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Population dynamics of Clethrionomys and Peromyscus in southwestern Yukon 1973–1989

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Clethrionomys rutilus and *Peromyscus maniculatus* occur together in the boreal forest of southwestern Yukon and we studied their population dynamics on unmanipulated live-trapping grids for 17 yr. *Peromyscus* showed a regular seasonal change in numbers each year with little interannual variation. *Clethrionomys* by comparison, showed low density fluctuations during one period (1976–1982) followed by changes in number in the next period that are consistent with a typical 3–4 yr microtine cycle. During one of two years of peak numbers adult males had unusually heavy body weights. The sexual maturation of juvenile *Clethrionomys* varied inversely with density. In most years *Clethrionomys* showed higher rates of population increase from spring to late summer than *Peromyscus* and this may be partly attributed to the vole's longer breeding season. Juvenile female *Clethrionomys* often reached sexual maturity during their first summer when population density was low but *Peromyscus* never matured during their first summer. Finally, there was no correlation between the two species in year to year changes in overwinter survival rates. This is the first report of a cyclic Norh American population of *Clethrionomys* and it underlines the need to search for hypotheses of population regulation that explain both annual and multi-annual cycles within the same population.

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Introduction

Temporal changes in the size of animal populations are highly variable but show one common theme – no population is capable of unlimited increase. Microtine rodents may fluctuate in abundance in a regular cycle of 3–4 yr or they may show annual changes in numbers (Taitt and Krebs 1985). Some species of mice, on the other hand, like *Apodemus* spp. or *Peromyscus* spp., are noted for the constancy of their pattern of annual density changes, marred only by occasional irruptions in numbers (Terman 1966, Flowerdew 1985). These patterns of population changes invite comparisons; why should one species show such stability while another species fluctuates widely. In recent years a more complex question has emerged with the realization that some microtine populations can exhibit regular, annual changes in number intermixed with periods when numbers go through a 3–4 yr cycle. What mechanism of population regulation can reconcile both features?

There are geographical patterns in the population dynamics of several microtine species in Scandinavia and northern Europe. Populations of *Clethrionomys glareolus* in northern Fennoscandia show 3–4 yr cycles in abundance (Wiger 1979, Hansson and Henttonen 1985b) while populations in southern Sweden show annual changes (Hansson 1979). Investigation of this problem has taken two paths. Several elegant studies have used voles from northern and southern populations to test for differences in reproductive and behavioural characteristics (Gustafsson et al. 1983, Hansson 1986, Ebenhard 1987). These studies address the proxi-

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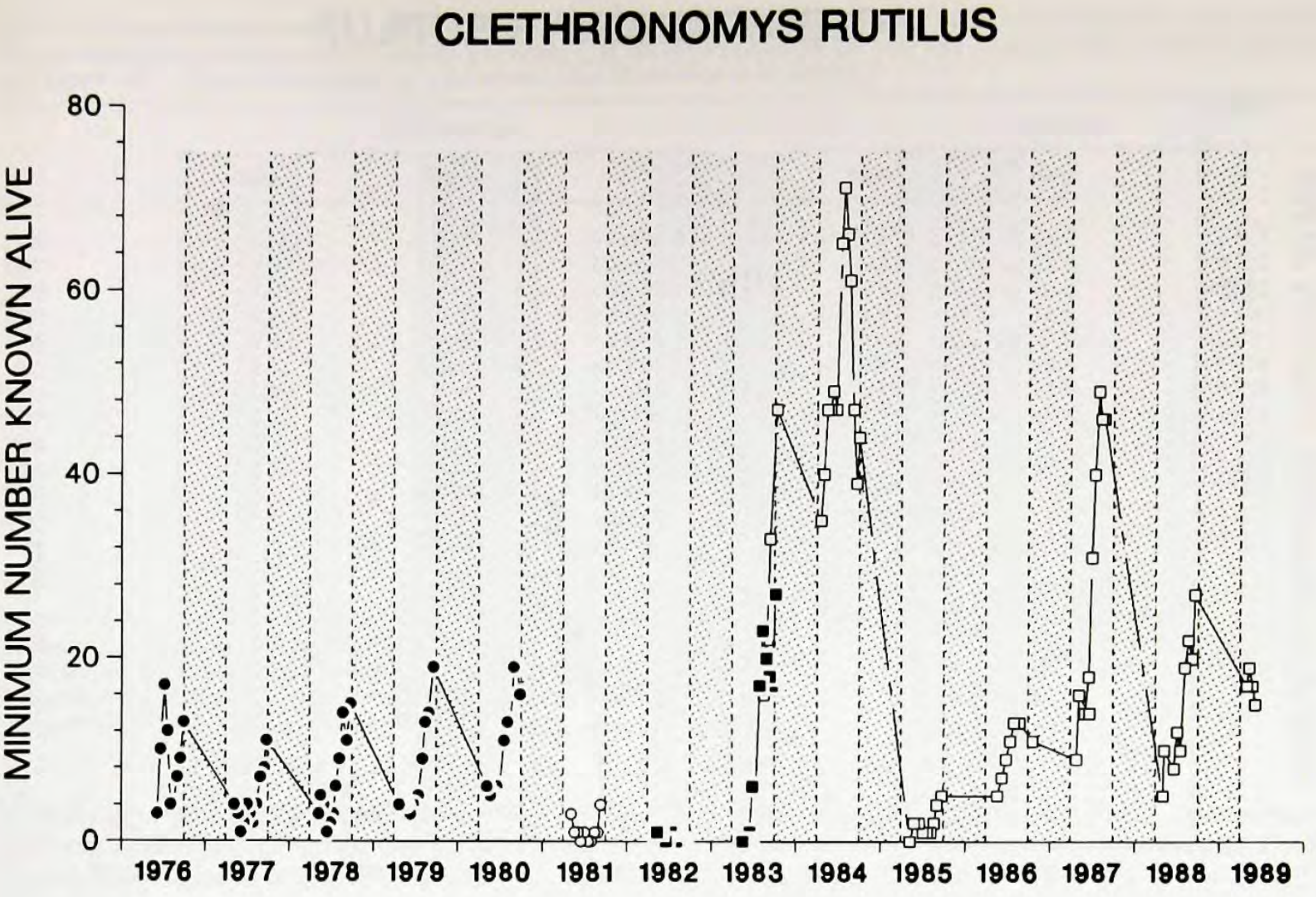
CLETHRIONOMYS RUTILUS



PEROMYSCUS MANICULATUS

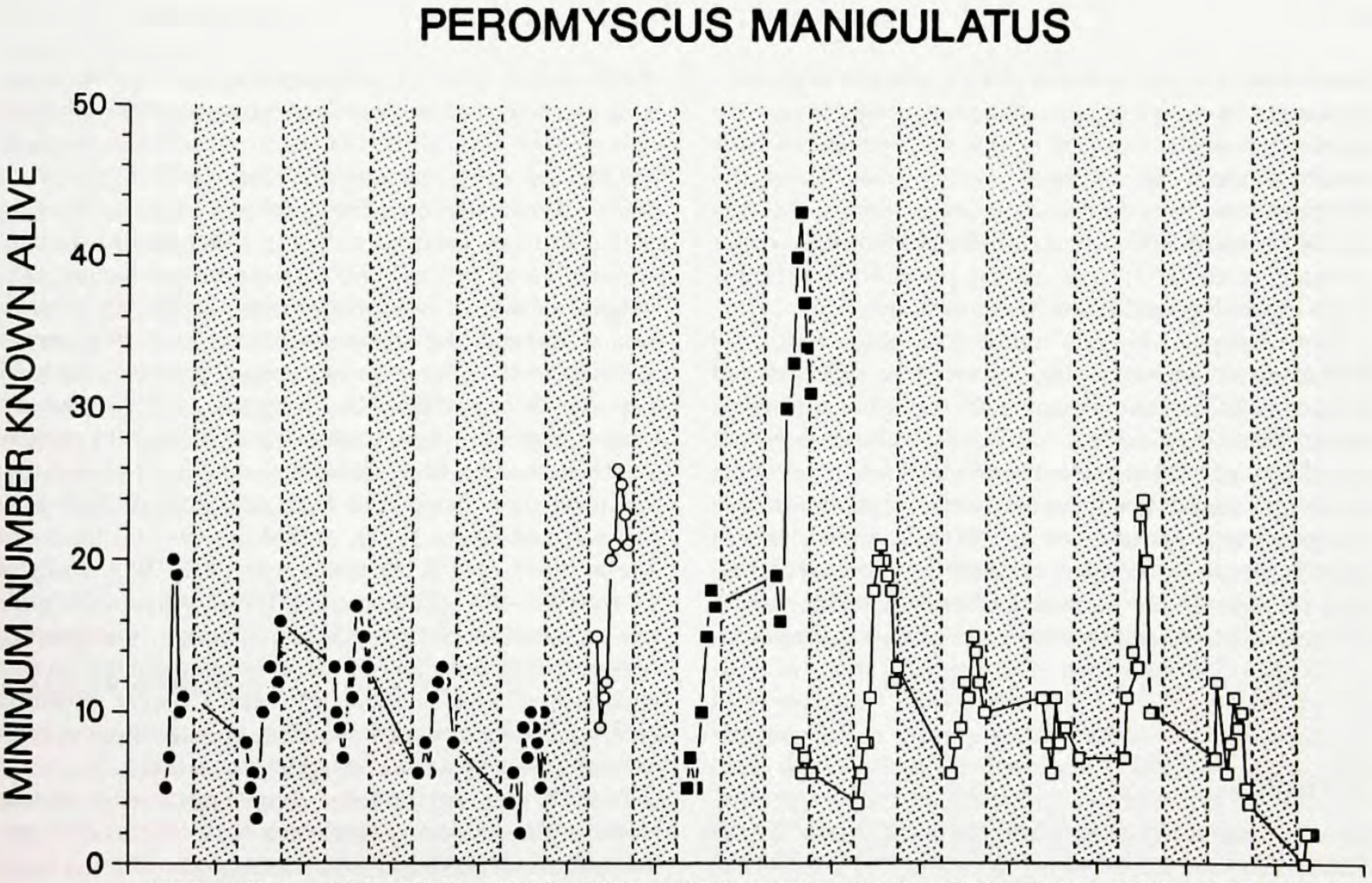


Fig. 1. Changes in minimum number alive on control grids, in forest habitats, for *C. rutilus* and *P. maniculatus*, sexes pooled. ● – grid I, ○ – grid H, ■ – grid X, and □ – grid C1.

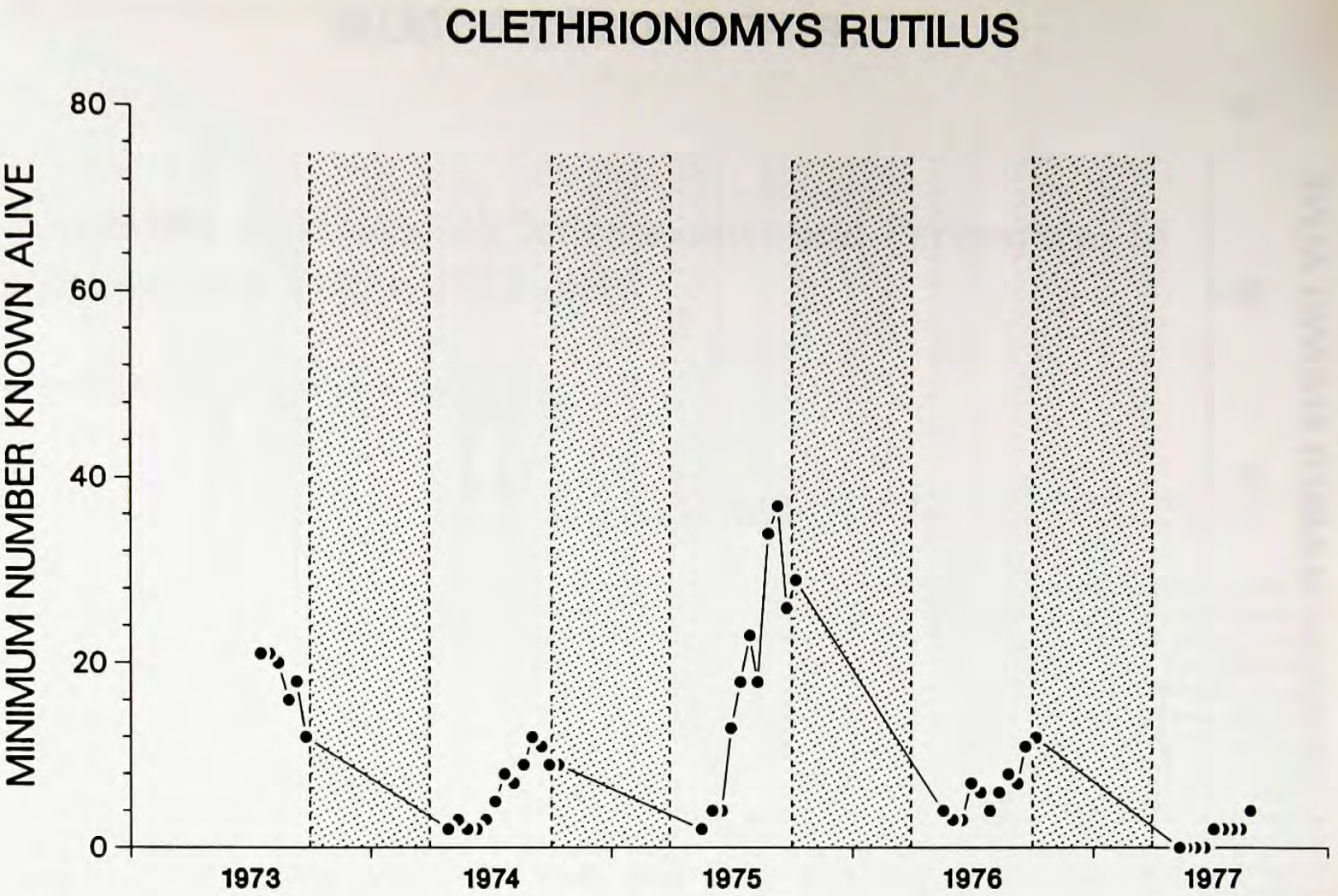


Fig. 2. Changes in minimum number alive on control grid D, open willow habitat for *C. rutilus* only, sexes pooled.

mate reasons for differences observed in the population dynamics of northern and southern populations. The other approach has sought to explain the differences by finding underlying differences in extrinsic factors between the two regions such as plant productivity (Laine and Henttonen 1983), predation by generalist predators (Erlinge et al. 1983) or predation pressure modified by snow cover (Hansson and Henttonen 1985a).

In this paper we examine the long term population dynamics of two coexisting rodents, the northern red-backed vole, *Clethrionomys rutilus* and the deer mouse, *Peromyscus maniculatus*. We adopt a comparative demography approach (Grant 1976) and ask what differences and similarities these sympatric populations have. *Clethrionomys* populations in North America, by most reports, do no show 3–4 yr cycles (Hansson and Henttonen 1985a) and our second goal is to describe how *C. rutilus* populations in southwestern Yukon compare.

Methods

Small mammal live-trapping began in 1973 near Kluane Lake, southwestern Yukon Territory (61°N, 138°W). All live-trapping plots (except grid X) were 10 × 10 checkerboard grids (2.3 ha) with 15.2 m between stations and a single Longworth live-trap at each of the 100 stations. We trapped in two different habitats. Grid D was located in an open willow habitat with little spruce cover (*Picea glauca*) and was subject to some flooding during May of each year during snow melt. Trapping began here in July of 1973 and continued during each snow-free season until September 1977. We include data collected for *Clethrionomys* only from this area as we caught few *Peromyscus* during the five years of trapping in this habitat. Our remaining data come from control populations located in forest habitat 3 km away where we caught both *Clethrionomys* and *Peromyscus*. We used data from grid I for the period 1976–1980 (Gilbert and Krebs 1981), grid H for 1981 (Gilbert and Krebs 1984), grid X for the period 1982–1983, and grid C1 for 1983–1989 (Gilbert et al. 1986). All of these grids were located in the same block of forest; the distance between different pairs of grids varied from 400 m to a maximum of 1100 m. Grids H, I and C1 were in similar habitat; a spruce-moss forest that had an understory of willows (*Salix* spp.) and *Shepherdia canadensis*.

Grid X was an irregular shaped grid with 50 trap stations placed along a dry creek bed – forest ecotone. We will avoid making comparisons of *Peromyscus* numbers on grid X with numbers on other grids because this

Tab. 1. Average minimum number alive of *C. rutilus* and *P. maniculatus* during May and August in forest habitat. Sexes pooled. The instantaneous rate of population change per week, r, is calculated based on the May and August density estimates (Alibhai and Gipps 1985). The cyclicity index, s, is calculated after Henttonen et al. (1985).

	Clethrionomys			*Peromyscus*		
	May[1]	Aug[2]	r	May[1]	Aug[2]	r
1976	5.5[3]	8.0	+0.038	8.5[3]	11.0	+0.026
1977	3.5	7.5	+0.048	6.5	11.5	+0.036
1978	4.0	12.5	+0.074	11.5	16.0	+0.021
1979	4.0	16.5	+0.086	7.0	10.0	+0.022
1980	5.5	19.0	+0.073	5.0	7.5	+0.024
1981	2.0	2.5	+0.014	12.0	22.0	+0.038
1982	1.0	0.0[4]	−0.083	6.0	17.5	+0.074
1983	0.0[4]	19.0	+0.296	17.5	40.0	+0.059
1984	47.0	54.0	+0.009	7.3	18.5	+0.062
1985	1.0	3.0	+0.076	7.0	13.0	+0.043
1986	5.0	13.0	+0.068	11.0	9.0	−0.014
1987	15.0	46.0	+0.075	12.0	8.0	−0.027
1988	7.5	21.0	+0.064	9.5	7.5	−0.015
1989	17.7			1.3		
	s = 0.57	s = 0.60		s = 0.15	s = 0.21	

1. Mean density of overwintered animals, 1 May – 3 June.
2. Mean density of adults and juveniles, 20 Aug. – 18 Sept.
3. Spring density is based a June sample when trapping began.
4. Assumed to be 0.3 for calculation purposes.

ecotonal area produced higher catches of *Peromyscus* than we recorded in other areas. Our decision to use the *Clethrionomys* data from grid X is based on an analysis of 13 trapping periods over 1983 and 1984 when we trapped both grids X and C1. There was a significant correlation between numbers on these two grids (Spearman $r_s = 0.66$, $p < 0.05$). In calculations of overwinter survival and spring weights we also included data from other populations during periods when they were unmanipulated.

We tried to conduct trapping at two week intervals during the snow free season from 1 May to 30 September and averaged 10 trapping sessions per year. Trapping frequency was lowest in 1986 and 1982 (six and seven trapping sessions respectively). Males with scrotal testes were defined as mature, while mature females had a perforate vagina (an indication of estrous) or showed signs of pregnancy or lactation. We used the weight of animals as an index to age and classified new animals < 21 g as juveniles for *Clethrionomys* and juvenile *Peromyscus* as animals < 20 g.

Results

Changes in number

The pattern of changes in numbers of *Clethrionomys* on forested grids (Fig. 1) has two notable features. First numbers were low each summer from 1976 to 1982. Secondly there were two fluctuations in numbers from 1983 to 1989 with peak numbers in 1983–84 and again in 1987. In Fig. 2 we extend our time series for *Clethrionomys* back to 1973, although this makes comparisons across two different habitats. Numbers on grid D, in open willow habitat, show a more drastic low in 1977 compared with the forest grid the same year (Fig. 1); there was a year of high numbers in 1975, and the partial trapping results for the 1973 season do not reveal if this was another peak year.

In summary the strongest support for a *Clethrionomys* cycle comes from the forested grid with peaks in 1983–84 and in 1987. Secondly, the data do not support our previous conclusion (Gilbert et al. 1986) that *Clethrionomys* peaks occur at 9–11 yr intervals; the three years of highest numbers occurred in 1975, 1984 and 1987.

Clethrionomys exhibited large fluctuations in numbers during the study compared with *Peromyscus* (Fig. 1). The density of breeding adult *Clethrionomys* in May ranged from 1 to 47 animals per grid (Tab. 1), while *Peromyscus* numbers varied from 1 to 12 animals per grid. We looked for possible correlations in May or August densities between species and found no significant relationship. The rate of population change (r) was different between the two species over the May to August interval. *Peromyscus* tended to show lower rates of population increase each season (mean $r = 0.027$ wk^{-1}, $n = 13$, S.D. $= 0.031$) compared with *Clethrionomys* (mean $r = 0.064$ wk^{-1}, $n = 13$, S.D. $= 0.083$). Thus *Clethrionomys* usually realized more population growth each season than *Peromyscus*. *Clethrionomys* in 1984 was an important exception. Population growth that season was $< 1\%$ wk^{-1}; the already dense population in May failed to increase appreciably by late August.

Were the population fluctuations related to the initial

Tab. 2. Female *Clethrionomys* reproduction during 1976–1988. The number of females estimated to have had a litter is sorted by age: adult mothers and young of the year mothers (juv).

	Total No. litters	No. adult	No. juv	Number of recruits
1976	2	2	0	31
1977	0	0	0	12
1978	1	1	0[1]	31
1979	2	1	0	18
1980	3[2]	1	2	26
1981	0	0	0	3
1982	0	0	0	1
1983	12	4	5	33
1984	44	19	0	125
1985	0	0	0	5
1986	8	3	1	24
1987	21[3]	6	4	73
1988	2	1	1	36

1. One female present for one trapping session only.
2. Litter of one adult died at birth in trap.
3. Litters of two adults both died at birth in trap.

Tab. 3. Female *Peromyscus* reproduction during 1976–1988. No young of the year female was scored as having litter during its first number season.

	Total No. litters	No. females	Number of recruits
1976	9	5	20
1977	2	2	22
1978	6	4	23
1979	6	4	22
1980	4	3	20
1981	9	7	23
1982	7	4	18
1983	11	5	23
1984	11	6	18
1985	9	4	21
1086	6	4	11
1987	12	7	19
1988	7	4	11

spring density of adults; i.e., did population growth show some density dependent relationship with spring numbers? The correlation between May numbers and the rate of population change (r) was negative but not significant for either *Clethrionomys* ($r_s = -0.25$, df = 9, $p > 0.05$) or *Peromyscus* ($r_s = -0.42$, df = 9, $p > 0.05$).

We calculated a cyclicity index, s, the standard deviation of the density estimates after they have been converted to logarithms (Stenseth and Framstad 1980, Henttonen et al. 1985). The low values of s for *Peromyscus* (0.26 and 0.21), is based on May and August densities (including data from grid X) and reflects the regular pattern of annual changes in number. The cyclicity index calculated for *Clethrionomys*, from 1976 to 1989, was 0.56 and 0.60 and this indicates a moderately high degree of cyclicity.

Reproduction

Three aspects of reproduction are considered here: i) female breeding success, ii) the breeding activity of young of the year, and iii) length of the female breeding season. We used mark-recapture data to estimate the number of litters each female had in a season and then summed these numbers for the entire grid. We also tallied the number of new juveniles that appeared in traps over the season. Both of these estimates include some uncertainty. We must assume for this analysis that our estimates of the number of litters born on the grid are accurate (e.g. no females are missed entirely) and that juveniles that appear in traps were actually born on that grid and were not immigrants.

For *Clethrionomys* there was great variation in the number of breeding females (range 0 to 19, Tab. 2). A similar amount of variability shows up in the estimates of the number of recruits. In some years, even though no females were thought to have had litters on the grid, there were juveniles recorded on the study area. Many of these juveniles must be immigrants because it is unlikely that, in 1978 for example, we could have missed the 5 to 10 litters necessary to give rise to 31 recruits (assuming a litter size of 6.25, Krebs and Wingate 1985).

Juvenile female *C. rutilus* contributed significantly to the breeding success of the population as a whole in some years. In 1980 and 1983 juveniles were responsible for 66% and 50% of the number of litters estimated to have been born in the study population. In contrast during years of high densities, juveniles were responsible for few of the litters, 0% in 1984 and 19% in 1987.

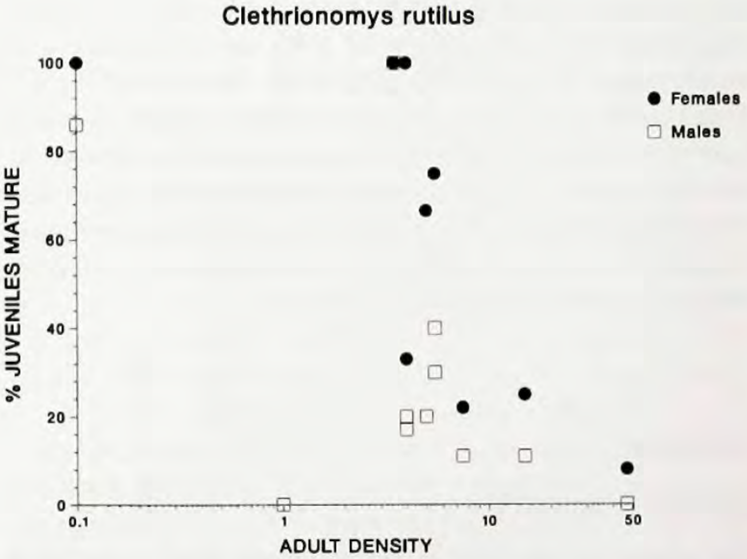


Fig. 3. Percentage of young of the year voles reaching sexual maturity during their first season plotted against May density of overwintered animals. Only juvenile voles weighing > 10 g, and appearing in traps before 10 August of each year are considered. As juveniles often fail to mature later in August this analysis should reveal maximum rate of sexual maturation.

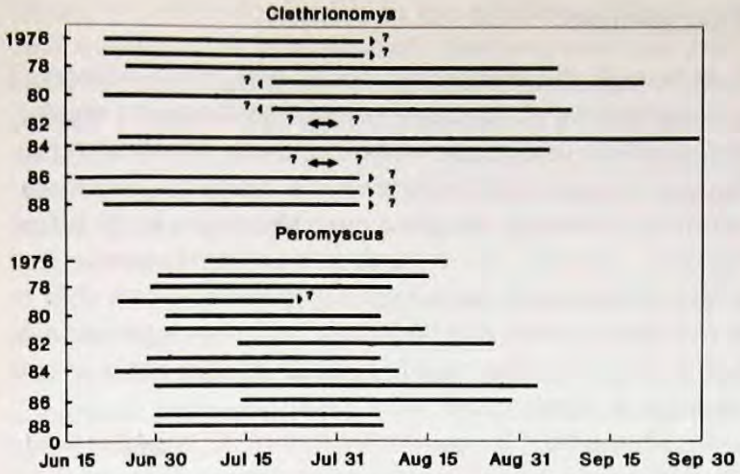


Fig. 4. Approximate time limits of breeding season for *C. rutilus* and *P. maniculatus* based on i) date and weight of juveniles first caught in traps and ii) the date on which the last female was lactating. Insufficient data are available for *C. rutilus* in 1983 and 1985. Only partial data available for some seasons (question mark).

Peromyscus exhibited much less year to year variation in female reproduction (Tab. 3). Each year an average of four to five females had litters on the study area and in most years c. 20 recruits joined the trappable *Peromyscus* population. In contrast to *Clethrionomys* we never recorded a juvenile female having a litter in its first summer of life.

In *Clethrionomys* the percentage of sexually mature juveniles varied inversely with density (Fig. 3). In the year with highest May numbers (1984) few juveniles matured while in years with low spring numbers maturation rates were higher. Those female juveniles that did become pregnant usually had a single litter during their first summer; only during a year of population increase (1983) did we estimate that juveniles were able to have two litters.

Clethrionomys females bred for six to eight weeks longer than *Peromyscus* females (Fig. 4). *Clethrionomys* juveniles usually appeared in traps about mid-June, c. two weeks before *Peromyscus* young appeared. Female *Peromyscus* usually finished lactating during the first two weeks of August although the season appeared to end earlier in 1983 and 1987, and later in 1982 and 1985. It is difficult to make generalizations about the end of the *Clethrionomys* breeding season as sample sizes were small in many years. In most years voles continued breeding several weeks longer into autumn than *Peromyscus*. There is one final point of interest in the *Clethrionomys* data. In 1984, a high density year, the female breeding season ended by early September, while in 1983, a year of massive population increase, lactating females were recorded until the end of September.

In summary, several differences in reproduction between the two species are evident. *Peromyscus* had a comparatively short breeding season, young of the year never participated in breeding during their first season and year to year recruitment seemed relatively constant. In *Clethrionomys* the breeding season was six to eight weeks longer and juveniles of both sexes sometimes bred in their first season; the frequency of sexual maturation of juveniles was inversely related to population density.

Overwinter survival

Survival of individuals from September to May has critical consequences for population size as breeding activity stops in winter. Rodent populations in our study area endure the major part of the year in a winter environment – plant production has ceased and snow cover persists for seven months. Since winters vary in severity, we may expect good and bad winters to fall on both rodent species simultaneously. This was not the case. No significant correlation was found between winter survival of the two species ($r_s = 0.16$, df = 10, $p > 0.05$, Tab. 4).

Peromyscus showed relatively constant overwinter survival rates with the winter of 1979–1980 and 1988–1989 being exceptionally low. *Clethrionomys* showed greater variation as revealed in the higher coefficient of variation (Tab. 4). Survival rates of *Clethrionomys* from 1983 to 1987 changed with the stage of population growth. During a winter following increasing numbers (1983–1984), autumn density was 40.0, and overwinter survival was high (64%). In the autumn of the peak year (1984–1985), although density was similar (41.5), overwinter survival was much poorer (0%). Survival then improved during the next two years of low and increasing populations (1985–1987).

We looked for a relationship between overwinter survival and the number of animals the next spring. There

Tab. 4. Overwinter survival of *Clethrionomys* and *Peromyscus*, sexes pooled, standardized to an 8-month period. These estimates are minimum survival rates. Animals were tagged and released during the last two trapping sessions in autumn (September) and recaptured in the spring of the next year. Sample size of number released in autumn in brackets. C.V. = coefficient of variation.

	Clethrionomys	*Peromyscus*
1976–77	0.07 (14)	0.44 (9)
1977–78	0.33 (12)	0.21 (14)
1978–79	0.05 (18)	0.26 (15)
1979–80	0.15 (15)	0.08 (15)
1980–81	0.00 (21)	0.34 (12)
1981–82	0.00 (4)	0.28 (20)
1982–83[1]	– (0)	0.54 (16)
1983–84	0.64 (50)	0.52 (9)
1984–85	0.00 (49)	0.34 (22)
1985–86	1.0 (4)	0.51 (32)
1986–87	0.46 (15)	0.66 (9)
1987–88[1]	0.09 (46)	0.16 (8)
1988–89	0.59 (26)	0.00 (7)
	C.V. 1.15	C.V. 0.58

[1] Animals released in only one autumn trapping session.

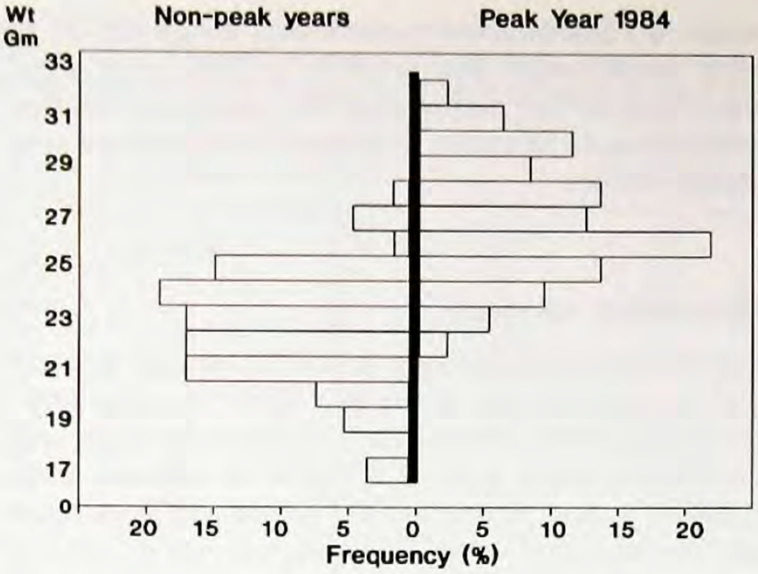


Fig. 5. Frequency distribution of spring body weights of overwintered male *Clethrionomys* for the peak year of 1984 (n = 67) versus all other years except 1987 (n = 76). There was no significant effect of weight in 1987 (peak year).

was a correlation for *Clethrionomys* ($r_s = 0.76$, df = 9, $p < 0.05$) but not for *Peromyscus* ($r_s = 0.44$, df = 10, $p > 0.05$).

Spring body weights

Next we consider the weights of individuals during May of each year and ask two questions, first, is there any year to year pattern in changes in weight? Second, is there any evidence that *Clethrionomys* are heavier in years of high density than during years of low numbers?

We carried out a one-way analysis of variance on the weights of males caught in May of each year (1976–1989), although we had to drop three years from the analysis (1981–1983) because of small sample sizes. *Clethrionomys* weights differed between years ($F_{10,143} = 17.1$, $p < 0.0001$) and a Tukey test indicated that males, in 1984 only, differed from males in all other years except 1978, 1987 and 1988. Fig. 5 illustrates the increased body size of males in 1984 (Gilbert 1987).

A similar analysis of *Peromyscus* males for the years 1977 to 1988 revealed significant differences between years ($F_{11,102} = 4.1$, $p < 0.001$). Males in the spring of 1983 (mean weight of 28.0 g) were heavier than males in other years except 1977, 1979, 1981, 1982 and 1986. We detected no other significant differences and our main conclusion is that the year of heaviest individuals varied between species: 1984 for *Clethrionomys* and 1983 for *Peromyscus*.

Discussion

In this study the demography of *P. maniculatus* diverged strikingly from *C. rutilus*. *Peromyscus* showed a regular, annual cycle in numbers with relatively constant reproductive output each year and less variable overwinter survival. Young of the year never matured in their first summer season. In comparison *Clethrionomys* had wider fluctuations in numbers, juveniles were able to breed during their first summer and overwinter survival had a more significant role in determining the numbers of voles in May.

In Manitoba, *P. maniculatus* and *C. gapperi* were studied over a 14 yr period and spring numbers of these species were positively correlated (Vickery et al. 1989). We failed to find such a relationship in our study. Our demographic analysis does show differences in rates of population increase. *Clethrionomys*' superior rate of population change (r, Tab. 1) may stem from two causes. *Clethrionomys* has a greater capacity for population growth than *Peromyscus* due to its longer breeding season and the occasional reproductive contribution of juvenile females. The other possibility is that behavioural interactions may limit the population increase of *Peromyscus* but not that of low density *Clethrionomys* populations.

We turn now to consider each species separately. Our working hypothesis (Gilbert et al. 1986) in following *Clethrionomys* populations was that periodic irruptions would be linked to the 10-yr cycle of snowshoe hares *Lepus americanus*, either by a predation, or plant productivity interaction (see also Hansson and Henttonen 1985a). The additional time series data provided in this study seem to refute a simple connection between *Clethrionomys* irruptions and predation that is driven by the snowshoe hare cycle. Peak vole numbers occurred in 1975, 1984 and 1987 (Figs 1 and 2) yet our original prediction was that the 1984 peak would be followed by a high in 1983 or 1984. We now discard the hypothesis that there is a simple interaction between the snowshoe hare cycle and *Clethrionomys* peaks.

Our live-trapping results on grid D (Fig. 2) began mid-way through the summer of 1973 and we were unable to indicate if this was another peak year. Population indices, based on snap-trap results from this region, suggest that numbers of *Clethrionomys* in 1973 were as high or even higher than in 1975 (Krebs and Wingate 1985). In summary there appear to have been four years of high numbers: 1973, 1975, 1984 and 1987. We still reject the suggestion that peaks occur at 9–11 yr intervals.

There is little support in the literature for the idea that North America *Clethrionomys* populations are cyclic. Studies in Alaska by Whitney (1976) and Whitney and Feist (1984) both showed that *Clethrionomys rutilus* lacked a 3–4 yr cycle in numbers. West (1982) reached the same conclusion after five years of live-trapping in a forest habitat in the same region. Fuller (1985) provided details of a five year study in the Northwest Territories that looked at the dynamics of *Clethrionomys* and *Peromyscus* populations. He concluded that neither *C. rutilus* nor *C. gapperi* showed a multi-annual cycle because of a low index of cyclicity ($s = 0.35$ for both May and August numbers of *C. rutilus*) and because *C. gapperi* males in the spring failed to show signs of the Chitty effect in body size or weight.

Our *C. rutilus* data are suggestive. Numbers rise and fall between 1982 and 1987 in a typical 3–4 yr cycle. The Chitty effect in 1984 is striking and the reproductive inhibition associated with high densities is also present (Figs 3 and 5). The cyclicity value of 0.57 and 0.60 for May and August numbers between 1976 and 1989 is also well within the range of values reported for cyclic populations in Europe (Henttonen et al. 1985). We are unable to explain why large bodied individuals were absent during the 1987 high and further, why there was no obvious decline after that peak year. At best this vole population may be judged to display both annual cycles in numbers (1976–1982) as well as a multi-annual cycle. Several alternative explanations are possible.

Hestbeck (1987) has proposed a tripartite model of population regulation for small mammals that predicts populations may be held near a low density equilibrium by predation until a "transition state occurs", e.g. predation pressure is relaxed. At intermediate vole densities, the model predicts that emigration is responsible for population regulation while at high densities, resource depletion slows population growth. At first glance our results for *Clethrionomys* seem consistent with the Hestbeck model – densities fluctuate at low numbers with poor overwinter survival from 1976 to 1982. There are, however, two incongruities. If predators, tracking the snowshoe hare population, are keeping *Clethrionomys* numbers low then how can one explain our observations. Vole numbers reached high density in 1987 when the snowshoe hare cycle was at an early increase phase and hare predators were nearly absent, yet voles failed to show any increase during the same period of the last snowshoe hare cycle (1976–1978). In both of these periods there were low numbers of snowshoe hares and their attendant predators yet vole populations behaved differently in each period.

If predation limits low density rodent populations, as predicted by Hestbeck's model, then providing extra food should have little effect on numbers. Experimental evidence from this population goes against the prediction (Gilbert and Krebs 1981). Supplemental food did cause numbers to at least double in 1978 and 1979, however adult survival rates were unchanged and this could be interpreted as a consequence of predation and support for Hestbeck's prediction.

Our *Clethrionomys* populations showed periods of both annual and multiannual cycles (Fig. 1). These results are similar to some *Microtus* populations that have been reported to intermix periods of annual and multiannual cycles at the same site over time (Taitt and Krebs 1985). In central Europe *C. glareolus* display small annual fluctuations with occasional population outbreaks following years of large seed production (Jensen 1982). We know from supplemental feeding experiments that *C. rutilus* are food-limited and suspect that the 1984 Yukon peak, at least, was preceded by a high spruce cone crop. Do our *Clethrionomys* populations follow the northern Scandinavian model of repeated multiannual cycles or the southern Scandinavian-central Europe pattern of annual cycles with occasional outbreaks following good mast years? We may be able to answer this question in the future by comparing local *Clethrionomys* populations from two different habitats: boreal forest and alpine tundra. If abundant spruce cone crop production is the key to *Clethrionomys* irruptions than we should see large differences in density between these habitats.

Bondrup-Nielsen and Ims (1988) present an hypothesis that predicts whether *Clethrionomys* populations will display stable or cyclic changes in number. They argue that the key to predicting whether a *Clethrionomys* population will reach a cyclic peak is assessing how much of the space available to the population is filled with occupied territories. Stable *Clethrionomys* populations, according to their hypothesis, will occur in areas where habitat heterogeneity prevents the population from reaching saturation. *Clethrionomys* in homogeneous habitats will be more likely to establish territories in all areas and thus the population will be poised to reach high densities – the antecedent of a population cycle.

Our data set challenges the hypothesis of Bondrup-Nielsen and Ims (1988). As we interpret their prediction our population must have been experiencing habitat changes over time to account for the transition between stable, annual cycles (1976–1982) and multiannual cycles (1983–1989). Is it reasonable to predict that the habitat on our study area changed sufficiently to support their hypothesis? The answer may be yes if one considers the overall impact that cyclic populations of snowshoe hares have on the boreal forest. We have difficulty in evaluating the Bondrup-Nielsen and Ims hypothesis further because of confusion with the definition of the terms "homogeneous" and "heterogeneous" habitat. They define habitat in terms of a population's response in a certain habitat (r, the intrinsic rate of population growth); thus the smallest unit of habitat that can be described must be the area that would permit measuring the population parameter, r. The authors are silent on the question of how to distinguish between homogeneous and heterogeneous habitat when the habitat varies on a fine scale (e.g. habitat patches smaller than the area needed to measure the rate of population growth, r).

Most microtine populations that exhibit multiannual cycles, show predictable changes in mean body weight – animals from peak populations are up to 30% heavier than animals from low or decreasing populations (Boonstra and Krebs 1979, Taitt and Krebs 1985). The association we found between size and density of *Clethrionomys* was not straight forward. Although the Chitty effect, the presence of these large-sized individuals, was clear in 1984 there was no obvious change in size in 1987. The link between body size and high density has been reported for several species of *Clethrionomys: C. glareolus* (Wiger 1979), *C. rufocanus* (Kalela 1957, Andersson and Jonasson 1986) and *C. rutilus* (Koshkina and Korotkov 1975). The underlying reason(s) why large-sized animals are associated with peak populations is unknown. A partial explanation comes from experimental results with *Microtus*; body mass increases after supplemental food is provided (Taitt and Krebs 1983). Thus the large-sized *Clethrionomys*, present in the spring of peak numbers in 1984, may be explained as a response to abundant natural food. It may be difficult to explain why *Peromyscus,* that shared the same habitat, did not also respond to the presumed food abundance by increasing in body weight. Our unusual results in 1987 are similar to those reported by Chernyavskii and Korolenko (1979), who described a cyclic population of *C. rutilus* from northeastern Siberia, with little variation in the weights of males caught each spring.

The correlation between overwinter survival of *Clethrionomys* and numbers in spring points the way to future experiments. At most densities this species shows strong population growth during summer and it is difficult to draw up realistic hypotheses to explain how the breeding population could do better. Winter survival shows great variation between years and is the key factor causing population changes. One explanation is food shortage therefore supplemental feeding experiments during the winter may resolve this question (S. Schweiger pers. comm.).

The population increase of *Peromyscus,* during the breeding season, may be limited by the aggression of adult males towards both juveniles and other males (Petticrew and Sadleir 1974), or by female aggression towards unrelated juveniles (Halpin 1981). In *Apodemus sylvaticus* numbers remain stable during the breeding season and then show a rise in numbers at the end of the breeding season (Flowerdew 1985). At least two factors are implicated – an increase in food supply and a reduction in the effects of adult male aggression (Flowerdew 1974). Future field manipulations that altered these variables (adult aggressiveness and late summer food supply) may show what limits Yukon populations of *Peromyscus.*

Wolff (1985) questioned the notion that all *Peromyscus* populations are stable. *P. maniculatus,* in our study area, are within a few hundred kilometers of their northern distributional limit, so their relative year to year stability seems more remarkable. However the last two years have been exceptionally poor for them in our study area. We have recorded the lowest juvenile recruitment, overwinter survival and spring densities since we began live-trapping in 1976. We recognize the importance of ongoing work to monitor these changes in the long term.

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