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LONG-TERM DYNAMICS OF THE BANK VOLE *CLETHRIONOMYS GLAREOLUS* AT PALLASJÄRVI, NORTHERN FINNISH TAIGA

ABSTRACT: The whole rodent community (eight arvicoline species) has been followed at Pallasjärvi, at the northern limit of *Clethrionomys glareolus* in Finnish Lapland, since 1970. Dynamics were cyclic until the mid 1980's, but since then the pattern has been stable. Also the species abundances have changed. The delayed density dependence, characterising the cyclic period, is not found during the stable period. Causes for this change in cyclicity are discussed. The bank vole is the most common rodent species in forests up to its northern limit. The long-term, year around live trapping studies and feeding experiments suggest e.g. that delayed maturation of young is not optimal but due to social constraints. Food addition resulted in higher densities, but the effect on the density-dependent structure was negligible and the dynamics were not affected by food addition.

KEY-WORDS: bank vole, *Clethrionomys glareolus*, arvicoline species, cycles, Lapland, density-dependence, interspecific competition

1. INTRODUCTION

The Pallasjärvi area (68°30'N, 24°09'E), in the southern part of the Pallas-Ounas National Park in western Finnish Lapland, has been a core place for an intensive rodent research since 1970. There are several reasons why this area in particular is so suitable for long-term ecological research on voles and lemmings. The population cycles of voles and lemmings have been a very characteristic feature in northern Fennoscandia. These cycles are, in turn, reflected in many other components of northern nature, like small game and vegetation (Hansson and Henttonen 1989). The very special feature of the Pallas rodent assemblage is the high number of syntopic species (Henttonen *et al.* 1977). The rodent fauna includes three species of *Clethrionomys*, bank vole *C. glareolus*, red vole *C. rutilus* and grey-sided vole *C. rufocanus*, two species of *Microtus*, field vole *M. agrestis* and root vole *M. oeconomus*, two species of lemmings, Norwegian lemming *Lemmus lemmus* and wood lemming *Myopus schisticolor*, and the water vole *Arvicola terrestris*. Also the muskrat *Ondatra zibethicus* is occasionally observed. These arvicoline species have, however, different habitat characteristics and diets. In addition, the small mammal fauna consists of four species of *Sorex* shrews, *S. araneus*, *S. caecutiens*, *S. minutus* and *S. minutissimus*, and the water shrew *Neomys fodiens*.

The high number of species allows for studying dynamical processes at various levels, i.e. the whole small mammal community, the rodent community and population level. As a consequence, it is possible to differentiate between the factors affecting simultaneously the whole small mammal or rodent assemblage or only the population of single species (Henttonen 1985, Henttonen

1987, Hansson and Henttonen 1988). Basically this is the difference between extrinsic *vs.* intrinsic population regulation (Henttonen *et al.* 1987), i.e. predation, food and diseases against social stress and behavioural mechanisms (self regulation), even though species specific resource interaction could affect only one species.

The high number of rodent species is partly a result of the encounter of northern and southern faunal elements, but it may also be partly facilitated by the pronounced population cycles of the rodent species (Henttonen and Hansson 1984, Hanski and Henttonen 1996). The habitat selection of these rodent species overlap, and interspecific competition at least for space during the population peaks is a common phenomenon (Henttonen *et al.* 1977, Henttonen and Hansson 1984, Jortikka 1990, Hanski and Henttonen 1996). The deep population crashes affecting all species simultaneously could be one factor promoting species coexistence. In respect of the bank vole, the Pallasjärvi area has one more specific feature: the study area is only some 40–50 km from the northern border of the species.

2. EXTENSIVE MONITORINGS AT PALLASJÄRVI

The Pallasjärvi area is characterised by an isolated mountain group. The forests on the slopes are characterised by Norway spruce *Picea abies*, downy birch *Betula pubescens* and Scots pine *Pinus silvestris*. The valleys are covered by pine bogs and mires. The dominant feature in the forests is the continuous and dense cover of the bilberry *Vaccinium myrtillus* in the field layer and the mosses *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum* spp in the bottom layer. The snow usually melts in late May, and permanent snow covers prevails since late October. The maximum snow cover on the study sites is around 1 meter in March–April.

The basic monitoring on three main habitats (old taiga forests, bogs and mires, and clear cuts) is done with snap trapping on the permanent sites twice a year. Additional trappings have been done at the tree line and in the alpine zone. The results on the bank voles in this article are presented primarily from taiga forests. Characterisation of other habitats can be found in Henttonen *et al.* (1987). 30 permanent small quadrats (grids of

15 × 15 m with three snap traps at each corner (Myllymäki *et al.* 1971)) on each of the main habitats have been used. In old taiga forests and peatlands, trapping is done in groups of 3–7 quadrats. In each group, the distance between quadrats is at least 50 m, usually more. The distance between groups is 0.5–5 km. One large clear cut area is used. Trappings have been done immediately after the snow melt at the turn of May and June–early June, and again in September. For more details, see Henttonen *et al.* (1987).

The main purpose of these basic monitoring trappings has been to describe the general features of the population dynamic patterns on a larger area, to obtain estimates of population densities on the main habitats, to collect data on demographic and reproductive parameters, as well as material for parasitological studies (e.g. Henttonen 1985, 1987, 1997, Henttonen *et al.* 1977, 1987, Hansson and Henttonen 1985b, Haukisalmi *et al.* 1987, 1988, 1996, Hanski *et al.* 1994). The data from small quadrats on a larger area serve as background and comparison for more detailed live trapping studies on more restricted sites (Henttonen *et al.* 1987, Hanski *et al.* 1994).

3. INTENSIVE LIVE-TRAPPING STUDIES AT PALLASJÄRVI

Intensive live-trapping studies have been done to follow the populations of individually marked animals. Depending on the purpose of the specific study, a variable number of study grids varying in size from 1 to 4.5 ha have been in use. Depending on the number of replicates, a 10 × 10m or 15 × 15m grid pattern has been used. Thus, the number of live traps per site has usually been 80–130. The trapping routine and the number of trap checkings per a trapping period has also depended on the number of replicated sites. Of course, within a specific experiment or program the protocol has been fixed.

The following main live trapping projects have been running in old taiga forests.

1) *The large control grid* (4.5 ha) was started in 1977, and since spring 1980 it has been yearly trapped several times from spring to autumn. During 1982–1992 the grid was intensively live trapped year around. 10 × 10 m grid pattern was used but at each moment traps were situated at 20-m intervals. In snow free seasons, a trapping period consisted of 16 trap checkings at 6-hour intervals. Each point was

trapped for 24 hours and then the trap was moved 10 m to the next point. During snowy seasons (late October to late May) permanent trap chimneys were used at 20-m intervals. In winter, trapping was done in day time starting at 8 a.m. and traps were checked at 2–3 hour intervals until 5–6 p.m. It should be noticed that in winter time bank voles are day active (though twilight in mid winter lasts only for few moments). Due to this very intensive trapping schedule, the sampling error is very low, only about 2% (Yoccoz et al,. in press).

2) *The large food grid* (2.8 ha) was started in spring 1982 and live-trapping run identically to the large control grid until autumn 1996. The first experiment with additional food (oat seeds) lasted from June 1982 to September 1996. The second experiment with oat seeds and mouse chow ran from spring 1998 to autumn 1992. Details of these two grids and projects have been given by Henttonen *et al.* (1987) and Prévot-Julliard *et al.* (1999).

3) *Replicated live-trapping grids.* Nine grids, each 1.8 ha with 10 × 10 trapping points at 15-m intervals, were established in spring 1986. Traps were permanently at the same points. In winter trap chimneys were used at every point. In summer time, each trapping period included 8 trap checkings at 8-hour intervals. In winter, three trap checkings during each of the three trapping days were done. To have replicates, we had to compromise in trapping efficiency and grid size.

In snow free seasons in 1986 and 1987, the interspecific competition between the bank vole and red vole was studied. Once a month, bank voles were removed on three grids, red voles from three grids, and three grids remained as controls (Jortikka 1990). Starting in spring 1988, a replicated experiment with supplemental food (mouse chow) was started on six of these grids (three food and three control grids). Three remaining *C. rutilus* grids where bank vole had been removed in 1987, were monitored in snow free seasons until 1992 to document the return of interspecific relations to the normal situation. The replicated food experiment lasted from spring 1988 to autumn 1992, and experiment ran year around. After the experiment with extra food was finished, the food grids were monitored in snow free season until autumn 1994. In snow free seasons 1993 and 1994 the three controls of the previous experiment and the above mentioned three former *C. rutilus* grids were used in an experiment where bank

voles were medicated with an antihelminthic (see Haukisalmi and Henttonen 2000).

4) *Two meadows* dominated by the root voles have been live trapped from 1981 to 1996 and have been snap-trapped twice a year since then.

The live-trapping studies have had (at least) the following purposes:

– To give real density values in comparison to estimates obtained with snap-trappings. Live trappings are much more labourous to do than snap-trappings, and therefore intensive live-trapping data can be obtained only in restricted sites. As a contrast, snap-trappings can cover larger areas, but snap-trappings give only indices. Combining these two approaches is fruitful (Henttonen *et al.* 1987, Hanski *et al.* 1994).

– In experiments with supplemental food, the role of food in the population dynamics of bank voles has been studied (Henttonen *et al.* 1987, Prévot-Julliard *et al.* 1999, Yoccoz *et al.,* in press).

– As told, interspecific competition among the rodent species is common. This is especially so between the breeding individuals of *Clethrionomys* species. Breeding females of *Clethrionomys* species have exclusive territories also between the species, and this is directly related to the space available to a species in accordance with the competitive interspecific hierarchy (Henttonen *et al.* 1977, Henttonen and Hansson 1984, Jortikka 1990, Hanski and Henttonen 1996).

– We have studied experimentally e.g. whether helminth parasites can affect the survival and dynamics of the bank vole by medicating voles in the experimental populations in the field. In these experiments individual performance and worm burden (measured by counting the worm eggs in the feces of individual voles) were monitored.

– In addition to rodent and parasite monitoring, we have followed the abundance of small mustelids (least weasels *Mustela nivalis* and stoats *M. erminea*). In summer time we have obtained data from live trappings and winter also from snow trackings (Henttonen *et al.* 1987, Oksanen and Henttonen 1996).

4. SOME BASIC CONCLUSIONS ON MICROTINE CYCLES AT PALLASJÄRVI

The very characteristic feature of the rodent cycles in northern Fennoscandia is (or at
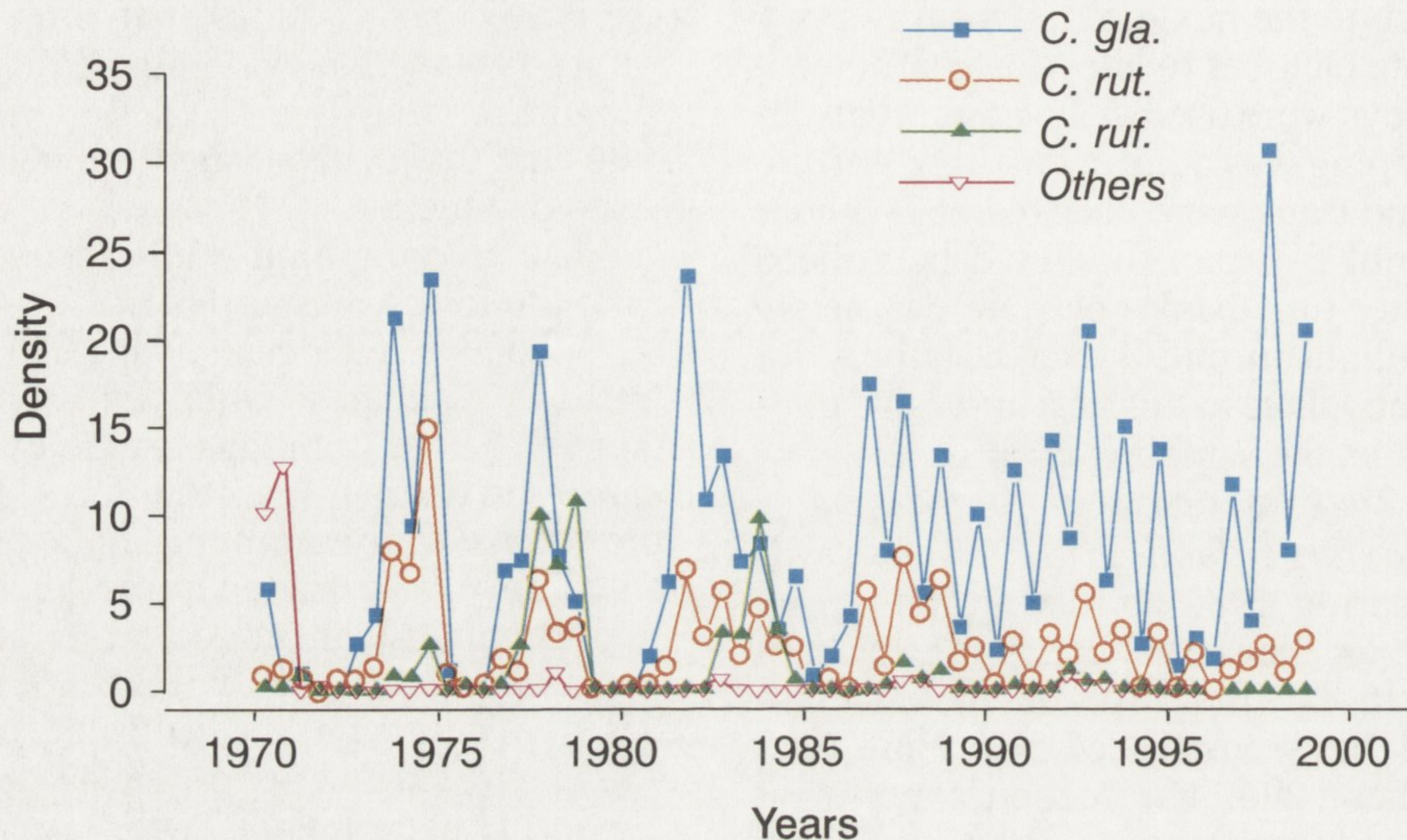
Fig. 1. Long-term dynamics of arvicoline rodents in old taiga forests at Pallasjärvi, western Finnish Lapland. *Others* refer primarily to *Lemmus lemmus*. Data based on snap-trappings twice a year. Density index is number of voles per 100 trap nights

least has been) the synchronous deep crash in all species (Fig 1). This is *the* reason to emphasize the community approach in the research of rodent cycles (Hansson and Henttonen 1985a, 1988, Henttonen 1987, Henttonen *et al.* 1987, Henttonen and Hanski 2000, Henttonen and Wallgren 2000, Hanski and Henttonen 1996, Hanski *et al.* 1991, 1993, 1994). These synchronous crashes cannot be explained by intrinsic factors alone. Of course the population increase of rodents can be first slowed down by social factors, but this does not mean that these same factors cause the crash. Why would all species commit a suicide together? The only reasonable explanation for the synchronous crashes is a common extrinsic factor (Henttonen 1985, Henttonen *et al.* 1987, Hansson and Henttonen 1988) and the most probable factor is the predation by small mustelids. In cyclic times at Pallasjärvi, this interspecfic synchrony extended also to insectivorous shrews (Henttonen 1985), but has disappeared since then. The role of specialist predation is further corroborated by studies elsewhere in Fennoscandia (e.g. Norrdahl and Korpimäki 1995, Korpimäki and Norrdahl 1998; it should be remembered, however, that in the three-year cycles in western Finland the abundance and role of avian predators is clealy higher than in the north, see also Hanski *et al.* 1991).

Some other features in the Pallasjärvi data set speak for community approach, too.

Even if the rodent community as a whole cycled together until mid 1980's, the abundances of individual species changed from cycle to another. Yet, very different densities of a species during successive cyclic peaks normally lead to similar total crashes. Furthermore, the second high density year during the peak phase (like in 1970, 1974, 1978, 1982) does not automatically lead to crash as found during the extended peak in 1983. In other words, direct density-dependent intrinsic mechanisms do not alone cause the cycle (Henttonen *et al.* 1987). This is further supported by the data from the last 15 years when the pattern of rodent dynamics at Pallasjärvi (and in Lapland generally) has changed. Even though the bank voles now often reach the same autumn densities as they did earlier only during the cyclic peak phases, their dynamics remain multi-annually rather stable. Recent time-series analyses also indicate that delayed density-dependence is prevalent in the long-term data sets on small rodent fluctuations in northern Fennoscandia suggesting that cycles are caused by a trophic interaction (Hanski *et al.* 1993, Stenseth 1999, Hansen *et al.* 1999). For the reason told above, the predation by small mustelids seems as the most probable cause. However, for the recent stable period with low weasel abundanace at Pallasjärvi, the analysis of Yoccoz *et al.* (in press) showed no detectable delayed density-dependence in the bank vole dynamics on the large control and food grids.

In mid 1980's and at the turn of 1980's and 1990's, a drastic change in the dynamics of small rodents has occurred in northern Fennoscandia. Starting in early 1980's the small mammal dynamics at Pallasjärvi began to change and since mid 1980's the dynamics have been very different from the earlier ones. After an extended cycle in 1982–84 and a the subsequent low phase in 1985, the dynamics of the bank vole and red voles in forests have turned to seasonal. The prevalent trend is the density increase in snow free season and decline in winter. The multi-annual pattern has disappeared. The rodent cycle has prevailed in northern Fennoscandia at least for decades. Therefore the change in cyclicity has been quite puzzling.

The large scale geographic synchrony broke down, and the dynamics of small agile species turned much more stable than earlier (e.g. *C. glareolus* and *C. rutilus*) while some earlier abundant large and competitively dominant species have become much less common, even rare (e.g. *C. rufocanus* and *M. agrestis*). Similarly, the least weasel *M. nivalis* has declines and the stoat *M. erminea* is more common, or at least dominating now. Since then this "Pallasjärvi syndrome" has occurred elsewhere in Lapland (Henttonen and Wallgren 2000) and in northern Sweden (Hansson 1999). Henttonen (1987) and Henttonen *et al.* (1987) suggested that the simultaneous long-term phase of low densities in *M. agrestis*, the favoured foor item of least weasels, resulted in poor reproduction in weasels, and the change in weasel abundance and dynamics caused the change in rodent dynamics. In other words, earlier cycles in the bank vole were not caused by bank voles themselves but were rather a side effect of *Microtus-Mustela* interaction. In a way, bank voles were alternative prey for weasels. Hanski and Henttonen (1996) and Oksanen and Henttonen (1996) have discussed the problem further. Models with a specialist predator and two competing prey species, the dominant of which is the preferred prey, yield patterns similar to those observed at Pallasjärvi (Hanski and Henttonen 1996).

The essence of this model is that in the present more stable situation, the predation by stoat in summer time is enough to prevent the increase of the preferred prey items, the larger and clumsier *Microtus*, *C. rufocanus* and also lemmings in the birch forest, while stoats are maintained in winter by smaller *Clethrionomys* (*C. glareolus* in taiga and *C. rutilus* in the birch forest). Predation by stoat keeps optimal prey low, below the threshold density needed for breeding of least weasels, and least weasels cannot increase. In proper cyclic times the least weasel dominated over stoats in abundance, especially in the late peak-decline phase (Viitala 1977, Henttonen *et al.* 1987). Now, during more stable rodent dynamics, stoats seem to dominate (Henttonen *et al.* 1987, unpubl., Oksanen *et al.* 1999). Our food addition experiments (Henttonen *et al.* 1987; Prévot-Julliard *et al.* 1999, Henttonen, unpubl.) show that in the present more stable situation, the impact of supplemental food on the densities of various rodent species depends on the susceptibility of the vole species to predation. In other words, supplemental feeding does not increase the densities of larger and clumsier species, which supposedly are heavily preyed by stoats in summer time, but it increases the densities of small agile species like *C. glareolus* and *C. rutilus*.

A core question is why the change has occurred. The model of Hanski and Henttonen (1996) shows that this kind of change in a system characterized by two competing prey species, which differ in their susceptibility to predation, and a shared predator, is fully possible due to inherent (chaotic?) properties of the system. The model predictions resemble very closely what has really happened e.g. at Pallasjärvi and Kilpisjärvi. A dynamic change from one state to another may happen suddenly, the new pattern can last for some decades, and the system can return to the old state again.

Hansson and Henttonen (1985a), and Hanski *et al.* (1991) related the gradient in Fennoscandian rodent cyclicity (increasing amplitude and cycle length to north) to the length of winter and snow depth. If something drastic had happened in the winter circumstances in the north, the resulting change in animal community structure could well have been reflected in the rodent dynamics, too, but there is no real evidence of such environmental change. The role of the introduced American mink has been mentioned (Oksanen and Henttonen 1996), but does not seem strong enough, especially in the long snowy winter as at Pallasjärvi. Hansson (1999) suggested that the change is due to the landscape change, especially the change in modern forestry. Briefly, the change in the age structure of boreal forests has resulted less food for forest rodents and also lower densities in open habitats in the increase phase. Earlier the dispersal by forest rodents

into open habitats in the early increase phase buffered predation on *Microtus* which gave them potential to increase. This was followed by increase of least weasel and subsequent crash, as described above. In the present situation, predation on *Microtus* is not buffered, weasels do not increase, and dynamics have changed to a different state.

The core conclusion of all of this is that the dynamics of any small mammal species should not be analysed out of its community context.

It remains to be seen how long this "exceptional" phase in Lapland will last. However, the change in dynamics have several consequences. First of all, the high spring densities characterising cyclic rodent peaks are now missing. The breeding of many predators and birds of prey depends crucially on the high peak spring densities of rodents. It is probable that the numbers of some birds of prey in Lapland have already declined. Another consequence of missing cyclic peak densities and subsequent heavy grazing pulses may be that the bottom and field layer on habitats favoured by voles and lemmings may change; species abundances may change if the most preferred plant species escape heavy grazing for long periods (see alsoVirtanen *et al.* 1997).

5. SOCIAL PATTERNS AND INTERSPECIFIC COMPETITION

At Pallasjärvi, the bank vole densities can vary from zero to about 50–60 individuals per hectare (Henttonen 1987, Henttonen *et al.* 1987, Prévot-Julliard *et al.* 1999). During the cyclic crash phases the snap trapping effort of 7000 trap night could produce only 5 animals (spring 1979), and during the deepest crashes (autumn 1979) the snap trapping based on permanent small quadrats (over 2000 trap nights) could have been without any catch. On the other hand, the highest densities of *Clethrionomys* (based on live trappings on the large grid) after snow melt in spring have been around 10 breeding voles/ha. Highest autumn densities have been found in cyclic increase phases and sometimes during the stable period, and have been around 50–60 *Clethrionomys*/ha. The bank vole is clearly the dominating species in the taiga forests at Pallasjärvi (Fig. 1, Henttonen 1997, Henttonen *et al.* 1987, Henttonen and Hanski 2000, Prévot-

Julliard *et al.* 1999), but there are always some *C. rutilus* amongst the bank voles. In some years also *C. rufocanus* has been quite common. Because breeding *Clethrionomys* females have exclusive territories also between the species, the dynamics of competitively dominant species *(C. rufocanus)* are reflected in the abundance of subordinate species. Notice, however, that these inverse competitive interactions take place in the course of increase and peak years; during the deep crash phases all species are around zero densities due to reasons related to cyclicity, not to interspecific competition.

The length of the breeding season of the bank vole varies considerably at Pallasjärvi. Males mature under snow in early April, 1.5 months before snow melt, and first litters are born in early June. The variation in timing of the first litter is about two weeks. In high density years young animals do not mature at all but in the early increase phase (like 1972) young females pregnant for the first time can be found in still October. Young born later in summer usually delay their maturation to the following spring. Based on the long-term live trappings on the large grid, winter survival of subadult females is clearly higher than survival of adult females (Prévot-Julliard *et al.* 1999). On the other hand, empirical values for the difference in survival were not consistent with survival values suggested by theoretical models if the delayed maturation was supposed to be optimal. Instead, our evidence suggests that delayed maturation is due to social constraints (Prévot-Julliard *et al.* 1999). There was a density-dependent relationship between maturation rate of young voles and the density of established breeding females. Furthermore, Yoccoz *et al.* (in press) found marked seasonal structure in direct density-dependence that was stronger in summer than in other seasons.

Communal nesting has often been suggested for bank voles in winter time, but our unpublished analyses of the space use by bank voles in winter time do not support aggregated distribution, i.e. communal nesting. On the other hand, there is some variation in the space use among winters, and furthermore, the winter distributions are often more aggregated on the food grid.

Our extensive field experiments (Jortikka 1990, Jortikka and Henttonen, unpubl.) showed that the abundance of *C. rutilus* is drastically limited by *C. glareolus*. When the bank voles were removed, the densities of red voles increased to the same level
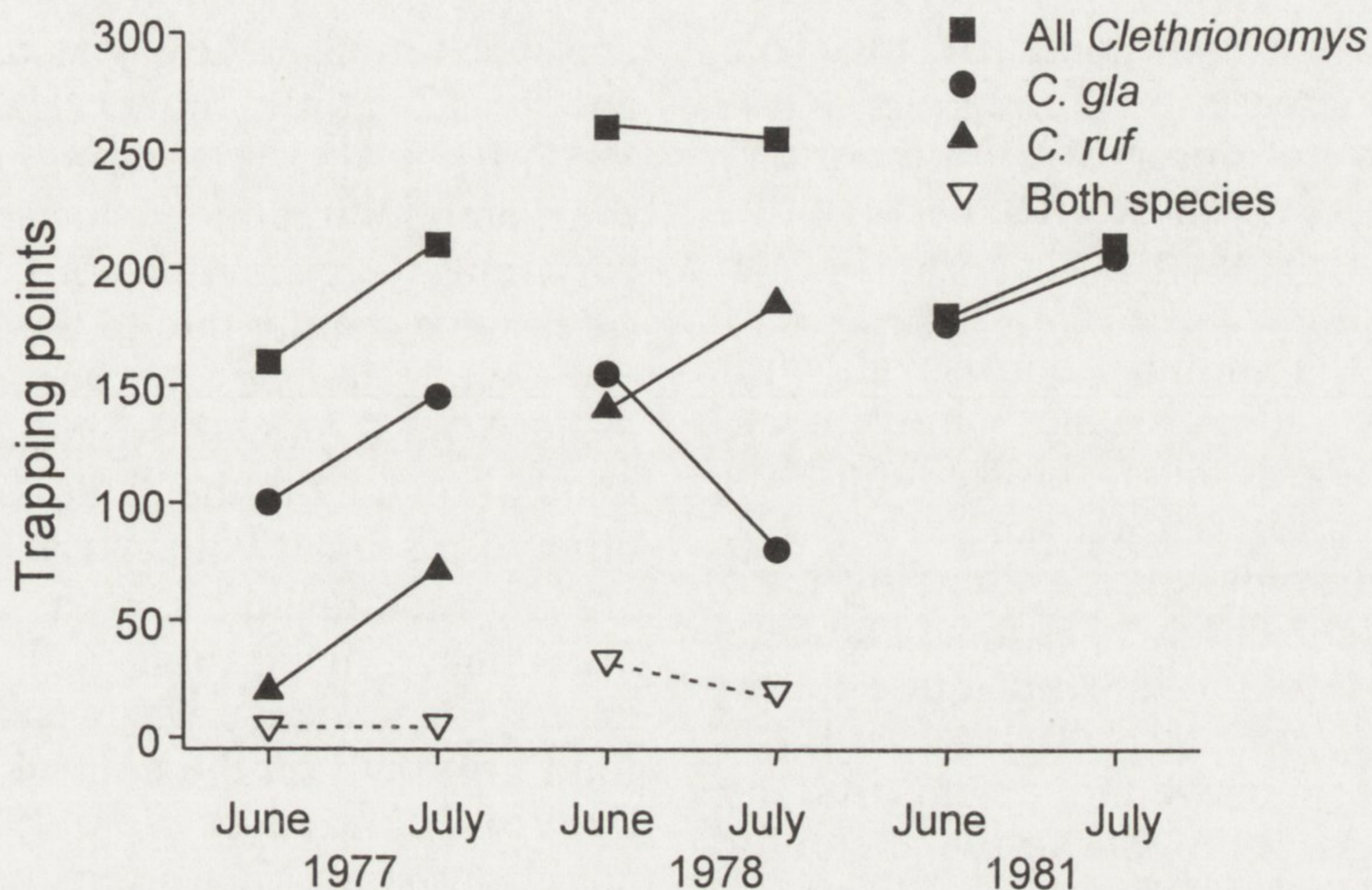
Fig. 2. Early summer space use, expressed as the number of trap stations inhabited, by breeding *Clethrionomys* at various species abundances. In 1981 *C. glareolus* was alone on the grid (4.5 ha), in 1977 *C. rufocanus* had low density and both species could still expand their space use. In 1978 during high density of *C. rufocanus*, the area occupied by *C. glareolus* declined while that by *C. rufocanus* expanded. See also the same years in Fig. 1

as those of bank voles in the controls or where red voles were removed. Removal of red voles did not have any significant effect on the bank vole abundance. Red voles are found only in old taiga forest at Pallasjärvi while bank voles are found on all habitats up to the tree limit of Norway spruce on the mountain slopes. The overlap zone of these two *Clethrionomys* species in western Lapland is 100–150 km. Red voles have been found on all permanent forest quadrats, but there seems to be a preference to drier habitats. Similarly, on the large grid the few red vole territories are usually found in the same, drier part of the grid. In winter time both the bank and red voles climb to trees to feed on lichens (*Usnea* and *Alectoria*). The stomach analyses show that e.g. in February the red voles rely almost exclusively on arboreal lichens whereas the bank voles have usually also some green material (*Vaccinium myrtillus* shoots) in the their stomachs.

The third *Clethrionomys*-species, the grey-sided vole is clearly larger and competitively dominant over the two smaller congenerics. Due to the territorial behaviour in breeding *Clethrionomys*, the occasional abundance of grey-sided voles in taiga forests reduces the space available for smaller species (Fig. 2). The number of trap stations on the large grid inhabited by breeding individuals of either species in early June and July is shown at different species abundances. In 1977 and 1981 the total area inhabited by

Clethrionomys was about the same, in 1978 it was somewhat higher. In 1981 total *Clethrionomys* was *C. glareolus* alone. In 1977 both species expanded their inhabited area from June to July, even though the number of trap station where both species were found, remained minimal. However, in 1978 with highest density of *C. rufocanus*, the area inhabited by *C. glareolus* drastically declined when that of *C. rufocanus* expanded. Simultaneously the overlap declined a bit. During low to moderate densities of *C. rufocanus*, its impact on *C. glareolus* is not drastic, but with the increasing density and space use of *C. rufocanus*, *C. glareolus* clearly loses ground. This can also be seen in those years when the grey-sided voles have increased towards the end of the peak like in 1978 and 1983 (Fig. 1), when the density of bank voles has declined already in the course of the peak year.

The Pallastunturi mountain group is the southernmost area in western Lapland where *Lemmus lemmus* is permanently found, and therefore *Lemmus* is a very interesting part of the local rodent fauna. It should be remembered that the dynamics of *Lemmus lemmus* differ drastically between south-central and northern Fennoscandia. Instead of the regular 3–4-year cycles found in the southern Norway, the pattern is much more irregular in Lapland (Henttonen and Kaikusalo 1993), where the lemming peaks coincide with those of voles, but there are not lemming peaks during every vole peak. In Fig. 1, the

others primarily refer to lemmings. Either lemmings totally miss some of the vole peaks, or the increase in lemmings is so minor that we do not observe it. Furthermore, lemming peaks occur more often in the northern mountain areas than further south in the boreal zone.

The great lemming outbreaks, with highly visible long-distance movements south into the boreal taiga, show a long-term pattern (Henttonen and Kaikusalo 1993). These great lemming years, extending even south of the Arctic Circle in Finnish Lapland, have occurred 1970, 1938 (not quite to the AC), 1902–03, 1872, 1840, 1810, 1787, 1755. After the intensive movements into the taiga, lemmings seem to survive there for some time. After the 1970 large-scale movements, local lemming peaks were again observed in many areas in Lapland in rhythm with the vole dynamics in 1974, 1978, and 1982. For example in forests and mires at Pallasjärvi, lemmings were found in 1974 and 1978. During the outbreak years, lemmings are the most abundant rodents in all habitats in northern taiga, like in 1970 at Pallasjärvi (Fig. 1) (Henttonen *et al.* 1987, Henttonen and Kaikusalo 1993), and have a strong impcat on other syntopic vole species, as well as on the vegetation (Kalela and Koponen 1971).

The periodic disappearance of lemmings from the taiga has been explained by at least three ways (Henttonen and Kaikusalo 1993):

1) winter food supply in taiga is not satisfactory to lemmings,

2) large and clumsy lemmings are more sensitive to predation than sympatric voles,

3) parasites (like *Babesia*) or pathogens occurring in other rodent species in the taiga could be harmful to lemmings.

In the second and third case, bank voles clearly have an advantage over lemmings through shared predators and/or parasites and pathogens. Our unpublished results both from Pallasjärvi and Kilpisjärvi suggest that lemmings are preferred by predators over smaller and agile voles of *C. glareolus/rutilus* type.

6. EXPERIMENTS WITH SUPPLEMENTAL FOOD

In the long-term experiment on the large control grid and large food grids, as well as in replicated experiments, the *Clethrionomys* densities were always higher on the food grids than on the controls. When oat seeds were used, the difference was 1.5–2 times, and when mouse chow was used, the difference was 2–3 times higher (Henttonen *et al.* 1987, Prévot-Julliard *et al.* 1999). However, on both treatments the seasonal density variations were simultaneous. Increased densities were mainly due to the higher number of breeding females per hectare on the food grids. Mouse chow also induced occasional winter breeding in the bank vole which is not otherwise seen at Pallasjärvi.

I mentioned earlier the density-dependent maturation of young. This density-dependency was weaker on the large food grid than on the control grid (Fig. 4 in Prévot-Julliard *et al.* 1999). More young could probably obtain territories at a given density level of breeding females, obviously because food addition allowed for smaller territories of breeding females. Even though food addition resulted in higher densities, its effect on the density-dependent structure was negligible. Moreover, stability analyses of the deduced model suggested that the dynamics were not affected by food addition. Variation in food resources is therefore probably not the cause for the multi-annual fluctuations in bank voles at Pallasjärvi (Yoccoz *et al.*, in press).

Finally, based on my experience at Pallasjärvi, I would seriously warn about the potential problems in live-trapping studies. It has been a common practice in many studies to prebait live traps, or use considerable amounts of bait food in the traps or in trap boxes. It is not known how much these practices affect the food-related density-dependent processes in vole populations. As shown by Prévot-Julliard *et al.* (1999), regulation of density-dependent maturation in the bank vole is clearly affected by additional food. In the first years of the food experiment on the large food grid, we used no more than 300 kg oat seeds per year on 2.8 ha, and the impact was clear. Rodents need only 2–3 grams of extra food per day to turn their energy balance positive, i.e. weight decrease turns to weight increase (my unpubl data). Because of our intensive trapping schedule, we use only 2–3 grams of bait in the trap on our control grids, and we do not throw the bait trash onto the field but collect them in a waste bag. It may be that most of the live-trapping studies in fact are unintentional experiments with supplemental food without controls.

7. PARASITOLOGICAL RESEARCH

Since the late 1970's intensive research on parasites of rodents and shrews has been going on at Pallasjärvi with Voitto Haukisalmi. This work was started by faunistical and taxonomical analyses (e.g. T e n o r a *et al.* 1983, 1985, H a u k i s a l m i and T e n o r a 1993), but one of the main purposes has been to monitor the long-term dynamics of vole helminths in their fluctuating host populations, primarily in the bank voles (e.g. H a u k i s a l m i *et al.* 1988, H a u k i s a l m i and H e n t t o n e n 2000). The change in the vole dynamics has introduced an additional interesting element into the parasite dynamics (H a u k i s a l m i and H e n t t o n e n 1993a, H a u k i s a l m i and H e n t t o n e n 2000). The interacting role of moisture and earlier host density seems to be the critical factors for helminth abundance (H a u k i s a l m i and H e n t t o n e n 1990). The role of rainfall is understandable because all the helminths have stages in their life cycle that have to survive outside of the host. We have not been able to demonstrate that helminths affect the population dynamics of rodents (H a u k i s a l m i and H e n t t o n e n 2000).

From the original work on long-term monitoring of the parasites dynamics in the bank vole and the possible impacts of parasites on rodents, the parasite research has expanded to analyze various other aspects in the population dynamics of helminths. These include interspecific relation of helminth species in a very restricted space, the intestine of the host (H a u k i s a l m i and H e n t t o n e n 1993b, c), and the general dynamic strategies of so-called common and rare (core and satellite) helminth species of bank voles (H e n t t o n e n and H a u k i s a l m i 1995, H a u k i s a l m i and H e n t t o n e n 1999). The last mentioned aspect has a strong connection to biodiversity problems: a great proportion of existing species are parasites, and therefore understanding of factors affecting the abundance and dynamics of parasites is of great importance.

8. CONCLUSIONS

So far, the material of Pallasjärvi rodent project has been used in more than 50 refereed publications as well as in a number of Finnish articles, congress abstracts and academic theses – altogether some 150 items. The close connection of the protected national park and the experimental forests of Finnish Forest Research Institute in near vicinity offers splendid opportunities for further long-term research. At Pallasjärvi, the two main expectations are in mind: when do the cycles return, and when is the next great lemming outbreak?

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