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A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters[1]

Erkki Pulliainen

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Gross activity, habitat selection and population fluctuations in the red fox *(Vulpes vulpes)*, pine marten *(Martes martes)*, stoat *(Mustela erminea)* and pygmy weasel *(Mustela rixosa)* were studied in the Värriötunturi fell area, eastern Finnish Forest Lapland, in the winters of 1968/69—1980/81. The populations of the food generalists, the red fox and the pine marten, fluctuated less than those of the rodent specialists, the stoat and the pygmy weasel. During the very marked peak in small rodent populations which culminated in the winter of 1978/79 there was good conformity with the trends in the predator populations. The pine martens preferred spruce-dominated mixed forests and the red foxes mixed forests characterized by juniper or pine and open bogs. The stoats occurred most frequently in forests characterized by juniper or spruce, and were found in different habitats from the pygmy weasels, probably depending primarily on the availability of food. The interspecific differences in habitat use enable reduction of competition. No clear trends were recorded in the gross activity of these carnivores from November to April.

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1. Introduction

Fluctuations in the numbers and habitat selection of the small rodents of the subarctic and northern taiga of Finland have been dealt with in a number of studies (e.g. Kalela 1949, 1957, 1962, Tast 1966, 1968, 1974, Tast & Kalela 1971, Kalela et al. 1971, Lahti et al. 1976, Henttonen et al. 1977, Järvinen & Tast 1980, Henttonen 1980), but there are only scattered notes on the small land carnivore populations inhabiting the same areas (e.g. Nyholm 1972a, b, Tast & Kalela 1971, Lahti et al. 1976; see also Hörnfeldt 1978). Of course, predator-prey interactions have been taken into account in more theoretical contributions (e.g. Andersson & Erlinge 1977, Stenseth 1977, 1978, Finerty 1980).

The present author began a census of red fox *(Vulpes vulpes)*, pine marten *(Martes martes)*, stoat *(Mustela erminea)* and pygmy weasel *(Mustela rixosa)* on the basis of tracks on a subarctic fell in eastern Finnish Forest Lapland in the winter of 1968/69 (see also Pulliainen 1981d). Results from 13 successive winters are now available. The purpose of the present paper is to provide records on gross activity, habitat selection and numbers of tracks during these winters.

2. Study area

The study area lies in eastern Itäkaira, Finnish Forest Lapland (Fig. 1). The area includes two fell ridges (Pulkkatunturi-Sauoiva and Värriötunturi) running in a north-south direction about 5 km apart. It is in a virgin state, with the following proportions of natural habitats in an area of approximately 200 km^2: spruce forests *(Picea abies)* 26.5 %, Scots pine forests *(Pinus sylvestris)* 18.5 %, birch forests (*Betula* spp.) 3.0 %, mixed forests 22.0 %, open bogs 13.5 %, mountain birch forests *(Betula pubescens* ssp. *tortuosa)* 7.0 % and treeless fell summits 9.5 %. The forests are old and mature, including a large number of standing and fallen dead trunks. The density of the trees is generally very low, and in some places there are young spruce, pine and birch saplings among the very old trees. Some of the lowland birch forests were killed by larvae of the geometrid *Epirrita autumnata* in 1965—1966 (see Pulliainen 1976). The study area lies 266—475 m above sea level.

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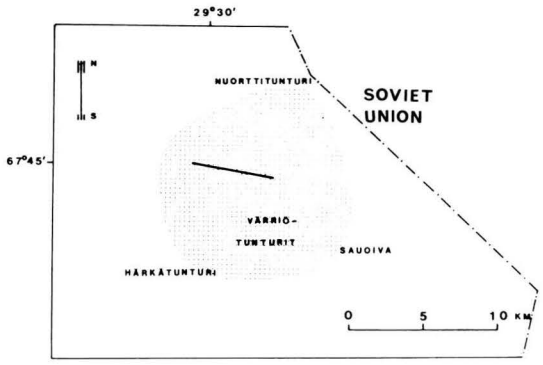

Fig. 1. The study area in eastern Finnish Forest Lapland.

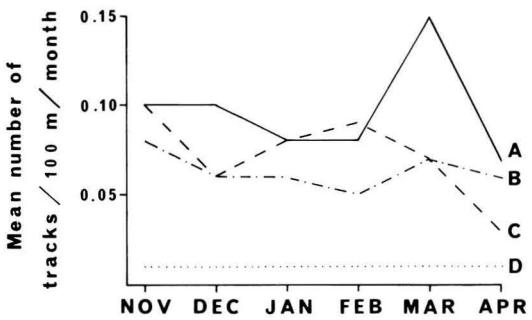

Fig. 2. Mean numbers of red fox (A), pine marten (B), stoat (C) and pygmy weasel (D) tracks (per 100 m of observation line per 4 recordings each month) in all habitats in November-April in the winters of 1968/69—1980/81.

3. Methods

The tracks of red fox, pine marten, stoat and pygmy weasel crossing an observation line 5970 m long running westwards from the summit of Värriötunturi were counted in the winters of 1968/69—1980/81 by skiing along this line once a week during the snowy season of the year. Only tracks that were at most two days old when recorded in November-April are taken into account in the present calculations. If the same individual had crossed the line more than once within a few minutes at points lying between two recording sticks 20 m apart, this was regarded as only one crossing.

In order to render the results for the different months comparable, all monthly means (per 100 m of the observation line) were calculated per four observation times on the basis of those observations in which fresh tracks were visible.

The observation line ran through the following habitats (distances covered in parentheses):

A) Almost treeless summit of the Värriötunturi fell (510 m).

B) Mountain birch forest on the western slope of Värriötunturi, where mountain birches comprised half of the trees, the other half consisting of pine (20—40 %), spruce (0—10 %) and juniper *(Juniperus communis)* (10—20 %) (570 m).

C) Spruce-dominated forests, the proportion of spruce varying between 40 and 85 %, that of pine between 0 and 40 %, that of birch between 5 and 30 % and that of juniper between 0 and 10 % (1860 m).

D) Pine-dominated forest, the proportion of pine being 70—80 %, that of spruce 0—10 %, that of birch 5—10 % and that of juniper 10—15 % (1200 m).

E) Mixed forest characterized by juniper, the proportion of juniper varying between 55 and 75 %, that of spruce between 5 and 15 %, that of pine between 0 and 20 % and that of living birches (some having been destroyed by *Epirrita autumnata*) between 10 and 20 % (1200 m).

F) A bog with 80 % willows (*Salix* spp.), 10 % birch and 10 % spruce (30 m).

G) A treeless marsh (600 m).

In order to obtain information on the abundance of the small rodent populations, an important food source for the present carnivores in wintertime, the recording of the occurrence of the vole damage on small pines, birches and spruces is the most practical method. *Microtus agrestis, M. oeconomus, Clethrionomys rufocanus, Cl. rutilus* and *Cl. glareolus* among the local small rodent species may cause this damage, which is mainly top damage in northern Finland (Teivainen 1979a). When the populations of these rodents are at their peak, the damage caused by them is also greatest, and vice versa (Larsson & Hansson 1977, Hörnfeldt 1978, Teivainen 1979a). Teivainen (1979a, b, 1980, 1981) has collected systematic data of this kind for northern Finland, her figures for the numbers of tree saplings (in thousands) damaged or destroyed by small rodents in eight winters being as follows:

1972/73:16 1973/74:369 1974/75:1 1975/76:31
1976/77:91 1977/78:839 1978/79:17580 1979/80:0

Field observations of the Värriö staff support these findings. The peak previous to the winter of 1973/74 was in 1969/70. The fluctuations in the local *Lemmus lemmus* population have coincided relatively well with those for the other small rodents, although the former were still abundant in the springs of 1971 and 1974, for instance. No notable fluctuations have been observed so far in the local *Myopus schisticolor* population.

4. Results and discussion

4.1. Gross activity

Fig. 2 shows the mean numbers of red fox, pine marten, stoat and pygmy weasel tracks recorded crossing the observation line in November-April in the winters of 1968/69—1980/81. These vary within a narrow range and no special trends are visible. All these species are mainly active during the dark part of the day. The short (twi)light period of the day in mid-winter is thus not reflected here. January is the coldest month of the

winter in this area (Helimäki 1974), but this did not have an effect on the gross activity pattern of these small carnivores as it did on that of the red squirrel (*Sciurus vulgaris;* Pulliainen 1973). Erlinge (1977) found increased movements of male stoats in spring, but these were not yet visible here in April. Vaisfeld (1972) reports that air temperature does not affect the length of the stoat's hunting trails to any great extent, these trails being closely related to the structure, density and depth of the snow cover. Loose snow makes hunting under the surface easier for the stoat (Vaisfeld 1972), whereas the pine marten may have difficulties in moving in the soft, deep snow (Pulliainen & Heikkinen 1980).

4.2. Habitat selection

The 30 m of transect crossing a bog characterized by willows (F, see Section 3) is omitted here, since only one red fox and one pine marten track were recorded there during the 13 winters. Tables 1—4 show the mean numbers of small carnivore and red fox tracks per 100 m of observation line in the remaining six habitat types (see Section 3) during each of the winters. The spruce-dominated mixed forests were clearly the most favoured movement habitats for the pine martens which avoided openings (Table 1). The order of use of the different habitats by the red foxes was mixed forest characterized by juniper = open bog = pine-dominated mixed forest > spruce-dominated mixed forest = mountain birch forest > treeless summit (Table 2). Tracks of the stoat (Table 3), like those of the red fox, occurred in all the available habitats, but most frequently in the mixed forests characterized by juniper and in the spruce-dominated mixed forests. Tracks of the pygmy weasel occurred in all habitats other than the treeless summit, but in many cases only in the winter of 1978/79 (Table 4).

The spruce-dominated mixed forests were mainly used by the stoats at the beginning of the study period, but later by the pine martens. There also were a lot of tracks of the stoat (two peaks) in the mixed forest characterized by juniper, but this was simultaneously an important habitat for the red fox throughout the study period, the pine marten even being absent in certain winters.

Aspisov & Popov (1940), Tarasov (1959), Vaisfeld (1972), Vershinin (1972) and Danilov & Tumanov (1976) report that the stoat prefers flood-plain scrubs, but may be found in all habitats which have potentially high food resources and provide adequate shelter, whereas Nyholm (1972a) describes the Lappish habitats of the species as follows: "Their tracks are found on the riversides and brooksides, and very seldom on the fells'. According to Nyholm (1972b) pygmy weasels occur in all kinds of habitats in Lapland, but seem to prefer burned areas, edges of forests, bogs and old riverside meadows.

The present small carnivores preferred lowlands rather than the summit and slopes of the fell,

Table 1. Mean numbers of pine marten tracks (per 100 m of the observation line) recorded crossing the observation line in different habitats (for descriptions, see Section 3) in the winters of 1968/69—1980/81.

Winter	Habitats					
	C "spruce-dom. forest"	D "pine-dom. forest"	E "juniper-characterized forest"	B mountain birch forests	G open bog	A treeless summit
1968/69	0.56	0.08	0.08	—	—	—
1969/70	0.61	0.30	—	0.14	—	—
1970/71	0.18	0.08	—	—	—	—
1971/72	1.04	0.28	0.27	—	0.17	—
1972/73	0.70	0.28	0.07	0.18	0.17	—
1973/74	1.95	0.42	0.08	—	0.13	—
1974/75	2.85	0.55	0.62	—	0.30	—
1975/76	1.52	1.03	0.50	0.18	0.17	—
1976/77	1.27	—	—	0.58	0.38	—
1977/78	1.27	0.42	1.14	1.18	—	—
1978/79	2.94	0.52	0.38	0.53	—	—
1979/80	0.96	0.73	0.67	—	—	—
1980/81	0.54	0.36	0.08	—	—	—
Mean ± *SE*	1.26 ± 0.24	0.39 ± 0.08	0.30 ± 0.10	0.21 ± 0.10	0.10 ± 0.04	0
t-test	4.019 $P<0.01$	1.083	0.917	1.082	2.808 $P<0.05$	

Table 2. Mean numbers of red fox tracks (per 100 m of the observation line) recorded crossing the observation line in different habitats (for descriptions, see Section 3) in the winters of 1968/69—1980/81.

Winter	Habitats					
	E "juniper-characterized forest"	G open bog	D "pine-dom. forest"	C "spruce-dom. forest"	B mountain birch forest	A treeless summit
1968/69	0.65	0.50	0.65	0.11	0.67	—
1969/70	1.67	0.13	1.18	0.74	0.53	0.39
1970/71	0.58	0.17	0.48	0.25	0.61	—
1971/72	1.12	0.47	0.08	0.60	0.35	0.20
1972/73	1.17	0.43	0.63	0.39	0.18	0.20
1973/74	1.70	1.33	1.38	1.19	0.67	—
1974/75	1.65	1.40	1.40	1.20	0.53	0.51
1975/76	0.50	0.67	0.61	0.27	0.40	—
1976/77	0.19	1.38	0.50	0.23	—	—
1977/78	0.08	2.00	0.17	0.05	—	—
1978/79	1.93	—	0.88	1.01	0.88	0.59
1979/80	1.33	1.60	0.37	0.20	—	—
1980/81	0.33	0.17	0.08	0.05	—	—
Mean ± *SE*	0.99 ± 0.18	0.79 ± 0.18	0.65 ± 0.13	0.48 ± 0.12	0.37 ± 0.09	0.15 ± 0.06
t-test	1.160	0.641	2.340 $P<0.05$	1.325	2.973 $P<0.05$	

Table 3. Mean numbers of stoat tracks (per 100 m of the observation line) recorded crossing the observation line in different habitats (for descriptions, see Section 3) in the winters of 1968/69—1980/81.

Winter	Habitats					
	E "juniper-characterized forest"	C "spruce-dom. forest"	D "pine-dom. forest"	B mountain birch forest	G open bog	A treeless summit
1968/69	0.75	0.53	—	—	0.17	—
1969/70	3.52	1.86	0.73	0.81	0.33	—
1970/71	0.79	2.04	1.63	0.37	0.47	—
1971/72	0.42	1.12	0.62	0.49	—	0.20
1972/73	0.33	0.25	—	—	—	—
1973/74	0.33	0.15	0.08	0.18	0.17	—
1974/75	0.55	0.90	0.42	1.23	0.33	0.63
1975/76	0.42	0.55	0.58	0.18	—	—
1976/77	0.11	0.07	—	—	—	—
1977/78	0.23	0.22	0.33	0.40	0.33	—
1978/79	2.27	1.27	0.90	1.23	0.60	—
1979/80	0.17	0.10	—	—	—	—
1980/81	0.07	—	—	—	0.50	—
Mean ± *SE*	0.77 ± 0.28	0.70 ± 0.19	0.41 ± 0.14	0.38 ± 0.13	0.22 ± 0.06	0.06 ± 0.05
t-test	0.353	3.122 $P<0.01$	1.967	1.466	2.088	

although due to temperature inversion, it was warmer at the higher altitudes, though more windy (Helimäki 1974, the present study). All these species, but especially the mustelids, may seek their resting sites under the snow surface in places into which the cold, heavy air does not flow and where there is no wind effect (see also Pulliainen 1981b). This subnivean life is especially important to the pygmy weasel, since its basal metabolism is 2—3 times higher than that represented by the standard curve for mammals (Scholander et al. 1950, Iversen 1972; see also Erlinge 1974). According to Vaisfeld (1972) the stoat may remain under the surface of the snow for more than 24 hours when the snow cover is thick and there is plenty of food available.

Table 4. Mean numbers of pygmy weasel tracks (per 100 m of the observation line) recorded crossing the observation line in different habitats (for descriptions, see Section 3) in the winters of 1968/69—1980/81.

Winter	Habitats					
	C "spruce-dom. forest"	E "juniper-characterized forest"	D "pine-dom. forest"	B mountain birch forest	G open bog	A treeless summit
1968/69	0.22	0.08	—	—	—	—
1969/70	0.11	—	—	—	0.17	—
1970/71	—	—	0.11	—	—	—
1971/72	—	—	—	—	—	—
1972/73	—	—	—	—	—	—
1973/74	0.05	0.08	—	—	0.17	—
1974/75	0.20	0.08	—	—	—	—
1975/76	0.22	0.50	—	—	—	—
1976/77	—	—	—	—	—	—
1977/78	0.07	0.08	—	0.18	—	—
1978/79	0.62	0.57	0.50	0.53	0.27	—
1979/80	0.04	—	—	—	—	—
1980/81	—	—	—	—	—	—
Mean ± *SE*	0.12 ± 0.05	0.11 ± 0.05	0.05 ± 0.05	0.05 ± 0.04	0.05 ± 0.03	0
t-test	0.375	1.511	0.454	0.242	1.834	

4.3. Numbers of tracks

Fig. 3 shows the total numbers of tracks recorded crossing the observation line (calculated as described in Section 3) in each of the 13 winters. When assessing this data and comparing the different species, it is worth remembering that the pygmy weasel lives more of a subnivean life than the other mustelids. Three peaks (in the winters of 1969/70, 1974/75 and 1978/79) were recorded for the stoat and the red fox, two for the pine marten (1974/75 and 1978/79) and two for the pygmy weasel (1975/76 and 1978/79). Thus the third peak coincided very well in all four species.

5. General discussion

The red fox has a reddish brown winter coat and the pine marten a brown one, whereas the stoat and pygmy weasel have white coats. The red fox is too large to be particularly vulnerable to predation from the air, whereas a pine marten may become the victim of an eagle owl *(Bubo bubo)* or golden eagle *(Aquila chrysaetos)* on light nights in late winter and spring (e.g. Nyholm 1970, Huhtala et al. 1976, Pulliainen 1981b) since it is easy to observe on the white snow. The stoat and pygmy weasel are probably not so vulnerable under similar conditions, also because of their subnivean habits.

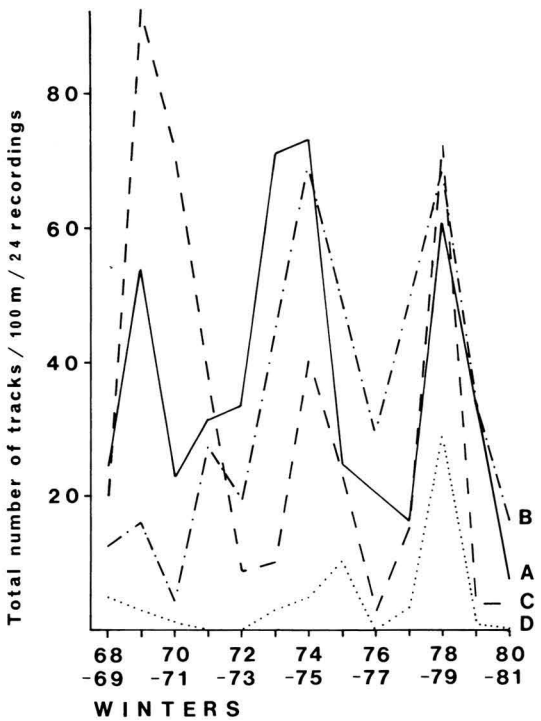

Fig. 3. Total numbers of tracks of red foxes (A), pine martens (B), stoats (C) and pygmy weasels (D) recorded crossing the observation line during the winters of 1968/69—1980/81 (numbers calculated per 24 recording occasions).

Thus it is understandable that the pine marten avoids entering areas with no overhead cover (Table 1; see also Hawley & Newby 1957), a fact which emerged very clearly during tracking of the species in the present study area (Pulliainen 1981b). When tracking a red fox, one soon observes how its trails cross those of the three other species, revealing that they are sympatric in the forest area. The present long-term study, however, reveals some differences in the use of the different available habitats. The pine marten clearly preferred the spruce-dominated forests (Table 1), thus confirming the results of the tracking study (Pulliainen 1981b), whereas the stoat and pygmy weasel occurred equally in the spruce-dominated forests and in mixed forests characterized by juniper (Tables 3 and 4). In contrast, the tracks of the red fox occurred most frequently in the mixed forests characterized by juniper or pine and on the open bogs, the spruce-dominated mixed forests being only second in order of importance (Table 2). Unlike the pine marten, the red fox also moved about on the almost treeless summit of the fell.

This habitat use pattern in the different carnivore species should reflect not only anti-predatory behaviour but also other factors such as the availability of food. The stoat and the pygmy weasel are specialists adapted to hunting and killing rodents, whereas the red fox and the pine marten are generalists which exploit a wide range of food items (e.g. Andersson & Erlinge 1977). Small rodents (voles and lemmings) are the most important food of the pine marten when available in plenty, but when these are scarce it will consume a variety of items from berries and mushrooms to all kinds of carcasses, birds and mammals (for details, see Pulliainen 1981a). The pine marten digs up burrows in the snow when hunting small rodents, searching for caracasses and picking berries, as do the local red foxes, as well.

During two winters (1971/72 and 1980/81) red foxes were tracked for a total of 281 km, and were found to visit carcasses an average of 0.22 times/km and 0.25 times/km, respectively, while the frequencies of digging in the snow were 0.43 and 0.25 times/km, respectively. During the former winter the red foxes tracked (for 182.5 km) only succeeded in killing one arctic hare *(Lepus timidus)* and during the latter (98.5 km) one willow grouse *(Lagopus l. lagopus)*. The author's observations (a few stomach analyses and field observations) confirm the importance of small rodents to the nutrition of the stoat and the pygmy weasel (see also Nyholm 1972a, b), but when the rodent populations are scarce even the latter can kill a young arctic hare (Pulliainen & Iivanainen 1979), and all carcasses are utilized effectively.

Whereas small rodents may occur in a sub-nivean environment in the snow drifts in mountain birch forests on the slopes of fells, in conifer-dominated forests and mixed forests characterized by juniper and on open bogs (e.g. Kalela et al. 1971, Danilov & Tumanov 1976, Henttonen et al. 1977), the summit of the Värriötunturi fell has a thin covering of hard-packed snow, and practically no snow drifts, so that usually no small rodents overwinter there. The stoat and the pygmy weasel probably accept a variety of vole and lemming species, and are thus found wherever these are available (see Tables 3 and 4), as also suggested by Aspisov & Popov (1940), Tarasov (1959), Vaisfeld (1972) and Vershinin (1972).

A number of authors (e.g. Lund 1962, Lloyd 1980, Sequeira 1980, v. Schantz 1980) suggest that the red fox prefers hunting *Microtus* spp., which may be due to the fact that these voles make their tunnels in the litter and consequently are within reach of the foxes in snowy conditions (v. Schantz 1980). *Microtus agrestis* and *M. oeconomus* are encountered in Finnish Lapland in places where vegetation consists of grasses (Kalela et al. 1971, Lahti et al. 1976, Henttonen et al. 1977; also confirmed during the present study by snap-trapping). Grasses are particularly common in the mixed forests characterized by juniper in the present study area, in which the larvae of *Epirrita autumnata* killed many of the birches in the 1960s, and on the open bogs. Thus it is easy to explain why the local red foxes are frequently found in these habitats (Table 2). Even so, as opportunistic feeders they also range widely over other habitats, utilizing their resources, and when moving from one habitat to another they may even cross the summit of the fell, which the pine marten does extremely seldom. In earlier times, when wolverines still occurred fairly regularly in the area, the red foxes often followed their tracks. Nowadays the foxes still follow the trails of the semi-domestic reindeer, which lead from one grazing site to another. In both cases the red foxes have learned that there may be carcasses available along these routes (see also Haglund 1966). In contrast, the pine martens do not use the same game trails in their movements (Pulliainen 1981c). The fact that the different habitats available in the area are not equally inhabited by small carnivores naturally reduces interspecific competition.

The small rodents are evidently of great importance to the diet of the present small carnivores and the red fox. The local small rodent populations fluctuate considerably in size from

year to year, and the numbers of the crossings of the observation line by small carnivores also vary greatly, but what is the role of predation in the fluctuations in small rodent populations?

In a predator-prey cycle one would expect the predator cycle to follow the prey cycle. Aspisov & Popov (1940) studied fluctuations in the numbers of the stoat in the flood plain of the Kama River in the Tatar SSR, where the water vole *(Arvicola terrestris)* is its main food, and found that a drop in water vole pelt stocks was always followed by one in stoat pelt stocks and vice versa. A similar relationship was recorded by Vershinin (1972) between the number of voles and the yield of stoat pelts in the Kamchatka region, eastern Asia, in 1937—1964, and by Danilov & Tumanov (1976) in the Murmansk Region of the Kola Peninsula.

The present trackings reveal that the home ranges of the red fox (unpubl. data) and the pine marten (Pulliainen 1981b, c) may vary considerably in area and reach almost 100 km^2. The 6 km of observation line used here lay inside the home ranges of three or less red foxes and three or less pine martens. The sizes of the home ranges of the stoat and the pygmy weasel were not studied in this way, but they are known to be much smaller, that for the stoat studied by Vaisfeld (1972) varying between 11 and 160 ha. Tast & Kalela (1971) trapped ten pygmy weasels in an area of 100 × 200 m at Kilpisjärvi, northwestern Finland, from 17th July to 3rd August 1970 during the cyclic rodent peak, the traps being too small for stoats, which were abundant at that time.

Changes in the numbers of small carnivores are usually caused by natality and mortality and/or by immigration/emigration. The numbers of crossings of the observation line may also change if the carnivores present in the area extend or reduce their home ranges and/or their mobility. Finerty (1980) reviews a number of cases in which small mammals escape adverse circumstances created by high population densities and/or food shortages.

Both differences and similarities are found in the responses of the present small carnivore populations (Fig. 3) to the fluctuations in small rodent populations.

1) When small rodents were really scarce in the winters of 1971/72, 1972/73, 1976/77 and 1979/80, the numbers of tracks of the stoat and pygmy weasel crossing the observation line were relatively few or nil, while those of the red fox and the pine marten did not decrease so drastically.

2) During the small rodent peak in the winter of 1969/70 there were also peaks in the numbers of the red fox and stoat tracks, but not in those of the pine marten and the pygmy weasel.

3) During the second small rodent peak each of the predator species appears to have had a good breeding result, as reflected in the numbers of crossings of the observation line either in the winter of 1975/76 (the pygmy weasel) or the previous winter (the other species).

4) During the third small rodent peak there was a good coincidence in the trends in small carnivore populations. The fairly high small rodent populations of the winter of 1977/78 probably allowed the predators to maintain their populations, which crashed or dispersed after the small rodent populations had fallen sharply during the course of the following winter. The pine martens (see Pulliainen 1981c) expanded their home ranges in this situation, whereas there were still few stoats and perhaps no pygmy weasels present in the winter of 1980/81, although the small rodent populations had already increased to some extent during the previous summer.

The present data confirm the finding that food specialists (here the stoat and the pygmy weasel) are more vulnerable to fluctuations in small rodent populations than generalists (here the red fox and the pine marten) (see also Hörnfeldt 1978). The pygmy weasel appeared to be especially vulnerable, for it was completely absent during certain winters in which there was a small rodent shortage (for similar cases, see also Thompson 1955, Robina 1960, Erlinge 1974).

The following observation of J. Koski (cit. in Nyholm 1972b) suggests that the pygmy weasel may then have recourse to dispersal to refuges (see also Erlinge 1975). One pygmy weasel had covered a distance of about 300 m by the end of the first day, about 800 m by the second and over 2000 m by the third day. It did not succeed in killing any voles during this period.

During dispersal movements pygmy weasels may withdraw so far that they are unable to return to their starting area in the next increase year(s) of small rodents, when successful breeding is again possible, (as was probably the case here during the first rodent peak), even though the breeding potential of the species is high under favourable conditions. There are two litters a year and females born in spring can reproduce the same year (Deanesly 1944).

The semi-domestic reindeer act as a supplementary factor in the food economy of the food generalists in this area. In earlier times they were often killed by wolves and wolverines, thus producing carcasses, while nowadays, in the absence of these large predators, death of reindeer due to starvation on over-grazed pastures

produce the same result. With their great mobility, the red fox and pine marten easily find these carcasses, whereas the smaller carnivores are not so successful in this respect (see also Andersson & Erlinge 1977). The generalists can also disperse effectively, since Englund (1980) reports cases in which young red foxes moved 200—250 km from their tagging site, but he emphasized that "there is no reason to believe that food shortage as starvation *per se* caused the high dispersal rate among the young males". He further states that the patchy distribution of food in poor rodent years will result in a locally clumped distribution of foxes, possibly even at higher densities than those which occur when they are more evenly distributed in years of high rodent populations.

Under these subarctic and northern taiga conditions the existence of the large herbivores (especially the reindeer, but also the moose *(Alces alces);* see Pulliainen 1974) is essential for the survival of the food generalists, and the herbivore carcasses also offer refuges (food reserves) for food specialists. The presence of the wolves, which belong to this ecosystem, would make it more functional, because they kill ungulates throughout the year (e.g. Pulliainen 1965, Mech 1970).

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References

Andersson, M. & Erlinge, S. 1977: Influence of predation on rodent populations. — Oikos 29: 591—597.

Aspisov, D. I. & Popov, V. A. 1940: Factors determining fluctuations in the numbers of ermines (Translation by Translation Service, Department of Internal Affairs, Wellington, New Zealand). — Arb. Naturforsch. Ges. Univ. Kasan 6: 41—64.

Danilov, P. J. & Tumanov, J. L. 1976: Kuni severozapada SSSR. — Nauka, Leningrad.

Deanesly, R. 1944: The reproductive cycle of the female weasel (Mustela nivalis). — Proc. Zool. Soc. Lond. 114: 339—349.

Englund, J. 1980: Yearly variations of recovery and dispersal rates of fox cubs tagged in Swedish coniferous forests. — Biogeographica 18: 195—207.

Erlinge, S. 1974: Distribution, territoriality and numbers of the weasel Mustela nivalis in relation to prey abundance. — Oikos 25: 308—314.

—»— 1975: Feeding habits of the weasel Mustela nivalis in relation to prey abundance. — Oikos 26: 378—384.

—»— 1977: Spacing strategy in stoat Mustela erminea. — Oikos 28: 32—42.

Finerty, J. P. 1980: The population ecology of cycles in small mammals. Mathematical theory and biological fact. — Yale University Press, New Haven and London.

Haglund, B. 1966: Winter habits of the lynx (Lynx lynx L.) and wolverine (Gulo gulo L.) as revealed by tracking in the snow. — Viltrevy 4: 81—299.

Hawley, V. D. & Newby, F. E. 1957: Marten home ranges and population fluctuations. — J. Mammal. 38: 174—184.

Helimäki, U. I. 1974: On the climate of Lapland, especially on the hills. — Acta Lapponica Fenniae 8: 23—27.

Henttonen, M. 1980: Tunturisopuli (Summary: Norwegian lemming, Lemmus lemmus). — Luonnon Tutkija 84: 23—25.

Henttonen, M., Kaikusalo, A., Tast, J. & Viitala, J. 1977: Interspecific competition between small rodents in subarctic and boreal ecosystems. — Oikos 29: 581—590.

Huhtala, K., Rajala, P. & Sulkava, S. 1976: Uusin tieto kotkan ravinnosta (Summary: Feeding habits of the golden eagle). — Suomen Luonto 35: 25—29, 63.

Hörnfeldt, B. 1978: Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. — Oecologia (Berl.) 32: 141—152.

Iversen, J. A. 1972: Basal energy metabolism of mustelids. — J. Comp. Physiol. 81: 341—344.

Järvinen, A. & Tast, J. 1980: Pikkujyrsijä- ja kololintukantojen säätelystä subarktisella alueella (Summary: Regulation of subarctic populations of small rodents and box-nesting passerines). — Luonnon Tutkija 84: 26—30.

Kalela, O. 1949: Über Fjeldlemming-Invasionen und andere irreguläre Tierwanderungen. — Ann. Zool. Soc. Vanamo 13(5): 1—90.

—»— 1957: Regulation of reproduction rate in subarctic populations of the vole Clethrionomys rufocanus (Sund.). — Ann. Acad. Sci. Fenn. (A IV) 34: 1—60.

—»— 1962: On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. — Ann. Acad. Sci. Fenn. (A IV) 66: 1—38.

Kalela, O., Koponen, T. & Yli-Pietilä, M. 1971: Übersicht über das Vorkommen von Kleinsäugern auf verschiedenen Wald- und Moortypen in Nordfinnland. — Ann. Acad. Sci. Fenn. (A IV) 185: 1—13.

Lahti, S., Tast, J. & Uotila, H, 1976: Pikkujyrsijöiden kannanvaihteluista Kilpisjärvellä vuosina 1950—1975 (Summary: Fluctuations in small rodent populations in the Kilpisjärvi area in 1950—1975). — Luonnon Tutkija 80: 97—107.

Larsson, T.-B. & Hansson, L. 1977: Vole diet on experimentally managed afforestation areas in northern Sweden. — Oikos 28: 242—249.

Lloyd, H. G. 1980: Habitat requirements of the red fox. Biogeographica 18: 7—25.

Lund, M. K. 1962: The red fox in Norway II. The feeding habits of the red fox in Norway. — Medd. Statviltundersøkelser 2(12): 1—79.

Mech, L. D. 1970: The wolf. — Natural History Press, New York.

Nyholm, E. 1970: Näädän elintavoista, saalistuksesta ja ravinnosta. — Suomen Riista 22: 105—118.

—»— 1972a: Kärppä. — In: Siivonen, L. (ed.), Suomen nisäkkäät 2: 173—187. Otava, Helsinki.

—»— 1972b: Lumikko. — In: Siivonen, L. (ed.), Suomen nisäkkäät 2: 187—199. Otava, Helsinki.

Pulliainen, E. 1965: Studies on the wolf (Canis lupus L.) in Finland. — Ann. Zool. Fennici 2: 215—259.

—»— 1973: Winter ecology of the red squirrel (Sciurus vulgaris L.) in northeastern Lapland. — Ann. Zool. Fennici 10: 487—494.

—»— 1974: Seasonal movements of moose in Europe. — Natural. Canad. 101: 379—392.

—»— 1976: Birch forest damage caused by Oporinia autumnata Bkh. (Lep., Geometridae) in 1965—1966 in eastern Itäkaira, northeastern Lapland. — Ann. Entomol. Fennici 42: 166—170.

—»— 1981a: Food and feeding habits of the pine marten in Finnish Forest Lapland in winter. — In: Chapman, J. A. & Pursley, D. (eds.), Worldwide Furbearer Conference Proceedings: 580—598. Frostburg, Maryland, USA.

—»— 1981b: Winter habitat selection, home range, and movements of the pine marten (Martes martes) in a Finnish Lapland forest. — In: Chapman, J. A. & Pursley, D. (eds.), Worldwide Furbearer Conference Proceedings: 1068—1087. Frostburg, Maryland, USA.

—»— 1981c: Scent-making in the pine marten (Martes martes) in Finnish Forest Lapland in winter. — Zeitschr. Säugetierk. (in press).

—»— 1981d: Habitat selection and population fluctuations of an arctic hare population (Lepus timidus) on a subarctic fell in Finnish Forest Lapland. — Zeitschr. Säugertierkunde (in press).

Pulliainen, E. & Heikkinen, H. 1980: Näädän talvisesta käyttäytymisestä Metsä-Lapin itäosassa (Summary: Behaviour of the pine marten (Martes martes) in E Finnish Forest Lapland in winter). — Suomen Riista 28: 30—36.

Pulliainen, E. & Iivanainen, J. 1979: Lumikko tappoi jäniksenpojan (Summary: Young arctic hare killed by a pygmy weasel). — Luonnon Tutkija 83: 151.

Robina, M. A. 1960: Some features of weasel (Mustela nivalis L.) ecology based on observations in the Moscow Region. — Bjull. Otbel Biol. N.S. 65(4): 27—33.

Schantz, T. v. 1980: Prey consumption of a red fox population in southern Sweden. — Biogeographica 18: 53—64.

Scholander, P. F., Hock, R., Walters, V. & Irving, L. 1950: Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. — Biol. Bull. 99: 259—271.

Sequeira, D. M. 1980: Comparison of the diet of the red fox (Vulpes vulpes L., 1758) in Gelderland (Holland), Denmark and Finnish Lapland. — Biogeographica 18: 35—51.

Stenseth, N. C. 1977: Evolutionary aspects of demographic cycles: the relevance of some models of cycles for microtine fluctuations. — Oikos 29: 525—538.

—»— 1978: Demographic strategies in fluctuating populations of small rodents. — Oecologia (Berl.) 33: 149—172.

Tarasov, P. P. 1959: Intraspecific relations (territoriality) in sable and ermine (Translation by Translation Service, Department of Internal Affairs, Wellington, New Zealand). — Bjull. Mosk. O-va Isp. Prir., Otd. Biol. 64(6): 37—43.

Tast, J. 1966: The root vole, Microtus oeconomus (Pallas), as an inhabitant of seasonally flooded land. — Ann. Zool. Fennici 3: 127—171.

—»— 1968: Influence of the root vole, Microtus oeconomus (Pallas), upon the habitat selection of the field vole, Microtus agrestis (L.), in northern Finland. — Ann. Acad. Sci. Fenn. (A IV) 136: 1—23.

—»— 1974: The food and feeding habits of the root vole, Microtus oeconomus, in Finnish Lapland. — Aquilo (Zool.) 15: 25—32.

Tast, J. & Kalela, O. 1971: Comparisons between rodent cycles and plant production in Finnish Lapland. — Ann. Acad. Sci. Fenn. (A IV) 186: 1—14.

Teivainen, T. 1979a: Vole damage to forest tree seedlings in reforested areas and fields in Finland in the years 1973—76. — Folia Forest. 387: 1—23.

—»— 1979b: Myyräraportti. — Metsä ja Puu 1979 (5): 34—35.

—»— 1980: Myyräraportti. Eniten tuhoja Savossa ja Keski-Suomessa. — Metsä ja Puu 1980(1): 34.

—»— 1981: Metsäpuiden taimien myyrätuhot vuonna 1979/80 ja ennuste seuraavien vuosien tuhoalueista. — Metsäntutkimuslaitoksen Tiedonantoja 2: 1—5.

Thompson, D. Q. 1955: The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. — Trans. N. Amer. Wildl. Conf. 20: 166—176.

Vaisfeld, M. A. 1972: Ecology of the ermine in the cold season in the European North (Translation by Translation Service, Department of Internal Affairs, Wellington, New Zealand). — Zool. Žurnal 51: 1705—1714.

Vershinin, A. A. 1972: The biology and trapping of the ermine in Kamchatka (Translation by Translation Service, Department of Internal Affairs, Wellington, New Zealand). — Bjull. Mosk. o-va Ispyt. Prir. Otd. Biol. 77: 16—26.

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