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Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus* in northern Canada

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Data from more than 145 000 snap-trap-nights in the summers of 1969 to 1979, and a capture-mark-release study on two grids with areas of about 6 ha in the summers of 1975 to 1979 are analysed for a population of *Clethrionomys gapperi*, a sympatric population of *Peromyscus maniculatus*, a parapatric population of *C. rutilus*, and an allopatric population of *P. maniculatus*. Mean annual relative numbers (catch per 100 trap-nights) are positively correlated in all six pair-wise comparisons; mean August relative numbers in four of six comparisons; and mean May relative numbers in two of six comparisons. Instantaneous daily rates of increase (all years lumped) were identical for three of four populations ($r = 0.007$). Minimum numbers alive on grids paralleled mean relative numbers in a general way, but not in detail.

Population densities on islands in the Mackenzie River were consistently higher than those on adjacent mainland.

Similarity of spring numbers, both intra- and interspecifically, suggests that spring numbers are a function of a more or less constant winter (=subnivean) carrying capacity.

Fluctuation indices (s) ranged from 0.26 to 0.35 in *Clethrionomys* spp., and from 0.14 to 0.26 in *P. maniculatus*; therefore it is concluded that none of the populations is cyclic.

Frequent, positive correlations among numbers of all populations, especially between heterogeneric but sympatric species pairs, suggests that all populations were responding to a common factor, or factors.

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1. Introduction

Long term studies of *Clethrionomys* populations in North America are rare and confined to mid latitudes: Gunderson (1962), Grant (1976), Iverson & Turner (1972) and Mihok et al. (1985) studied *C. gapperi*. I know of no other studies of that species, and none at all of *C. rutilus*, that could be called long term.

The study that forms the basis of this report began in an exploratory fashion in 1960, entered a second phase with the establishment of a series of small (0.4 ha) live-trapping grids in 1964, and became a year round effort after a small building was erected to serve as winter quarters. The working hypothesis that stimulated me to begin the project came from a reading of the classic work on snow by A. N. Formozov (1946; English translation 1964): all classically cyclic species of birds and mammals are chionophiles, which suggested that cycles may be driven by events that take place in the subnivean environment (Fuller 1967).

Early results have already been summarized (Fuller 1969, Fuller et al. 1969). Some additional material on *C. gapperi* has also been published (Fuller 1977a, 1977b, 1979, 1984, Mihok & Fuller 1981, Mihok et al. 1983), but to date nothing has been published on *C. rutilus* or *Peromyscus maniculatus*. The present report deals mainly with the 10 summers of 1970 to 1979 inclusive.

2. Study area

The field station was located near km 130 (km 0 is at the Alberta-NWT border) on the Mackenzie Highway in the southern Mackenzie District of the Northwest Territories (Fig. 1). Its geographic coordinates were approximately 61

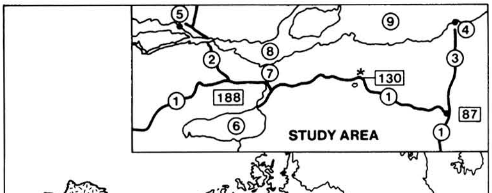


Fig. 1. Ranges of *Clethrionomys gapperi* and *C. rutilus* in North America, and location of the Study Area (Inset).
1) Mackenzie Highway
2) Great Slave Lake Highway
3) Hay River Highway
4) Town of Hay River
5) Village of Fort Providence
6) Kakisa Lake
7) Kakisa River (boundary between *C. gapperi* and *C. rutilus* from Kakisa Lake to Mackenzie River
8) Mackenzie River
9) Great Slave Lake

north latitude and 117 west longitude. Trapping was carried out from about km 110 to the junction of the Mackenzie and Great Slave Lake highways (km 188), thence along the latter to the Mackenzie River — a linear distance of about 100 km. However, effort was concentrated in two stretches of about 40 km, one at each end of the transect just described.

The Kakisa River, a stream with a width of about 30 m, forms the boundary between the ranges of *C. gapperi* and *C. rutilus* in the study area. The two species of *Clethrionomys* are sharply separated along the course of the Kakisa (McPhee 1977), which makes it possible to compare the population dynamics not only of the parapatric species of *Clethrionomys*, but also of the sympatric *Clethrionomys* species and *Peromyscus maniculatus*, and two allopatric populations of *Peromyscus*.

The forests of the study area fall mainly into the Hay River Section of the Boreal Forest Region (Rowe 1972), but the Mackenzie River and south shore of Great Slave Lake are bordered by the Upper Mackenzie Section. They consist of a mosaic of habitat types produced by differences in soils, elevation, and recent fire history. Most trapping was done in upland sites dominated by a mixture of white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) or nearly pure stands of jack pine (*Pinus banksiana*). Low-lying areas dominated by black spruce (*Picea mariana*) and larch (*Larix laricina*) were avoided because they are not much used by *Clethrionomys*.

3. Methods

Snap traps were set at intervals of about 8 m in lines that were seldom more than 0.5 km from the highway, which thus acted as a long transect. Individual lines usually crossed more than one habitat type. Locations of lines and trap stations were not permanently marked, but the same general locations were trapped at about the same time each year. Most lines consisted of 100 traps, but in the early years shorter lines were used. Traps were usually left in place for three nights, but again there were exceptions, especially in the earlier years. The number of trap nights was not corrected for sprung traps or traps occupied by other species.

In 1975 grids about 6 ha in area were established. They were covered by an orthogonal array of 96 Longworth traps set at intervals of 25 m. One grid (8 rows X 12 rows) was in the range of *C. rutilus*; the other, which was somewhat irregular in shape, was in the range of *C. gapperi*. (Live-trapping was conducted on grids 2.25 ha in area from 1970 to 1974. Results will not be discussed here because the grids were too small). Traps were opened in the evening of day 0, visited twice (or oftener if necessary) on days 1 and 2, and closed after the morning visit on day 3. They were supplied with laboratory chow, sunflower seeds, and terylene fibre. Individuals were marked for future identification by means of toe-clipping, weighed, examined for signs of breeding, and released at the point of capture.

Snap-trapped animals were weighed, measured and autopsied. Skulls were saved, cleaned, and used to place each individual in one of four age classes according to the morphology of the second upper molar (Koshkina 1955, Tupikova et al. 1968, Martell & Fuller 1979). In individuals belonging to age class 1 the anterior labial groove is open to the proximal end of the tooth; in age class 2 a neck has formed, which closes the groove at the proximal end; in age class 3 measurable (= 0.1 mm) roots are present, but roots are usually shorter than 0.6 mm; and in age class 4 roots are usually longer than 0.8 mm. In summer-caught samples all individuals in class 4 are overwintered (OW); the other three classes are young of the year. Mihok (1980) showed that the transition from class 1 to class 2 in known-aged individuals takes place at 32-35 days of age, and that measurable roots appeared at 62-72 days, with some of the variance being due to differences in sex and reproductive state.

4. Material

This analysis is based on the catches from 376 trap lines, with 101 919 trap nights (TN) of effort in the range of *C. gapperi*, and 170 trap lines, with 44 572 TN of effort in the range of *C. rutilus*. The chronological distribution of trapping effort was about the same each season from about 1 May to late August (*C. rutilus*) or late September (*C. gapperi*). The mean dates for all trap lines were July 6±2.18 days for *C. gapperi* and July 9±3.03 days for *C. rutilus*.

Table 1. Relative numbers of *Clethrionomys gapperi*, *C. rutilus* and *Peromyscus maniculatus* in May and August, 1970-1979. *N* = number of trap lines.

		1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	Total
Heart Lake												
May												
	N	15	15	5	14	6	16	9	12	18	7	117
C. gapperi	Mean	3.490	1.616	2.648	1.428	6.025	0.822	2.444	1.682	0.767	2.000	2.292
	SE	0.638	0.332	1.081	0.221	0.846	0.137	0.299	0.384	0.151	0.436	0.143
Perom.	Mean	1.512	0.599	1.689	0.903	1.366	1.002	1.741	0.566	0.778	0.524	1.068
	SE	0.550	0.265	0.672	0.371	0.374	0.192	0.511	0.156	0.166	0.176	0.044
August												
	N	8	7	6	3	4	5	8	7	12	4	64
C. gapperi	Mean	5.250	1.646	2.516	2.778	12.476	2.667	8.792	2.923	3.389	4.500	4.696
	SE	0.930	0.747	0.925	0.676	1.719	0.537	1.783	0.572	0.650	0.5 53	0.426
Perom.	Mean	1.500	1.611	3.139	0.889	2.405	2.467	4.083	2.8 94	2.370	0.583	2.194
	SE	0.751	0.837	1.950	0.401	1.312	1.014	0.936	1.070	0.670	0.394	0.133
Mackenzie River												
May												
	N	6	1	5	3	5	6	1	4	8	0	39
C. rutilus	Mean	3.456	0	2.744	3.336	3.117	0.505	1.000	3.062	0.627	-	2.086
	SE	0.770	-	1.071	2.167	1.178	0.283	-	0.591	0.312	-	0.342
Perom.	Mean	3.794	1.333	2.693	4.234	1.789	1.349	2.000	2.5 99	1.002	-	2.249
	SE	1.030	-	0.693	1.641	1.092	0.199	-	1.269	1.189	-	0.319
August												
	N	15	2	2	6	2	3	6	4	9	7	56
C. rutilus	Mean	6.485	2.075	3.667	2.000	3.148	0.663	9.667	0.901	2.991	3.454	4.317
	SE	0.902	0.925	0.667	0.755	0.185	0.166	2.301	0.615	0.632	0.560	0.507
Perom.	Mean	7.059	2.070	6.667	3.056	5.556	4.762	6.389	4.135	4.455	2.298	4.967
	SE	1.540	1.570	1.667	0.474	1.481	1.693	1.509	1.289	1.529	0.725	0.571

5. Results

5.1. Relative Numbers

Spring relative numbers

Mean May relative numbers (catch per 100 Trap Nights) of *Clethrionomys gapperi* showed a tendency toward a 2-year cycle from 1965 to 1975 (Fuller 1977a). That tendency continued through 1979 (Table 1). The pattern from 1968 to 1979 (Table 2) is random according to the "runs up and down" test (or "runs test") (Sokal & Rohlf 1969: $r_{crit} = 9.5$ for 11 events). Thus, the pattern would not be exceptional were it not nearly identical with the pattern for sympatric *Peromyscus*, which is clearly not random.

C. rutilus and its sympatric *Peromyscus* population both show random patterns, but the amount of concordance between them is striking (Table 2). Pairwise Spearman and Pearson correlations performed on May data were all non-significant except that between sympatric *C. rutilus* and *Peromyscus maniculatus* ($r_s = 0.72$, $p \simeq 0.01$; $r = 0.84$, $p < 0.01$).

The spring population of *C. gapperi* was anomalously high in 1974 as a result of winter breeding, which was revealed by the presence of placental scars on the uteri of 5 females, and by a large proportion of individuals in the May sample with short roots on M^2. According to Fuller (1977b; Fig. 2, and unpublished data) most summer-born individuals have roots at least 0.9 mm long by the following May. In the combined sample of 181 individuals from 1976, 1977, and 1978, for example, only 8 had roots less than 0.9 mm, and only 4 were less than 0.8 mm. In 1974, on the other hand, 69 of 117 had roots less than 0.9, and 44 were less than 0.8 mm. At growth rates presented for *C. glareolus* (Tupikova et al. 1968) individuals with roots 0.8 mm long could be 8 months old, but I consistently get growth rates of about 2.0 mm per month for *C. gapperi*, which gives a maximum age of 6 to 7 months. Breeding

Table 2. Direction of change in numbers (+ = up, − = down) in each of four populations (two sympatric pairs) in May and August, 1968-1979. Runs within parentheses. R = number of runs.

	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	R
May												
C. gapperi	(+	+)	−	+	−	+	−	+	(−	−)	+	9
P. maniculatus	−	+	−	+	−	+	−	+	−	+	−	11*
C. rutilus	−	+	−	(+	+)	(−	−)	(+	+)	−	0	7
P. maniculatus	(+	+)	−	(+	+)	(−	−)	(+	+)	−	0	6
August												
C. gapperi	(+	+)	−	(+	+	+)	−	+	−	(+	+)	7
P. maniculatus	+	−	(+	+)	−	(+	+	+)	(−	−	−)	6
C. rutilus	−	+	−	+	−	+	−	+	−	(+	+)	10*
P. maniculatus	−	+	−	+	−	+	−	+	−	+	−	11

* Distribution not random.

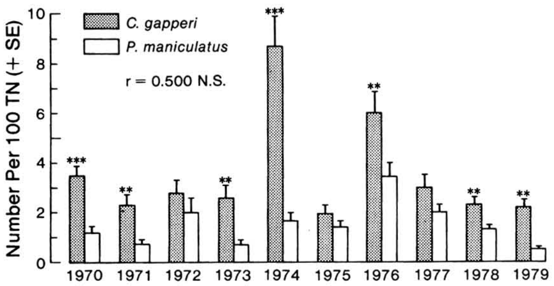


Fig. 2. Mean annual relative numbers of *C. gapperi* and sympatric *P. maniculatus*, 1970-1979. Asterisks refer to the probability that numbers of both species were equal. $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

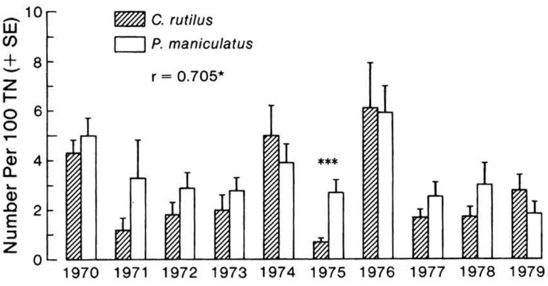


Fig. 3. Mean annual relative numbers of *C. rutilus* and sympatric *P. maniculatus*, 1970-1979. Asterisks refer to the probability that numbers of both species were equal. $^{***}p<0.001$.

probably began in November, and carried on until at least January (roots = 0.4 mm). There was no evidence for a similar amount of winter breeding in any other population.

In view of the above, it seems legitimate to remove 1974 from correlation analyses of spring numbers. Such removal has no effect on the Spearman correlation, but it makes the Pearson correlation between *C. gapperi* and sympatric *Peromyscus* marginally significant ($r = 0.63$, $0.10 > p > 0.05$).

Late summer relative numbers

August is the latest month for which I have estimates for all species. *C. gapperi* showed a weak 4-year periodicity from 1961 to 1975 (Fuller 1977a), but the pattern broke down after that. High numbers occurred in 1974 and again in 1976, which was followed by a decline in 1977 with modest recovery in 1978 and 1979 (Table 1). According to the run test, increases and decreases in the numbers of both *C. gapperi* and *Peromyscus* were random (Table 2), and they were out of phase about as often as they were in phase.

C. rutilus and sympatric *Peromyscus* clearly had 2-year cyclicity in August (Tables 1 and 2). Spearman correlations were significant between *C. gapperi* and *C. rutilus* ($r_s = 0.69$, $p \simeq 0.01$), and between *C. rutilus* and sympatric *Peromyscus* ($r_s = 0.64$, $p < 0.05$). Pearson correlations were significant between *C. gapperi* (1974 omitted) and allopatric *Peromyscus* ($r = 0.91$, $p < 0.01$), and marginally significant between two populations of *Peromyscus* ($r = 0.63$, $p \simeq 0.05$) and *C. rutilus* and sympatric *Peromyscus* ($r = 0.53$, $0.10 > p > 0.05$).

Mean annual relative numbers

For *C. gapperi* two years, 1974 and 1976, stand out (Fig. 2). For *P. maniculatus* there is only one less pronounced high in 1976. *C. gapperi* outnumbered *Peromyscus* in 7 of 10 seasons, but the direction of the changes in numbers from year to year is the same in both species. The similarity is especially striking for the last 5 years of record.

For *C. rutilus* 1974 and 1976 were also years of high numbers (Fig. 3). In contrast to *C. gapperi*, *C. rutilus* displayed a clear pattern in the subset of years 1970-1973, and the pattern was repeated in the subset 1976-1979. In spite of the shortness of the subsets they (1970-73 & 1976-79) are significantly correlated ($r = 0.982$, $p < 0.05$). Mackenzie *Peromyscus* tracked *C. rutilus* throughout the 10-year period. They also displayed a pattern in 1970-1973 that repeated itself from 1976-1979 ($r = 0.956$, $p < 0.05$). In only one year was there a significant difference between the mean numbers of the two species, and in that year *P. maniculatus* were more numerous than *C. rutilus* (1975; $F_{1,15} = 18.93$, $p < 0.001$).

Correlations among mean annual numbers are nearly universal. *C. rutilus* numbers are correlated with those of *C. gapperi* ($r = 0.80$, $p < 0.01$), sympatric *Peromyscus* ($r = 0.79$, $p < 0.01$), and marginally with allopatric *Peromyscus* ($r = 0.58$, $0.10 > p > 0.05$). The *Peromyscus* populations are correlated at the 5% level ($r = 0.72$). *C. gapperi* numbers, with 1974 included, are not correlated with *Peromyscus*, but when 1974 is removed, they are strongly correlated with both the sympatric ($r = 0.87$, $p < 0.01$) and allopatric ($r = 0.86$, $p < 0.01$) *Peromyscus* populations.

Seasonal rates of increase

Patterns of seasonal growth in numbers were variable. Some years there were spring declines, in other years there were not. In some seasons numbers continued to increase at least until mid September, whereas in other years they reached a plateau, or even declined, as early as the second half of August. For most years there appeared to be a period of exponential growth between early June and about August 20, regardless of what happened at the beginning and end of the season. Accordingly, two sets of regression equations were calculated for each population for each year. In one set only data for the period 1 June to 20 August (23 August for *C. rutilus*) were used. In the other all data from 1 May to 30 September were used for *C. gapperi*. Since there was no September trapping in the range of *C. rutilus* the cutoff date was 2 September. *Peromyscus maniculatus* begin to restrict their activity as the days become colder in September, so 2 September was also used as a cutoff date for them. Regression lines are graphed only for cases in which the regression was significant at the level of 10%. Common regression lines are based on all 10 years of data, and are all highly significant ($p < 0.001$ for all populations).

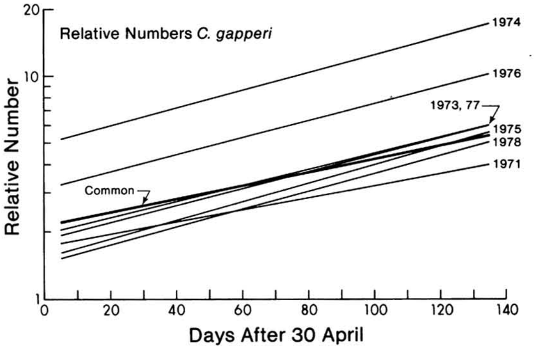
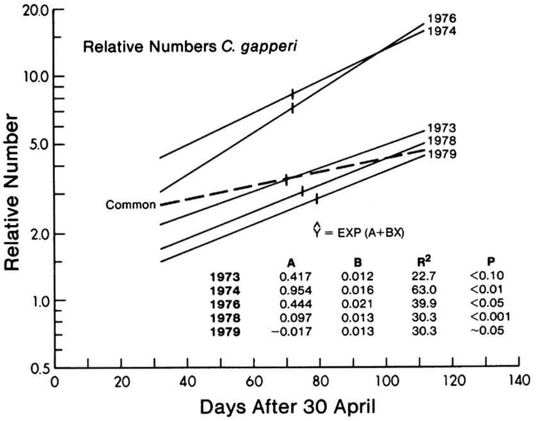


Fig. 4. Rates of increase in relative numbers of *C. gapperi* from 1 May to 30 September. Only years with slopes significantly different from zero at 10% are graphed.

Significant regression equations were found for 7 of the 10 years for *C. gapperi* when the $\ln(x+1)$ transform of data for the whole season was used (Fig. 4). The lines for 1974 and 1976, not unexpectedly, stand out clearly from the rest, including the common regression. Note that there is little difference among the slopes for years of high or low numbers. The slope of the common regression is depressed by inclusion of three years in which it did not differ from zero.

A similar pattern occurs when only data from 1 June to 20 August are used (Fig. 5), but there are differences in detail. For the 5 years that met the 10% criterion, slopes are higher than for the summer as a whole. The years of low numbers still have nearly identical slopes,



	A	B	R^2	P
1973	0.417	0.012	22.7	<0.10
1974	0.954	0.016	63.0	<0.01
1976	0.444	0.021	39.9	<0.05
1978	0.097	0.013	30.3	<0.001
1979	−0.017	0.013	30.3	~0.05

Fig. 5. Rates of increase in relative numbers of *C. gapperi* during the part of summer with rapid exponential growth (1 June to 20 August). Only years with slopes significantly different from zero at 10% are graphed.

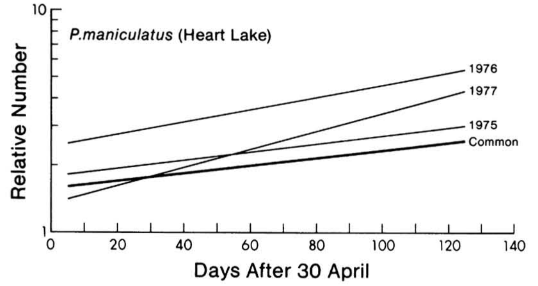


Fig. 6. Rates of increase in relative number of *P. maniculatus* sympatric with *C. gapperi* from 1 May to 2 September. Only years with slopes significantly different from zero at 10% are graphed.

but the years of high numbers, especially 1976, appear to have steeper slopes than the years of low numbers although they do not differ significantly from the rest.

Only four significant regressions were generated for *P. maniculatus* (Fig. 6) sympatric with *C. gapperi*. Estimated numbers predicted by the regression equations all fall within a narrow range, both in spring (1.5-2.5) and fall (2.5-5.5). The slope of the common regression for *P. maniculatus* is significantly less than that for *C. gapperi* ($t = 2.631$, $p < 0.01$).

For *C. rutilus* 1970 approached 1974 as a year of high numbers (Fig. 7). Numbers grew most rapidly in 1976, and in all other years there was a tendency toward less variation in August than in May.

A major change occurs when early and late records are dropped from the analysis (Fig. 8).

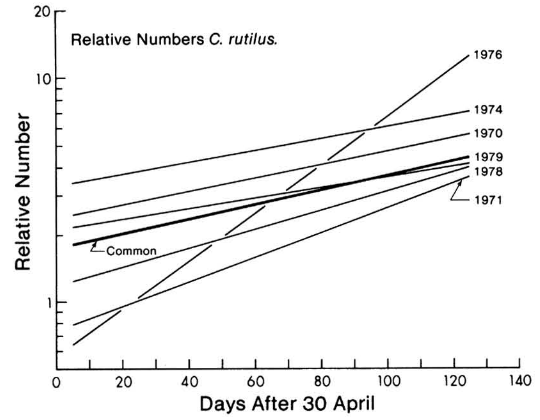
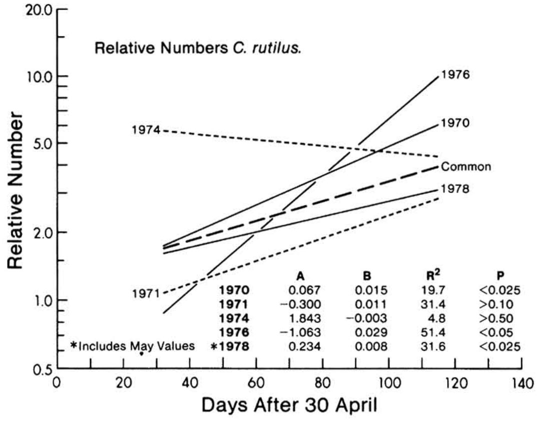


Fig. 7. Rates of increase in relative numbers of *C. rutilus* from 1 May to 2 September. Only years with slopes significantly different from zero at 10% are graphed.



	A	B	R^2	P
1970	0.067	0.015	19.7	<0.025
1971	−0.300	0.011	31.4	>0.10
1974	1.843	−0.003	4.8	>0.50
1976	−1.063	0.029	51.4	<0.05
***1978**	0.234	0.008	31.6	<0.025

Fig. 8. Rates of increase in relative numbers of *C. rutilus* during the part of summer with rapid exponential growth (1 June to 20 August). Only years with slopes significantly different from zero at 10% are graphed.

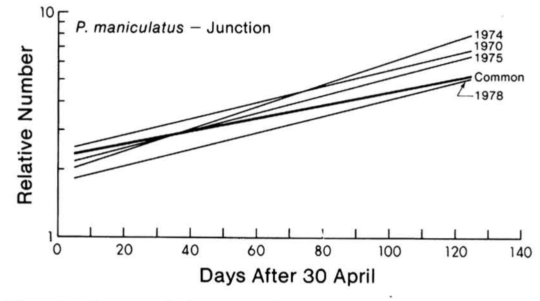


Fig. 9. Rates of increase in relative numbers of *P. maniculatus* sympatric with *C. rutilus* from 1 May to 2 September. Only years with slopes significantly different from zero at 10% are graphed.

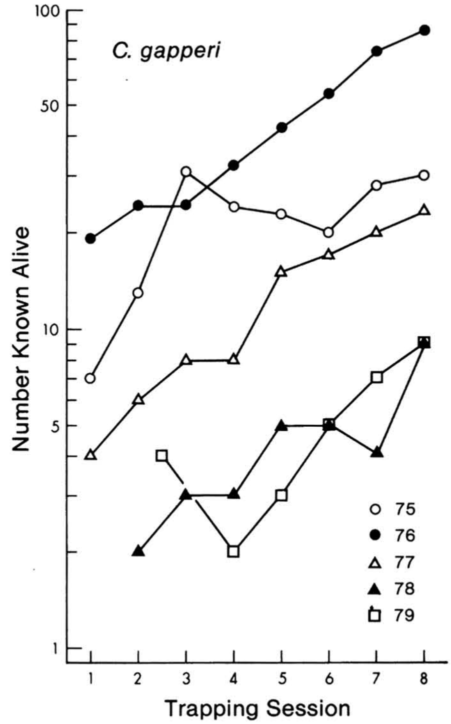


Fig. 10. Minimum number of *C. gapperi* alive on a 6-ha grid from mid May to late August. The interval between the start of one rota and the start of the next was 14 days.

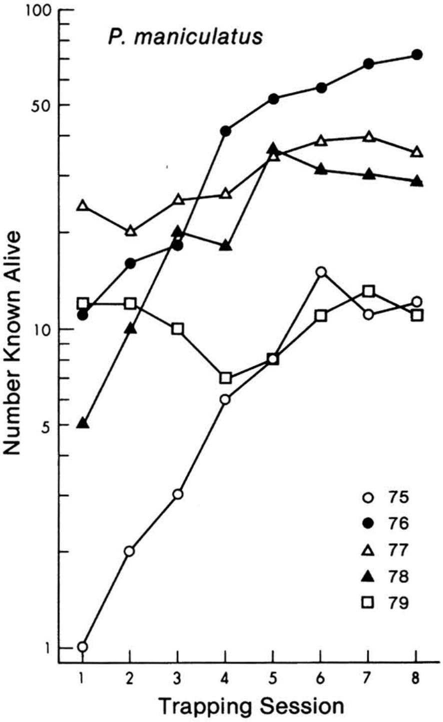


Fig. 11. Minimum number of *P. maniculatus* sympatric with *C. gapperi* alive on a 6-ha grid from mid May to late August. The interval between the start of one rota and the start of the next was 14 days.

Most significant is the fact that 1974 no longer has a slope significantly different from zero. Only low values early, and high values late in summer produce the significant regression of Fig. 7. Also no longer significant are 1979 and 1971, although I have included the latter year in Fig. 8 because it explains a reasonable amount of the variance in catches (31 %).

Mackenzie *Peromyscus* had significant regressions in only 4 years (Fig. 9). The slopes are all about 0.008, and all four span a remarkably small range of numbers.

The slopes of the common regressions for *C. rutilus* and sympatric *P. maniculatus* are identical (0.0070), and virtually the same as that for *C. gapperi* (0.0069). Although there are significant interspecific correlations in mean annual number, there are no such correlations among slopes of the regression equations except for the common regressions. There is a correlation between intercepts for *C. gapperi* and *P. maniculatus*, which, along with lack of a similar correlation between the two populations of *P. maniculatus*, and lack of correlation between the two species of *Clethrionomys*, suggests that similarity of winter conditions, rather than genetic similarity, plays the dominant role in setting spring numbers.

Slopes and intercepts are negatively correlated for three of the four populations studied (*C. gapperi* $r = -0.65$, $p < 0.05$; *C. rutilus* $r = -0.91$, $p < 0.01$; Mackenzie *Peromyscus* $r = -0.86$, $p < 0.01$)), which suggests that rate of increase is generally inversely related to spring numbers.

5.2. Minimum Number Alive

In many respects Minimum Number Alive (MNA) and relative numbers are in agreement, but in some they are not: *C. gapperi* increased rapidly and steadily to reach the highest number recorded in 1976 (Fig. 10). Obvious lows occurred in 1978 and 1979. Rapid exponential increase during the first three trapping sessions of 1975 was not seen in the snap-trap

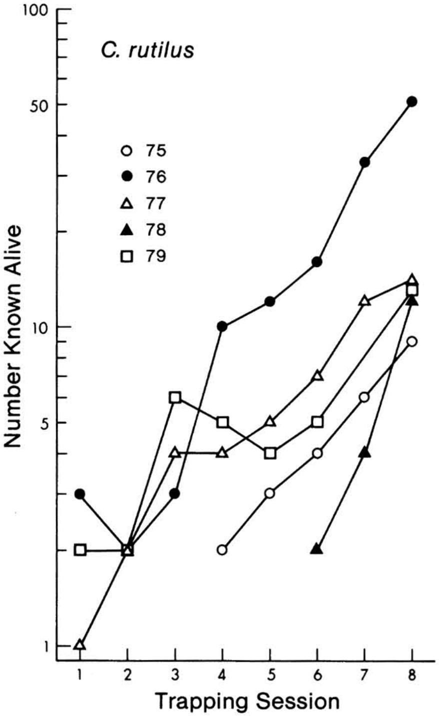


Fig. 12. Minimum number of *C. rutilus* alive on a 6-ha grid from May to late August. The interval between the start of one rota and the start of the next was 14 days.

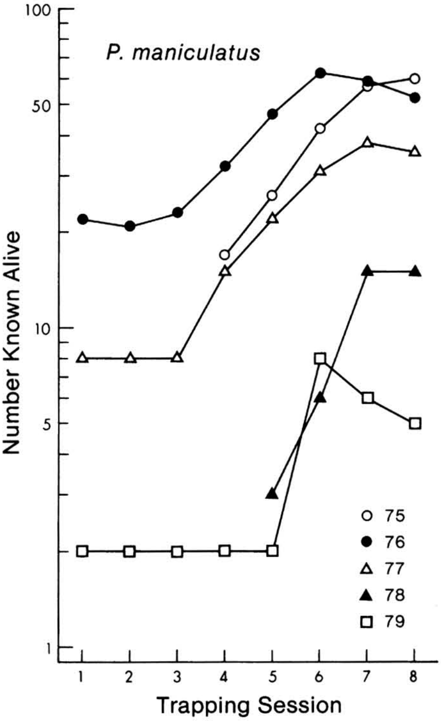


Fig. 13. Minimum number of *P. maniculatus* sympatric with *C. rutilus* alive on a 6-ha grid from mid May to late August. The interval between the start of one rota and the start of the next was 14 days.

samples. Note too that numbers were still increasing on the grid at the time of last enumeration every season.

Heart Lake *Peromyscus* also had a year of high numbers (1976), two years of moderate numbers and two of low numbers (Fig. 11), however, the positions of 1975 and 1978 are reversed between *C. gapperi* and *P. maniculatus*. Note that, except in 1976, *Peromyscus* numbers did not increase after the fifth or sixth trapping session.

C. rutilus numbers again showed a strong tendency to converge toward a constant late August number (Fig. 12), although numbers were still increasing every year when enumeration ended.

Mackenzie *Peromyscus* reached high numbers in two consecutive years (Fig. 13). They were the only population to do so. In 1976 and 1977 the curves seem to approach the classical logistic growth model. A tendency to reach a plateau, or even to decline, is again evident, but is less well-marked than in the Heart Lake population.

Regression equations were calculated for each population and each season for which there were at least 5 MNA points. There are occasional years in which slopes were nearly identical with slopes of relative number regressions (*C. gapperi* in 1975 and 1979), but there are also many striking differences (Table 3). There is no correlation between slopes of MNA regressions and those of relative number regressions within any population. However, the slopes of the MNA regressions for *C. gapperi* and Heart Lake *Peromyscus* are negatively correlated ($r = -0.913$, $df = 3$, $p < 0.05$).

One may also compare the four populations year by year: Late August numbers tend to cluster around three densities — high, from 50 to 80; moderate, around 30; and low from 9 to 15. Of 20 fall counts, 10 or 11 were in the low range, 4 or 5 where in the moderate range, and 5 were high (Table 4). All four populations were high in 1976 and all were low in 1979; every population had at least 2 low years out of 5; only 1 population had 2 high years.

Table 3. Instantaneous daily rate of increase based on Minimum Number Alive on grids, and on regressions of relative numbers caught in snap traps.

	1975	1976	1977	1978	1979
C. gapperi					
Live	0.0054	0.0080	0.0090	0.0071	0.0138
Dead	0.0053	0.0211	0.0078	0.0135	0.0132
C. rutilus					
Live	0.0132	0.0166	0.0125	-	0.0076
Dead	−0.0009	0.0292	−0.0039	0.0084	0.0035
P. maniculatus					
Heart Lake					
Live	0.0132	0.0101	0.0032	0.0083	0.0001
Dead	0.0182	0.0135	0.0130	0.0032	0.0020
Mackenzie					
Live	0.0118	0.0062	0.0097	-	-
Dead	0.0089	0.0021	0.0177	0.0166	−0.0080

Table 4. Frequency of occurrence of three qualitative levels of August numbers known to be alive on two 6 ha grids. H = high; M = moderate; L = low.

	1975	1976	1977	1978	1979
Heart Lake					
C. gapperi	M	H	M-L(?)	L	L
P. maniculatus	L	H	M	M	L
Mackenzie					
C. rutilus	L	H	L	L	L
P. maniculatus	H	H	M	M	L

Overall *Clethrionomys* numbers were low on 6 or 7 occasions, moderate on 1 or 2, and high on only 2. On the other hand, *Peromyscus* had 4 low, 3 moderate, and 3 high years.

5.3. Density estimates

Bondrup-Nielsen (1983) has shown that edge effect is a function of the ratio of grid size to home range size. Because home range size varies with sex, and probably also with age, separate density estimates should be made for at least immature and mature, males and females.

Mature females of *C. gapperi* had exclusive home ranges of about 0.3 ha (Fuller, unpubl. data). Mature males, on the other hand, had total ranges too large to measure on a 6-ha grid. Several males are known to have used half of the traps on the grid (i.e., 3 ha) in the course of a summer, and an unknown area beyond the grid boundaries. However, they do not have exclusive use of such large areas. Immatures of both sexes seemed to be clustered around a mature female, which was probably their mother, and therefore probably had home ranges no larger than hers.

If there were perfect packing of mature female home ranges into a 6 ha grid the maximum number of mature females to expect would be 20. The maximum number observed was 23. If the observed number was an overestimate by a factor of 1.6 (Bondrup-Nielsen 1983) the corrected number, allowing for edge effect, would be 15. Given a sex ratio of 55 males to 45 females we would then expect 19 mature males. If each mature female were accompanied by 3 surviving immature young the expected density would be 79 individuals per 6 ha, or about 13 per ha. The maximum number known alive at one time (88 in August 1976) does not permit a peak density much greater than that. As a minimum estimate of peak density we can simply discount the observed maximum by a factor of 1.6 ($n = 55$) and get a density of about 9 per ha. In years of low numbers density may not exceed 2 per ha.

The maximum number of *C. rutilus* known alive was only 51. However, the relative numbers of the two species were comparable and so were the numbers caught on 2.25 ha grids from 1969 to 1974 (unpublished data). I therefore suggest that the low number on the grid was a function of the poor quality of the habitat, and that the range of densities attained by *C. rutilus* is about the same as that reached by *C. gapperi*.

5.4. Fluctuation indices

Stenseth (1977) and Stenseth & Framstad (1980) recommended the use of an index, s (= standard deviation of $\log_{10}$ numbers), to distinguish between the cyclic and stable populations. Several values of s for each population are given in Table 5. All values fall well within the range for stable populations according to Henttonen et al. (1985). By this measure, too, numbers are no more variable in August than in May, and for *C. gapperi* the same is true even for September.

5.5. Winter survival of *C. gapperi*

Fuller (1984) used a number of characteristics of the September population of *C.*

Table 5. Indices of cyclicity, *s*, based on 10 years data for four populations.

	May	August	Sept.[1]	Annual
Heart Lake				
C. gapperi	0.2718	0.2607	0.2683	0.2099
P. maniculatus	0.2006	0.2641	0.1422	0.2584
Mackenzie				
C. rutilus	0.3535[2]	0.3522	-	0.2961
P. maniculatus	0.2131[3]	0.1897	-	0.1474

[1] No samples in 1979. October sample in 1971 included.
[2] $n = 8$. Zero catch in 1971 and 1979.
[3] $n = 9$. Zero catch in 1979.

gapperi (numbers, body weight, body length, age ratio, October temperatures, for each sex separately and for sexes combined) as possible predictors of numbers the following May, or of the instantaneous rate of decline during winter. Of 14 regressions, 10 failed to predict the high spring density in 1974, 9 failed to predict the low May density in 1978, and 5 failed to predict the extreme low in 1975. Seven predictors failed to predict at least two of 1974, 1975 and 1978, and four failed to predict all three. Nevertheless, September numbers explained about 80% of the variance in winter survival rates and May numbers for the remaining 6 years.

It is perhaps unrealistic to expect any feature of the fall population to predict winter breeding such as occurred in 1973-74. If that winter is omitted from the regressions, fall numbers account for 80% of the variance in 28-day survival rates of males, females and sexes combined in the remaining 8 winters. The correlations are strongly negative, which suggests that winter survival is density-dependent. However, there are no significant differences in spring numbers among any of the 8 years in question (spring number = 1.676± 0.241), which leads to an alternative explanation: If winter carrying capacity is fixed within narrow limits the apparent density-dependence is reduced to an arithmetic artifact. The biologically significant feature is the constancy of the winter carrying capacity.

Relative constancy of May numbers is not confined to *C. gapperi*. Mean spring relative numbers, exclusive of 1974 were 0.975±0.172 for *Peromyscus* at Heart Lake, 1.839±0.443 for *Peromyscus* at the Mackenzie, and 1.574±0.460 for *C. rutilus*.

It is a reasonable conclusion, therefore, that winter carrying capacity was low and rather constant for all populations.

5.6. *C. rutilus* on islands

Several islands in the Mackenzie River (Fig. 1) were sampled intensively in 1973 (Dickinson 1976) as a test of the "Krebs Effect" (MacArthur 1972; i.e., that a small island should act like a small enclosure and therefore density should be higher on small islands than on large ones). The smallest islands did not have the greatest density, but density of *C. rutilus* decreased monotonically with area from Island Two to the mainland (Table 6). *Peromyscus* densities showed no association with area. In terms of the total number of cricetids, Providence Island had the highest density. In 1976 density was again (or still?) high on Island Two, and there was not much difference between the mainland populations and those of small islands (Table 6).

In 1977 and 1978 a live-trapping study was undertaken on Island Two and Green Island (Burns 1980, 1981), but it was supplemented by some snap trapping. The MNA on Island Two reached 100 individuals by early July 1977 and showed little gain thereafter, which suggests that *C. rutilus* had attained saturation density. *Peromyscus* densities were about 75% of *C. rutilus* densities (Burns 1980). Clearly, no crash occurred on Island Two in 1977 as it did on Providence Island and the adjacent mainland. *C. rutilus* numbers fell in 1978 according to both the live-trapping results (Burns 1981) and the results of an attempted total kill at the termination of the project (Table 6). *Peromyscus* were twice as common as *C. rutilus* at the end of 1978.

Although these data are fragmentary, it is clear that island populations were consistently denser than those of the mainland (suggesting a "Krebs Effect"), and that the ratio of *Peromyscus* to *C. rutilus* on the islands altered radically between 1973 and 1978.

5.7. Morphometry and demography in *C. gapperi*

In a multivariate analysis of 19 skull measurements, plus body length and weight, of OW males taken in May, Mihok & Fuller (1981) failed to find any obvious types of individual. Subtle differences in skull shape were not related to demography, but each of the first three axes of canonical discriminance was associated with temperature — in the fall growth period, during midwinter, and during

Table 6. Relative numbers of *C. rutilus* (*C. r.*) and *P. maniculatus* (*P. m.*) on several islands in the Mackenzie River and on adjacent mainland. All sampling done in August. *N* = number of trap lines.

Islands	Size (ha)	1973			1976			1977			1978		
		N	*C. r.*	*P. m.*	*N*	*C. r.*	*P.m.*	*N*	*C. r.*	*P. m.*	*N*	*C. r.*	*P. m.*
Small[1]	1-2	752	9.92	2.26	400	11.25	3.00		-	-		-	-
Two	7.7	645	21.86	0	100	34	23[2]		-	-	515	8.16	16.12
Green	30.6	444	15.54	2.03		-	-	300	4.33	8.00	500	5.40	10.20
Providence	61.2	450	12.67	11.33		-	-	300	0.33	2.33		-	-
Mainland		1800	2.00	3.06	1200	0.67	6.39	1184	0.90	4.13	2470	2.99	4.45

[1] 4 islands in 1973, 2 in 1976.
[2] Single night of trapping.

the spring growth period. Bivariate analyses, however, showed that relative size is related to demographic change, but not in a direct way. Positive deviations from common regressions of body size on skull size occurred in years *following* a year with low spring density.

6. Discussion

The data presented herein shed light on the answers to two important questions in small mammal population biology.

1) Are these *Clethrionomys* populations examples of lack of 3- to 4-year cyclicity in a microtine? And,

2) do they have any bearing on the general question of population regulation?

The answer to question 1 seems to be rather clear cut: The index of cyclicity, *s*, falls well below the range of cyclic populations, not only in spring, but in all summer months. There is also a strong tendency toward a weakly developed 2-year cycle as revealed by the "runs up and down test". In addition, morphometric analysis of spring males failed to reveal a type of individual supposedly characteristic of either high or low density populations. Analysis of frequencies of transferrin alleles (Mihok et al. 1983) revealed only a general negative correlation between the frequency of Tf^J in young of a given year and an index of abundance in May of the previous year. The question of cyclicity in *C. gapperi* is examined further elsewhere (Fuller 1985).

The second question can be approached in the following way: If populations are regulated by forces entirely intrinsic to each population (i.e., as independent events), there is no reason to expect a high correlation between the numbers of a pair of sympatric species, especially when the species are in different subfamilies and have quite disparate life history characteristics. If both species were known to have cycles with a 4-year periodicity there would be a probability of about 0.25 that they would be in phase. But since neither the *Clethrionomys* nor the *Peromyscus* populations studied are cyclic in the study area the probability of chance concordance over a 10- or 12-year sequence must be much less than 0.25. Correlation might well be expected, however, between two populations of the same species in the same general area. If interspecific interactions were operating, densities of the interacting species might well be negatively correlated. Finally, if the populations are responding to the same environmental factors, sympatric species, even those with different life history characteristics, might well be positively correlated. Because the allopatric populations studied are only separated by 50 to 100 km it is not unreasonable to expect correlations among all four populations if they are responding to environmental factors.

Numerous positive correlations among populations have been reported in this paper — in May numbers, in August numbers, and especially in mean annual numbers. Furthermore, the correlations among intergeneric pairs of sympatric species are stronger than those between the conspecific, but allopatric, populations of *P. maniculatus*. To find so many positive correlations if each population is free to regulate its own numbers strains credulity. Positive correlations eliminate interspecific competitive interference. The conclusion must be that the populations are responding to a common factor, or factors, in the environment.

Even the 5-year record for the live-trapping grids (Table 4) supports this conclusion. The probability of a high population was 0.25 (5 highs in 20 population-years). The probability of four highs in a given year is thus 1 in 256, or about 0.004, if we are dealing with independent events. Lows were more common than highs — 7 occurrences in 20 population-years — but the probability of four of them occurring simultaneously is only about 0.015.

The foregoing analysis begs the question — to what factor, or factors, are the populations responding? I suggest two that need further investigation. First is the possibility of a more or less fixed winter carrying capacity. Some indication of how that might work is given by West (1977). Winter studies under extreme continental conditions are difficult, but need to be done.

Second, I am drawn by the tantalizing evidence for some sort of 2-year cycle to suggest a 2-year cycle in plant production as originally proposed by Kalela (1962). My evidence on this point is anecdotal. Crops of edible berries were certainly higher in even-numbered years, as opposed to odd-numbered years. The evidence consists of the number of pies made from *Amelanchier alnifolia* and the number of jars of preserved *Ribes hudsonianum* taken home for winter consumption. Unfortunately, precise records were not maintained. It seems to me fitting, however, especially since we are meeting in Finland, to end by urging reexamination of one of the important contributions of a great Finnish pioneer in *Clethrionomys* population biology.

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