Population Fluctuations in the Small Mammals of the Kluane Region, Yukon Territory

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From 1973 to 1977 we studied population changes in small rodents of the Kluane Lake region, southwestern Yukon. Six species were at maximal abundance in 1973 and were relatively scarce from 1974 to 1977. Only one species, *Microtus oeconomus* (Tundra Vole), showed a correlation between body size and population size (the Chitty Effect). Reproductive rates varied among species but were not related to population density in any species. *Peromyscus maniculatus* (Deer Mouse) had the lowest reproductive rate because of a short breeding season, so that females had only one or two litters in most years. There was no evidence of winter breeding in any species. We conclude that none of the small rodent species in the Kluane region, except *Microtus oeconomus*, show good evidence of 3–4 year population cycles. Density fluctuations are irregular and populations appear to be strongly *r*-selected in an unfavourable environment which is typically almost empty of rodents.

Key Words: population fluctuations, cycles, rodents, Yukon, Deer Mouse, *Peromyscus maniculatus*, Northern Red-backed Vole, *Clethrionomys rutilus*, Tundra Vole, *Microtus oeconomus*, Meadow Vole, *Microtus pennsylvanicus*, Heather Vole, *Phenacomys intermedius*, niche overlap, r-selection

An area of high diversity of microtine rodents in North America occurs in the mountains of the Yukon and Alaska (Hawes 1975). Although several surveys have been done in this area (Rand 1945; Baker 1951; Banfield 1961; see also Youngman 1975), there are no long-term data on population changes in the small rodents of the southern Yukon. From 1973 to 1977 we studied the small mammals of the Kluane Region, and we present here data on the population dynamics of the five most common small rodents.

Methods

This study was done in the area surrounding Kluane National Park in the boreal forest of the southwestern Yukon (as described in Krebs and Wingate 1976). The basic sampling technique used was a line of snap traps, 20 stations spaced at 15.2 m intervals in a straight line with three traps per station. Museum Special snap traps were used. Each line was left in position for three days and checked daily. Parallel lines were set out at least 61 m apart. Peanut butter was used as bait. The same general areas were trapped each year, although we were unable to place traps at exactly the same stations between years. Sampling was carried out from April to September each year.

All rodents captured were autopsied. We used the standard methods of autopsy as described in Keller and Krebs (1970). Females were classified as nulliparous, primiparous, or multiparous. Normal and resorbing embryos were counted. We did not try to count corpora lutea, corpora albicantia, or placental scars. Average number of litters per female was calculated as in Caughley (1977, page 79).

Habitat was classified around each snap-trapping station. It was difficult to place a trap line entirely within a single habitat. Our habitat classification followed Douglas (1974) but grouped some communities into a simpler classification. Krebs and Wingate (1976, Table 1) list the habitats sampled and the plant communities they contained.

Because not all the species occur in every habitat, we calculated indices of abundance for specific habitats. For *Peromyscus* six habitats were included: aspen, balsam poplar, balsam poplar-buffaloberry, willow, open spruce, and closed spruce. For *Clethrionomys* seven habitats were included — all of the *Peromyscus* habitats plus subalpine shrub tundra. For *Microtus pennsylvanicus* two habitats were included: marsh and shrub birch-meadow. For *Microtus oeconomus* three habitats were used: alpine tundra, subalpine shrub tundra, and marsh. For *Phenacomys intermedius* five habitats were used: aspen, balsam poplar, balsam poplar-buffaloberry, shrub-birch-meadow, and willow.

Results

Relative Abundance

We caught ten species of mice and voles in our snap traps; Table 1 gives the total catch and relative abundance for each species over the five years of study. *Peromyscus maniculatus* and *Clethrionomys rutilus* were the two dominant species every year; *Microtus pennsylvanicus* was a distant third, comprising an average of 8% of the catch. These three dominants together comprised 85–98% of the total catch over the five years. The other seven species were rare and usually comprise less than 5% of the catch, averaging only 1.3% each. These patterns of relative abundance fluctuated slightly from year to year but were remarkably stable.

TABLE 1. Total catch and relative abundances (%) of the ten species of voles and mice caught in snap-trap lines in the Kluane Region, 1973–1977.

Species	1973	1974	1975	1976	1977	Total
Peromyscus maniculatus	369	129	255	288	266	1307
Deer Mouse	(46.4)	(26.2)	(34.1)	(51.7)	(51.7)	(42.1)
Clethrionomys rutilus	293	202	369	192	215	1271
Northern Red-backed Vole	(36.9)	(41.1)	(49.3)	(34.5)	(41.7)	(40.9)
Microtus pennsylvanicus	23	88	64	52	23	250
Meadow Vole	(2.9)	(17.9)	(8.6)	(9.3)	(4.5)	(8.0)
Microtus oeconomus	50	11	14	5	6	86
Tundra Vole	(6.3)	(2.2)	(1.9)	(0.9)	(1.2)	(2.8)
Phenacomys intermedius	6	17	9	7	3	42
Heather Vole	(0.8)	(3.4)	(1.2)	(1.3)	(0.6)	(1.4)
Microtus miurus	14	26	30	2	0	72
Singing Vole	(1.8)	(5.3)	(4.0)	(0.4)		(2.3)
Microtus longicaudus	35	10	4	6	1	56
Long-tailed Vole	(4.4)	(2.0)	(0.5)	(1.1)	(0.2)	(1.8)
Synaptomys borealis	1	4	2	0	0	7
Northern Bog Lemming	(0.1)	(0.8)	(0.3)			(0.2)
Lemmus sibiricus	0	4	0	1	0	5
Brown Lemming		(0.8)		(0.2)		(0.2)
Zapus hudsonicus	4	1	1	4	1	11
Meadow Jumping Mouse	(0.5)	(0.2)	(0.1)	(0.7)	(0.2)	(0.4)

Population Density

Relative population density was estimated by the index of snap-trapping catch (number of animals per 100 trap-nights). Two major sources of variability are present in these data. Area effects occur because not all the Kluane Region operates in synchrony (see Krebs and Wingate 1976, p. 382). Temporal effects should be easier to visualize. None of these rodents has been found to breed during the winter. Thus population density should fall to its minimum in the spring or early summer, and then rise to a seasonal peak in later summer or early autumn.

Area effects were present, as described previously (Krebs and Wingate 1976), but the patterns of density changes over the five years were the same in all areas. One exception was Jacquot Island in Kluane Lake which was first trapped in the summer of 1977 and had very high densities of *Peromyscus, Clethrionomys* and *Microtus pennsylvanicus* at that time. For this reason we have lumped together data from all the Kluane Region (except Jacquot Island) in our analysis.

Figure 1 shows the seasonal and yearly variations in *Peromyscus* density from 1973 to 1977. These data fall into two groups: 1973 was a high-density year, and all the other years were low density years. The density in 1974 was particularly low. Numbers had dropped very much from September 1973 to April 1974, so that the high density occurred within one year.

Figure 2 shows the *Clethrionomys* indices for 1973–77. Again 1973 was a year of high density, and like *Peromyscus* none of this carried over into 1974. The autumn density of 1975 was also relatively high but otherwise every year had the same low density, averaging 1.0 individuals or less per 100 trap-nights.

Figure 3 gives the average indices of abundance for three of the less common species. In every case 1973 was a year of peak numbers, and density either declined or stayed low from 1974 to 1977. In contrast to *Peromyscus* and *Clethrionomys*, numbers seemed to decline only slightly from 1973 to 1974 in *Microtus pennsylvanicus* and *Phenacomys intermedius*.

Only one high density population of *Microtus longicaudus* was ever found, in 1973 near Sockeye Lake. *Microtus miurus* was at high density in subalpine and alpine tundra at Coin Creek in August 1975 and 1976. *Microtus miurus* was the only vole which did not seem to fit the pattern of peak density in 1973.

Table 2 summarizes the indices of population size for the five major species for 1973 to 1977. The coefficient of variation (SD/mean) of the average indices is highest for the two rare species and nearly the same for the two most common species.

To summarize: 1973 was the year of maximum

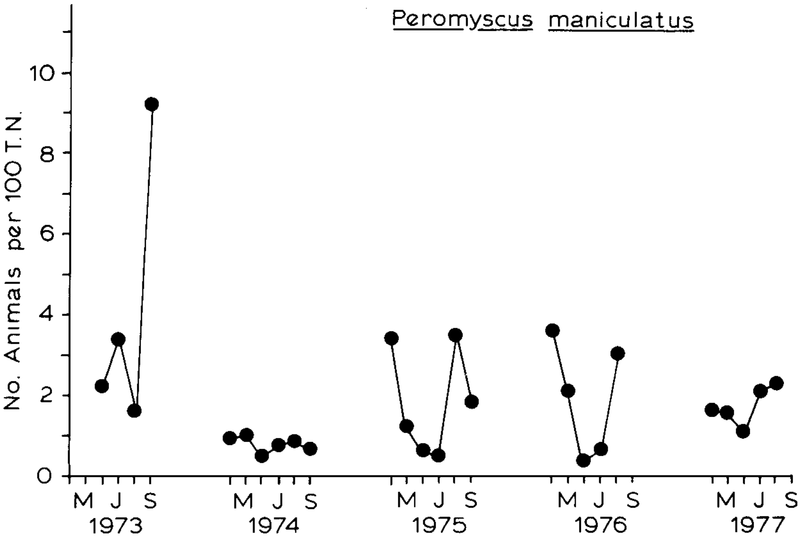

FIGURE 1. Abundance of *Peromyscus maniculatus* in the Kluane region, southwestern Yukon, 1973–1977. Abundance is estimated from snap-trapping of six habitats with samples averaged over months from April to September. T.N. = trap nights.

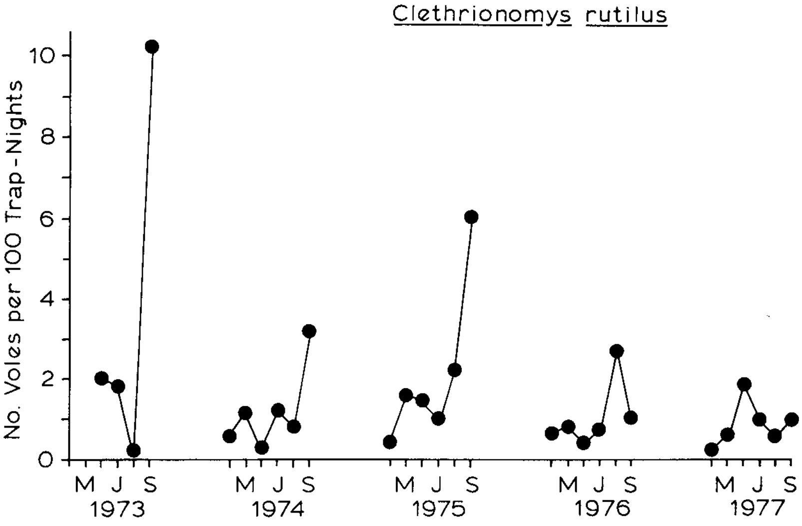

FIGURE 2. Abundance of *Clethrionomys rutilus* in the Kluane Region, 1973–1977. Abundance is estimated from snap-trapping in seven habitats with samples averaged over months from April to September.

TABLE 2. Average index of population size (no. caught per 100 trap nights) for combined samples, April to September. Numbers in parentheses are the number of trap-nights. Mean is the mean of all years. C.V. — coefficient of variation of population size among years (%).

Species	1973	1974	1975	1976	1977	Mean	C.V.
Peromyscus maniculatus	3.88 (7704)	0.86 (15066)	1.55 (16209)	1.52 (18810)	1.58 (16497)	1.87	61.9
Clethrionomys rutilus	2.69 (10224)	1.05 (19287)	2.03 (17649)	0.86 (21384)	1.08 (19377)	1.54	51.0
Microtus pennsylvanicus	2.92 (720)	2.47 (2961)	1.55 (3618)	1.34 (3654)	0.05 (2097)	1.66	66.8
Microtus oeconomus	0.52 (8280)	0.11 (6642)	0.12 (5193)	0.04 (6714)	0.14 (4383)	0.18	103.0
Phenacomys intermedius	0.18 (2745)	0.17 (4023)	0.04 (4509)	0.05 (5481)	0.03 (3519)	0.10	77.6
Total all rodents	4.65 (17100)	2.14 (22950)	3.34 (22365)	2.09 (26604)	2.38 (21609)	2.81 (110628)	

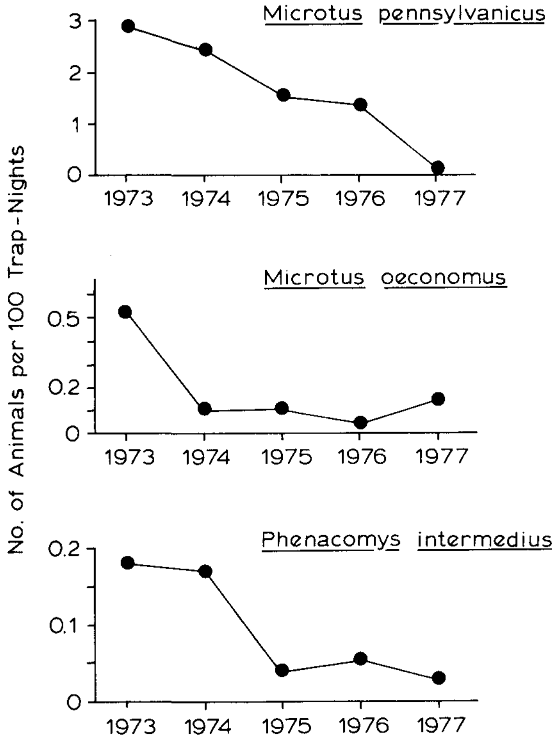

FIGURE 3. Abundance of the less common small rodents in the Kluane region, 1973–1977. *Microtus pennsylvanicus* abundance estimated from snap-trapping in two habitats, *Microtus oeconomus* from three habitats, and *Phenacomys intermedius* from five habitats. See text for details.

density for six of seven species, and numbers were lower in most species from 1974 to 1977.

Body Weight

Voles which fluctuate in abundance in a 3–4 year cycle typically show a cycle in adult body weight. Individuals in peak populations typically are 20–30% larger than individuals in declining or low populations (the Chitty effect; Boonstra and Krebs 1979). We looked for the Chitty effect in our data.

Table 3 gives the mean body weights of males of the four species with sufficient samples in May and June. Only overwintered adults are included in this table. The two dominant species, *Peromyscus* and *Clethrionomys*, showed no variation in average adult size from year to year. In particular, weights of adults were no larger in the high density year of 1973 than they were at other times. In *Microtus pennsylvanicus* there is also no sign of the Chitty effect. The largest male caught in the high density year 1973 was 44 g, compared with 43 g in 1976 and 45 g in 1977 when density was low. In *Microtus oeconomus*, by contrast, the Chitty effect is very clear. In the high density year of 1973 six of 16 breeding males exceeded 42 g, to a maximum of 52 g. In 1974 the largest male was 39 g, in 1975 41 g, in 1976 38 g, and in 1977 34 g.

Reproductive Rate

Table 4 summarizes the reproductive data for *Peromyscus, Clethrionomys, Microtus pennsylvanicus*, and *M. oeconomus* for the years 1973 to 1977. There was no indication of winter breeding for any of these species. No young animals were ever caught until the end of May and reproduction had always ceased by the time trapping stopped in late September or October.

TABLE 3. Mean body weight (g) of overwintered males in May and June (± 1 S.E.).

May	1973	1974	1975	1976	1977
Peromyscus	—	25.3 ±0.5	26.9 ±0.4	25.6 ±0.3	26.0 ±0.5
Clethrionomys	—	23.2 ±0.6	24.7 ±0.3	23.9 ±0.9	22.0 ±0.7
M. pennsylvanicus	—	26.0 ±0.9	23.5 ±4.5	27.0 ±2.6	—
M. oeconomus	—	28.0 ±1.7	22.0 ±2.0	29.5 ±0.5	—
June					
Peromyscus	25.8 ±1.1	23.8 ±1.0	26.5 ±1.1	26.2 ±1.1	25.7 ±1.1
Clethrionomys	19.9 ±1.7	23.9 ±1.8	28.7 ±1.0	25.9 ±1.2	22.8 ±0.5
M. pennsylvanicus	26.8 ±2.4	30.7 ±2.6	33.3 ±0.3	28.5 ±0.5	35.8 ±1.8
M. oeconomus	38.0 ±1.5	32.5 ±1.7	28.3 ±2.6	35.0 ±3.0	29.5 ±2.5

Pregnancy rates were determined for primiparous and multiparous females from the height of the breeding season. Since gestation periods in all these species range from 19–23 days, and embryos can be seen macroscopically only after five days of pregnancy, the theoretical maximum pregnancy rate should be 0.74 to 0.78 when every female is pregnant all the time. Observed rates in Table 4 are nearly all in the 0.6 to 0.7 range, and this is consistent with a model of continuous maximal reproduction of mature females with either a post-partum oestrous or an estrous cycle 4–5 days after parturition. When adult females are breeding, they seem to be doing it at a maximal rate.

Litter sizes do not vary significantly between primiparous and multiparous females, except in *Clethrionomys rutilus*. All four species seem to have an average litter size between five and six. We could detect no seasonal variation in litter size, but this may be a result of our small sample size.

The most striking difference between these species is in the length of the breeding season. *Peromyscus* has a very short breeding period, about half of the length of *Clethrionomys*. In some years (1973, 1975) most *Peromyscus* females could have only one or two litters, and none of the young mice bred during their first summer. The potential number of young produced per mature female averages only 14 in *Peromyscus*, compared with 28 in *Clethrionomys*. The two *Microtus* species are intermediate with potential production of 19–23 young per female.

Variations in the average number of litters produced set an upper limit to population growth in these species. With 100% survival *Peromyscus* populations could go up only 7-fold in one year, while *Clethrionomys* populations could increase 14-fold as a maximum. It would be surprising if the annual survival rate was as high as 50%, and we would expect the actual rate of increase to be approximately 3–4-fold in *Peromyscus*, 7-fold in *Clethrionomys*, 5–6-fold in *Microtus pennsylvanicus*, and 4–5-fold in *M. oeconomus* at best.

Table 5 gives the median weights at sexual maturity for *Clethrionomys, Microtus pennsylvanicus*, and *M. oeconomus* samples trapped in July and August each year. Weight or age at sexual maturity is one of the parameters most responsive to density changes in small rodents (Krebs and Myers 1974). Surprisingly, none of these species showed any year-to-year variation in size at maturity. In particular, none of the high density 1973 populations appeared to exhibit an increased size at maturity. We did not calculate median weight at maturity for *Peromyscus* because no young mice ever reached maturity in their first summer of life.

Niche Breadth

Different species of rodents in the Kluane Region occupy a variable habitat range (Krebs and Wingate 1976). *Peromyscus* and *Clethrionomys*, for example, occur in many different habitats whereas *Microtus* spp. are typically found in only a few. We quantified the range of habitats used by calculating standardized niche breadth (Pianka 1973) using the 18 habitat types listed in Krebs and Wingate (1976, p. 380). Table 6

TABLE 4. Reproductive rate estimates for *Peromyscus, Clethrionomys, Microtus pennsylvanicus,* and *M. oeconomus* for 1973–1977. Sample sizes in parentheses. F = female, M = male. Litter size: P = primiparous, M = multiparous.

Species	Year		Length of Breeding Season			Pregnancy Rate	Litter Size	% Embryos Resorbing	Ave. No. Litters per Female	Potential No. of Offspring
			Date Start	Date End	Days					
Peromyscus	1973	F	?	24 June	—	0.40(5)	6.5 (2)	7.1 (14)	—	—
		M	?	4 July	—					
	1974	F	17 May	14 July	58	0.62(8)	5.6 (7)	11.3 (44)	2.26	14.7
		M	29 April	2 July	65					
	1975	F	7 May	24 June	48	0.60(20)	5.8 (12)	1.4 (71)	1.80	10.1
		M	28 April	8 July	72					
	1976	F	30 April	17 July	79	0.71(38)	5.3 (14)	3.9 (77)	3.50	20.3
		M	24 April	23 July	90					
	1977	F	15 May	19 July	65	0.64(36)	5.8 (27)	3.1 (163)	2.60	15.1
		M	24 April	19 July	86					
	Mean	F	9 May	9 July	62	0.64(107)	5.71(62)	4.33(369)	2.48	14.2
		M	26 April	11 July	77					
Clethrionomys										
	1973	F	?	26 August	—	0.65(48)	P 5.6 (11)	2.3 (214)	—	—
		M	?	16 September			M 6.2 (24)			
	1974	F	30 April	5 September	129	0.60(30)	P 5.6 (23)	0.5 (193)	4.84	29.8
		M	28 April	10 September	136		M 6.3 (10)			
	1975	F	4 May	2 September	122	0.63(43)	P 5.8 (22)	1.9 (267)	4.80	29.0
		M	28 April	1 September	127		M 6.1 (22)			
	1976	F	30 April	12 August	111	0.72(36)	P 4.7 (13)	6.6 (197)	5.00	30.7
		M	24 April	20 September	150		M 6.5 (19)			
	1977	F	26 April	9 August	110	0.55(47)	P 5.7 (9)	1.2 (171)	3.78	22.9
		M	24 April	9 September	139		M 6.2 (19)			
	Mean	F	30 April	23 August	116	0.63(204)	P 5.50(78)	2.50(1042)	4.57	27.8
		M	26 April	11 September	139		M 6.25(94)			

TABLE 4. (concluded)

Species	Year		Length of Breeding Season			Pregnancy Rate	Litter Size	% Embryos Resorbing	Ave. No. Litters per Female	Potential No. of Offspring
			Date Start	Date End	Days					
Microtus pennsylvanicus										
	1973	F	?	29 August	—	0.69(13)	4.1 (9)	2.6 (38)	—	—
		M	?	1 September	—					
	1974	F	16 May	5 September	113	0.74(57)	5.2 (43)	2.2 (230)	5.23	27.2
		M	11 May	5 September	118					
	1975	F	26 May	20 August	87	0.57(14)	5.9 (8)	0.0 (47)	3.10	18.3
		M	11 May	13 September	126					
	1976	F	10 May	18 August	101	0.63(30)	4.7 (19)	9.2 (98)	3.98	18.7
		M	1 May	29 September	152					
	1977	F	?	?	—	1.00(8)	5.7 (8)	0.0 (46)	—	—
		M	?	8 September	—					
	Mean	F	17 May	26 August	102	0.70(122)	5.09(87)	3.27(459)	4.46	22.7
		M	8 May	11 September	127					
Microtus oeconomus										
	1973	F	?	21 August	—	0.78(9)	5.1 (11)	3.4 (58)	—	—
		M	?	29 August	—					
	1974	F	16 May	1 August	77	0.50(16)	5.4 (11)	4.8 (62)	2.41	13.0
		M	10 May	21 August	104					
	1975	F	23 May	21 September	122	0.50(10)	4.9 (8)	9.3 (43)	3.81	18.7
		M	11 May	13 September	126					
	1976	F	?	?	—	1.00(1)	7.0 (1)	0.0 (7)	—	—
		M	25 April	?	—					
	Mean	F	18 May	25 August	100	0.58(36)	5.19(31)	5.29(170)	3.63	18.8
		M	5 May	31 August	119					

TABLE 5. Median body weights (g) at sexual maturity for voles caught during July and August, 1973–1977.

	Males		Females	
	Median	95% C.L.	Median	95% C.L.
Clethrionomys rutilus				
1973	19.5	18.5–20.4	20.1	19.1–21.1
1974	19.0	17.9–20.0	19.4	17.7–21.2
1975	17.8	16.8–18.7	17.8	16.2–19.4
1976	16.8	15.8–17.9	20.2	19.0–21.5
1977	19.0	17.3–20.7	21.9	20.0–23.9
Microtus pennsylvanicus				
1973	20.8	18.4–23.5	17.9	15.4–20.7
1974	19.5	18.0–21.1	16.4	12.0–22.3
1975	19.4	14.9–25.4	19.9	14.7–27.0
1976	20.4	18.5–22.5	19.0	17.5–20.6
1977	18.0	16.1–20.1	20.4	16.6–24.9
Microtus oeconomus				
1973	25.5	24.0–27.1	20.6	16.8–25.4
1974	21.1	19.9–22.4	20.3	15.6–26.4
1975	22.4	19.7–25.4	21.3	16.8–27.1

gives these niche breadths for 1973 to 1977. Two points of interest emerge from this table. First, niche breadths were remarkably stable from year to year in spite of the variations in population density. Second, two groupings of species fall out of Table 6. The common species *Peromyscus* and *Clethrionomys* had equal and broad niches. The rare species, all *Microtus*, had narrow niches.

As with niche breadth, niche overlap in these rodents seems to remain relatively constant from year to year. Table 7 gives the average values of niche overlap for the 6 most common species. Only two values are noticeably high. *Peromyscus* and *Clethrionomys* overlapped greatly in their range of habitats occupied, and *Microtus pennsylvanicus* and *M. oeconomus* also had high overlap.

Discussion

Population cycles are commonly believed to be a characteristic feature of small rodents in northern ecosystems, and the first question we must address is whether the populations we have studied in the Kluane region of the Yukon show any evidence of cycles. We used three criteria to decide if a population is cyclic:

(1) peaks in density should recur at 3–4 year intervals;
(2) during population peaks mean body weights of overwintered adults are increased 20–30%; and
(3) reproductive rates are increased in expanding populations and reduced in declining populations.

All of these criteria are flexible because some exceptions occur to the classical cyclic syndrome (Krebs and Myers 1974).

From the density criterion, none of the five species shown in Figures 1–3 is cyclic. For an interval of five years we expect to see two population peaks, but only one possible 'peak' could be described — 1973. For the two dominant species (*Peromyscus* and *Clethrio-*

TABLE 6. Standardized niche breadths of small rodents sampled by snap trapping in 18 habitats, 1973–1977.

	1973	1974	1975	1976	1977	Mean
Peromyscus maniculatus	0.40	0.42	0.51	0.46	0.52	0.46
Clethrionomys rutilus	0.33	0.39	0.61	0.26	0.56	0.43
Microtus pennsylvanicus	0.07	0.12	0.16	0.09	0.12	0.11
Microtus oeconomus	0.24	0.13	0.19	0.11	0.09	0.15
Microtus miurus	0.12	0.12	0.06	0.11	—	0.10
Phenacomys intermedius	0.14	0.42	0.26	0.21	0.15	0.24
Microtus longicaudus	0.19	0.16	0.11	0.23	0.06	0.15

TABLE 7. Average niche overlap for seven small rodent species in the Kluane area. Values based on a mean of five values calculated for each year 1973–1977.

	Clethrionomys rutilus	*Microtus pennsylvanicus*	*Microtus oeconomus*	*Microtus miurus*	*Phenacomys intermedius*	*Microtus longicaudus*
Peromyscus maniculatus	0.51	0.05	0.16	0.06	0.26	0.31
Clethrionomys rutilus		0.15	0.08	0.02	0.20	0.27
Microtus pennsylvanicus			0.46	0.02	0.27	0.06
Microtus oeconomus				0.08	0.35	0.14
Microtus miurus					0.12	0.12
Phenacomys intermedius						0.29

nomys) the evidence is stronger because Gilbert and Krebs (1981) give two further years of live-trapping data for these species, and we have further unpublished data for 1980–83. Since 1973 there has been no high density of either *Peromyscus* or *Clethrionomys* for nine years. We are thus confident that neither of these species shows population cycles in the Kluane region. We are less confident in this conclusion for the *Microtus* species. Five-year cycles are not unknown among microtines and a five-year cycle could explain the results shown in Figure 3. Furthermore, we have observed outbreaks of *Microtus* in local areas in the Kluane region while doing other studies. For example, *Microtus pennsylvanicus* was abundant on Jacquot Island in Kluane Lake in the summer of 1977, and *Microtus* spp. were also seen there commonly in 1980.

Except for *Microtus oeconomus*, none of the species studied showed the body weight change characteristic of many cyclic small rodents (Krebs 1964). On this evidence we would classify *M. oeconomus* as cyclic in the Kluane area. We are surprised that *M. pennsylvanicus* seems to show no change in body weight of adults from year to year. Our samples, while small, are adequate to detect this striking effect if it occurred.

Finally, none of the species showed any sign of variation in reproductive rates that seems characteristic of many cyclic populations. Sample sizes are small for *Microtus oeconomus*, but we could detect no striking changes in the length of the breeding season or in the size at sexual maturity. These two components of reproduction change dramatically in most cyclic populations (Krebs and Myers 1974). We conclude that none of the rodent species in the Kluane region except *Microtus oeconomus* shows evidence of cycles in numbers. For *M. oeconomus* the evidence is weak but suggestive of cycles. We interpret the density changes shown in Figures 1–3 as irregular fluctuations.

Fuller (1969) studied *Peromyscus maniculatus* and *Clethrionomys rutilus* populations near Great Slave Lake, 1100 km east of our study area. He found high populations of *Peromyscus* in 1961 and 1966, and high populations of *Clethrionomys rutilus* in 1962 and 1967. Fuller (1969) observed no change in body weight of adults from year to year, a conclusion in agreement with our findings.

Martell and Fuller (1979) compared *Clethrionomys rutilus* populations in taiga and tundra areas near Inuvik, N.W.T. They found no winter breeding in either habitat. There was no sign of a population cycle in the tundra population and only a modest 4-fold fluctuation in spring densities in the taiga population. Martell and Fuller (1979) reported larger litter sizes for their populations. Whereas our mature females had litters averaging 6.25, their taiga females averaged 6.7–7.1, and their tundra females 7.3–7.9. But most of their females produced only two litters a year whereas our *Clethrionomys* averaged four or five litters a year. Thus overall production of young is higher in our population because of a longer breeding period.

Koshkina and Korotkov (1975) summarized 15 years of data on *Clethrionomys rutilus* populations in central Siberia. Our *Clethrionomys* populations never seemed to reach the high densities reported by Koshkina and Korotkov (1975). It is difficult to compare results directly but our densities appear to be only one-quarter those of Koshkina and Korotkov (1975). Furthermore, our populations showed much less year-to-year fluctuation. Spring densities varied less than 4-fold in our populations, but 7–10-fold in

Koshkina and Korotkov's populations. Whereas the summer peak in numbers was very similar in the Siberian populations (2–3-fold variation), it was more variable in our populations (5–6-fold variation). In years of high density Koshkina and Korotkov (1975) found a reduction in the maturation rate of young-of-the-year voles, so that the percentage of young voles sexually mature was inversely related to population density. We did not observe this effect in our *Clethrionomys rutilus* data because young voles mature every summer at the same size.

Whitney (1976) studied sympatric populations of *Clethrionomys rutilus* and *Microtus oeconomus* near Fairbanks, Alaska, about 640 km northwest of our study area. He trapped three populations for four years and found that *Clethrionomys* attained the same density every autumn, while *M. oeconomus* showed a population cycle with peaks three years apart. These results conform closely with our findings. Whitney (1976) postulated that population cycles were characteristic of species with narrow niches, and his hypothesis is supported by our data (Table 6). Whitney's hypothesis predicts that all our *Microtus* species and *Phenacomys* should show population cycles. Because of their low abundance we cannot definitely reject this prediction for our *Microtus* spp. We can, however, see no way of reconciling Whitney's hypothesis with Koshkina and Korotkov's (1975) data on *C. rutilus*.

Millar et al. (1979) analyzed latitudinal variation in reproduction in *Peromyscus*, and commented on the shortage of data from high latitude populations. Their data predict an average litter size of 5.93 for our populations, compared with our observed value of 5.71, and they predict a breeding season of 86 days compared with our observed 62 days for females. Our data are much closer to Fuller's (1969) values than they are to the predictions of Millar et al. Our *Peromyscus* are atypical because no young-of-the-year reach maturity during their first summer, which thus eliminates the most important component Millar et al. (1979) identified as increasing summer productivity. Millar and Gyug (1981) also reported that *P. maniculatus* from Hay River, N.W.T., did not reach sexual maturity until one-year old. *Peromyscus* appear to be unique among the small rodents of the Kluane area because it shows traits of a K-selected species — short breeding season, slow rate of maturation, large body size, and relatively constant population density.

We interpret all the voles in the Kluane region to be under extreme r-selection and thus selected for maximal reproductive rates in an unfavourable environment. The high mortality over the prolonged winter non-breeding season reduces the population every year to levels approaching local extinction. Population fluctuations result from changes in mortality rates in the face of a constant high reproduction. The most striking feature of these small mammal communities is that they are close to being empty most of the time. The selective premium is always on individuals trying to fill up a largely empty world, and we would predict competition for food both within and between species to be minimal.

More experimental work needs to be done on these northern populations to try to identify the factors limiting population sizes. We have already tried to increase population size by supplemental feeding (Gilbert and Krebs 1981). Manipulations designed to improve overwinter losses are badly needed. Fuller (1977) has rejected the hypothesis that variations in winter losses are determined by differences in winter weather conditions in the subnivean environment for *Clethrionomys gapperi*, so more complex hypotheses are needed. Year-to-year fluctuations in these Yukon populations are produced by events in the winter, non-breeding period and not determined by variations in reproductive success during the summer months.

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