Jahren. In allen Spitzenjahren wurden Wanderungen festgestellt. Bei Wanderungen verunglückte Tiere konnten gesammelt und gemessen werden. Die Grösse der Tiere und die Anzahl der Jungen war in den Jahren mit wachsender Populationsdichte grösser als in den Jahren, als die Populationsdichte sich verminderte. Das Verhältnis der Geschlechter wechselte von 15% bis 29% Männchen in verschiedenen Jahren, aber es gibt keine Korrelation zwischen dem Anteil der Männchen und der Populationsdichte.

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Author's address: OLAVI ESKELINEN, Department of Biology, University of Joensuu, Box 111, FIN-80101 Joensuu, Finland



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