Oecologia (1995) 103:481–489

ORIGINAL PAPER

Charles J. Krebs · Rudy Boonstra · Alice J. Kenney

Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada

Received: 2 May 1994 / Accepted: 1 April 1995

Abstract From 1987 to 1989 we monitored population changes during summer of the collared lemming *(Dicrostonyx groenlandicus)* and the tundra vole *(Microtus oeconomus)* at Pearce Point, Northwest Territories, Canada (69° 48′ N, 122° 40′ W). Populations on four study areas did not cycle but remained at low density (<3/ha) each year and continued at low numbers for the following 3 years (Reid et al. 1995). Lemming numbers often declined throughout the summer in spite of continuous reproduction, and population recovery occurred overwinter. Heavy predation losses of radio-collared lemmings occurred each summer and this lemming population may be trapped in a predator-pit. Collared lemmings breed in winter and only because of winter population growth do these populations persist. Tundra vole numbers increased rapidly in most summers but usually declined overwinter. Tundra voles do not seem able to sustain winter reproduction in this extreme environment and this prevents them from reaching high density because of the short summer. Population growth in both these rodents could be prevented by poor food or by predation losses, and landscape patchiness may also help to prevent population growth. For lemmings we do not think that a shortage of shelter or intrinsic limitations could be restricting population increase at Pearce Point. This is the first detailed study of a non-cyclic collared lemming population.

Key words Cycles · Lemmings · *Dicrostonyx groenlandicus* · *Microtus oeconomus* · Canadian Arctic

Introduction

Lemming populations in many parts of the Canadian Arctic fluctuate cyclically in abundance, reaching peak numbers every 3–4 years (Shelford 1943; Chitty 1950; Krebs 1964; Mallory et al. 1981). In spite of the great interest in lemming populations and their role in popular mythology, there have been very few quantitative studies of populations in the Canadian Arctic (Fuller et al. 1975a, b; Rodgers and Lewis 1986; Stenseth and Ims 1993). Collared lemming populations are commonly thought to be cyclic but cycles may not be clear or even occur in all collared lemming populations. Chitty and Nicholson (1942) noted for the mainland western Arctic of Canada that the lemming cycle was not clearly visible to natural history observers in some settlements. Fuller et al. (1975b) could not determine whether collared lemming populations on Devon Island were cyclic or not, although they peaked in 1969 and 1973, because in 1971 numbers were not low but intermediate. Collared lemmings show well-developed cycles on both Banks and Victoria Islands in the western Arctic (Chitty 1950).

In 1974 Krebs and Myers (1974) postulated that all vole and lemming populations fluctuated cyclically, but by the 1980s it was already clear that many vole and lemming populations fluctuated irregularly or not at all and it became important to determine why. Since we are interested in determining the causes of cyclic changes in rodent populations, we decided to begin work on lemmings in the western Canadian Arctic under the belief that they are the most strongly cyclic of all the microtine rodents. In 1987 we began a 6-year study of collared lemmings at Pearce Point, Northwest Territories, to examine the role of both intrinsic and extrinsic factors in causing cycles (Krebs 1985). We report here on the demography of these populations for the first 3 years of the study (1987–1989) and develop hypotheses which we tried to test experimentally during 1990–1993. In particular we have studied the impact of predation on this population (Reid et al. 1995), the social organisation of both the tundra vole (Lambin et al. 1992) and the collared lemming (R. Boonstra and C.J. Krebs, unpublished work), and the role of maternal effects and quantitative genetics on behaviour and growth of collared lemmings (R. Boonstra and W. Hochachka, unpublished work). In

C.J. Krebs (✉) · A.J. Kenney
Department of Zoology, University of British Columbia,
Vancouver, B.C. V6T 1Z4, Canada

R. Boonstra
Division of Life Sciences, Scarborough Campus,
University of Toronto, Scarborough, Ontario M1C 1A4, Canada

this paper we address three demographic questions which form the backdrop for all these other studies:

1. Do lemming and vole populations at Pearce Point show dramatic population fluctuations?
2. What changes occur in reproduction and growth in different years?
3. What are the major mortality factors affecting small rodents at Pearce Point?

Methods

Lemmings and voles were live-trapped with Longworth live traps and standard techniques (Krebs 1966). In 1987 we began using systematic grid trapping on 10×10 checkerboard grids with 30.5 m spacing. We caught few rodents and changed our strategy to adapt to low densities of lemmings (Boonstra et al. 1992). We used microscope slides coated with talcum powder to locate active lemming burrows and then live-trapped only at these active sites. Traps were set between 0600 and 2200 hours and checked every 4–6 h. We are confident that these methods allowed us to capture >95% of all lemmings on the study areas. During 1988 and 1989 we fitted all collared lemmings >34 g with radiocollars (Biotrack model SS1). Radiocollared individuals were located every 1–2 days throughout the summer with hand-held antennas. We attempted to weigh every individual once a week but cold not always achieve that goal. We located the nests of breeding female lemmings from their radio signals and in 1988 we dug up nests and marked the young by toe clipping at 6–9 days of age. We stopped doing this in 1989 because of concern for possible mortality of the juveniles from this nest disturbance.

Tundra voles and brown lemmings *(Lemmus sibiricus)* were much easier to locate and study because they use runways. They are also easier to live-trap than collared lemmings. Voles were marked only with eartags.

We live-trapped four main areas near Pearce Point. Habitats in these areas were classified into five types:

1. Rock – sand – mud flats with less than 20% vegetation cover
2. *Dryas integrifolia* heath with small amounts of *Salix arctica*
3. *D. integrifolia* heath with upland sedge *(Carex rupestris)* mixed and small amounts of *Salix* spp.
4. Sedge hummock, dominated by *C. membranacea* but with some *D. integrifolia*
5. Sedge marsh, principally with *C. aquatilis*. These habitat maps were digitized into the geographic information system SPANS and radio-locations and live trap captures of all animals were overlain and counted to provide a measure of habitat preference. Manly's α was used as a measure of preference (Krebs 1989, p 396).

Population sizes were estimated from mark-recapture data with the Jolly-Seber full model to reduce bias (Jolly and Dickson 1983). Because of the intensive trapping and radiocollaring procedures, the population estimate from the minimum-number-known-to-be-alive was only slightly less than the Jolly-Seber estimates.

Because we were live-trapping animals, only limited reproductive information was obtained. Sexual maturity was judged for males from descended testes and for females from perforate vaginal orifice, lactation, advanced pregnancy, or the presence of a litter in the trap. We estimated the median body weight at sexual maturity by fitting probit lines with the techniques described by Leslie et al. (1945). Body mass was obtained on Pesola spring scales to 0.5 g.

Survival rates were obtained from the radiocollared animals using the staggered entry design and formulae given in Pollock et al. (1989).

Results

Species composition

Three species of small rodents occur in the Pearce Point area. The collared lemming occurs in both dry and wet habitats. The tundra vole occurs in wet habitats almost exclusively. The brown lemming is extremely rare around Pearce Point, and we caught only three in the period 1987–1989, all in sedge marsh habitats. We do not know if the tundra vole excludes the brown lemming from wet habitats in the Pearce Point area. Alternatively,

Table 1 Habitat available and habitat utilized by collared lemmings at Pearce Point, N.W.T., 1987–1989 combined. Sample size includes radio-locations and live trap captures. Habitat available and habitat utilized are expressed as percentages. Manly's α is an index of habitat preference that scales from 0.0 to 1.0 and indicates preference when it is above 0.20 (except for Water Lake, which has only four habitats, above 0.25), and avoidance when it is below 0.20 (Krebs 1989, p. 396)

Grid area	Habitats						
	Rock-mud	*Dryas* heath	Heath-sedge	Sedge hummock	Sedge marsh	Sample size	No. individuals
AIRFIELD							
Available	21.99	38.81	21.96	16.83	0.42		
Utilized	2.58	14.16	43.40	39.80	0.05	1857	227
Manly's α	0.02	0.07	0.40	0.48	0.02		
WATER LAKE							
Available	28.61	14.50	42.55	14.34	0.00		
Utilized	3.12	7.63	50.16	39.08	0.00	1218	171
Manly's α	0.02	0.12	0.26	0.60	–		
OLD ROAD							
Available	9.74	45.55	21.35	22.11	1.24		
Utilized	0.82	18.80	29.56	49.09	1.73	1096	133
Manly's α	0.01	0.08	0.25	0.40	0.25		
POTENTILLA							
Available	6.54	72.94	11.68	8.44	0.40		
Utilized	2.31	43.42	34.44	19.4	0.43	1170	165
Manly's α	0.05	0.08	0.41	0.32	0.15		

Table 2 Habitat available and habitat ulitized by tundra voles at Pearce Point, N.W.T., 1987–1989 combined. Samples size includes live trap captures only. Habitat available and habitat utilized are expressed as percentages

Grid Area	Habitats						
	Rock-mud	*Dryas* heath	Heath-sedge	Sedge hummock	Sedge marsh	Sample size	No. Indiv.
WATER LAKE							
Available	28.61	14.50	42.55	14.34	0.00		
Utilized	0.90	1.20	38.40	59.50	0.00	333	49
Manly's α	0.01	0.02	0.17	0.80	–		
POTENTILLA							
Available	6.54	72.94	11.68	8.44	0.40		
Utilized	0.30	0.91	6.04	85.2	7.55	331	60
Manly's α	0.00	0.00	0.02	0.35	0.63		

the shortage of mosses, a principal winter food for brown lemmings (Batzli et al. 1980), may make the wetter habitats in this region unsuitable for the brown lemming.

For the collared lemming the highest preference value for three of the four trapping areas was for the wet sedge hummock habitat, and the second most preferred habitat was heath-sedge (Table 1). These habitat preferences were similar in all 3 years and are somewhat surprising in view of the usual belief that the collared lemming prefers dry sites (Shelford 1943; Krebs 1964). Rodgers and Lewis (1986) pointed out that in areas where the brown lemming is absent, the collared lemming may utilize wetter areas. There is a clear preference of tundra voles for the wet sedge hummock and sedge marsh habitats (Table 2). They tend to avoid the drier heath-sedge and *Dryas* areas which are much more extensive in area in this region.

Population density

Between June and August collared lemming numbers declined on Water Lake grid (Fig. 1). The summer rate of population change (*r*) varied from –0.06 to –0.15 per week on this area. On Airfield grid, by contrast, lemming numbers increased during the summers of 1987 and 1989 and remained stationary during the summer of 1988 (Fig. 1). On the two remaining areas lemming numbers remained unchanged each summer on Old Road or decreased in 1987 and 1988 and increased in 1989 on Potentilla. There is little concordance in density changes for lemmings among these four sites, and an analysis of variance on the rate of summer population change indicates no significant variation among sites or among years. The predominant pattern is for numbers to fall or remain constant during most summers (Table 3). In 1989 three of the four areas showed a summer increase in lemming densities.

Lemming densities were almost never above 2/ha in any habitat at Pearce Point (Table 4). Maximum densities recorded were 3.2/ha in August 1989 on Airfield grid. All four areas reached their highest density in 1989.

Overwinter population changes could not be monitored directly and we have available only densities at the end of summer and the beginning of the next spring to indicate overall winter population dynamics. Lemmings at Pearce Point typically increased in density over winter at an average rate of $r = 0.0128$ per week. There was a systematic trend from 1987 to 1989 toward lower rates of increase over winter for lemmings (Table 3). These overwinter rates of population growth are very low rates of population change for small rodents

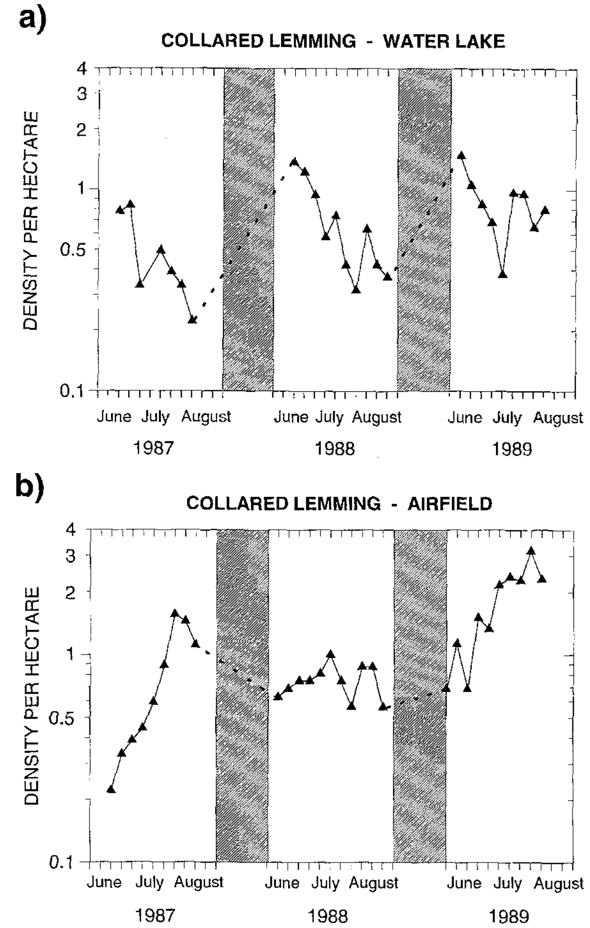

Fig. 1 Population density changes in the collared lemming at Pearce Point, 1987–1989. Estimates from Jolly-Seber model. Winter months are *shaded*. **a** Water Lake area, 20-ha trapping area. **b** Airfield area, 26-ha trapping area

Table 3 Average rates of population change per week (r) (±SE); $n = 4$ populations for lemmings, $n = 2$ populations for voles

	WINTER		
	1987–1988	1988–1989	1989–1990
Collared lemming	0.03 (0.0131)	0.02 (0.0075)	–0.01 (0.0073)
Tundra vole	–0.02 (0.0045)	–0.01 (0.0169)	–0.05 (0.0328)

	SUMMER		
	1987	1988	1989
Collared lemming	–0.15 (0.1569)	–0.05 (0.0330)	0.08 (0.0582)
Tundra vole	–	0.19 (0.0118)	0.20 (0.0427)

Table 4 Maximum summer density of collared lemmings at Pearce Point, 1987–1989. Densities per hectare, estimated from Jolly-Seber model

Grid	1987	1988	1989
Airfield (16 ha)	1.6	1.0	3.2
Old Road (20 ha)	0.7	1.0	1.1
Potentilla (25 ha)	1.0	1.1	1.8
Water Lake (19 ha)	0.8	1.4	1.5

(Krebs and Myers 1974) and indicate doubling times of 31 weeks for winter 1987–1988 and 46 weeks for winter 1988-1989.

Tundra voles were common only on two areas, Potentilla and Water Lake. Vole numbers increased during the summer months and declined over winter (Fig. 2). On average tundra voles increased at $r = 0.193$ per week in summer and declined at –0.027 per week in winter (Table 3). There is only slight variation from year to year in this pattern. Tundra voles never reached high numbers on any of our study areas at Pearce Point. Even in the better wet habitats the local density never exceeded 10–20 voles per hectare.

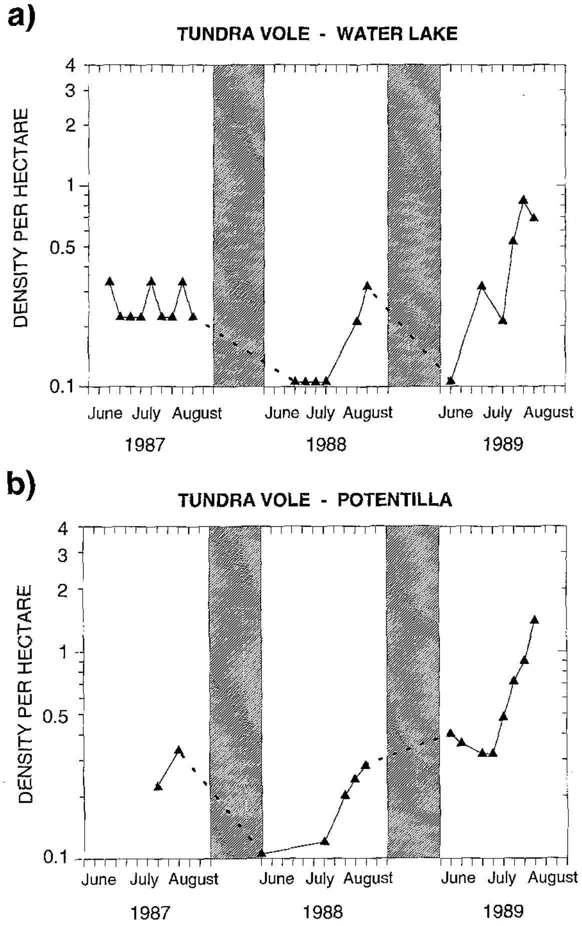

Fig. 2 Population density changes in the tundra vole at Pearce Point, 1987–1989. Estimates from Jolly-Seber model. Winter months are *shaded*. **a** Water Lake area, 20-ha trapping area. **b** Potentilla area, 30-ha trapping area

Reproduction

Collared lemmings reached sexual maturity on average at 29.5 g for males (95% confidence limits 28.5–30.5) and at 30.3 g for females (28.1–32.7). Tundra voles matured at lower weights, 27.6 g for males (25.6–29.7) and 24.5 g for females (21.0–28.7). Data from all years were combined to get these estimates. Small samples precluded year-to-year comparisons. There was no significant variation among the four trapping areas in size at maturity (ANOVA, $P > 0.5$).

We could not detect any differences in the length of the summer breeding period in the three summers of our study, and both lemmings and voles were breeding from the time we arrived in early June to the end of August when we left. Winter breeding in lemmings presumably occurred in each winter or the population would be extinct. Spring breeding under the snow in April and May occurred in lemmings every year, since we found juvenile lemmings in early June that were less than 6–8 weeks old. We had much less evidence of winter breeding in tundra voles. Only in June 1989 did we find juvenile *Microtus* that must have originated from spring breeding under the snow in April or May.

Lemmings and voles at Pearce Point seemed to be reproducing at near-maximal rates throughout the summer. For microtine rodents with a 20–21 day gestation period and a 14–16 day lactation period, we would expect 67–80% of females to be observed as lactating in random samples. From external examination 56% of all adult-sized lemmings (>34 g) were recorded as lactating when they were captured throughout the summer season, and 67% of tundra voles were judged to be lactating at capture. Individual lemming females that could be followed closely showed signs of advanced pregnancy every 20–24 days during the summer.

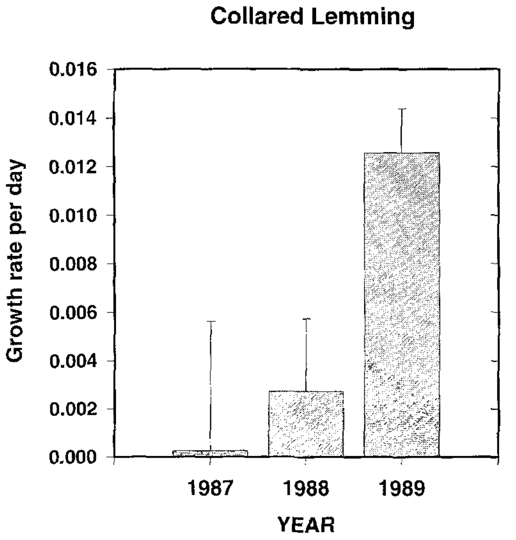

Fig. 3 Instantaneous relative growth rates (and SE) for collared lemmings at Pearce Point for 1987–1989 summers. Growth rates were much higher in the summer of 1989 than in the previous two summers

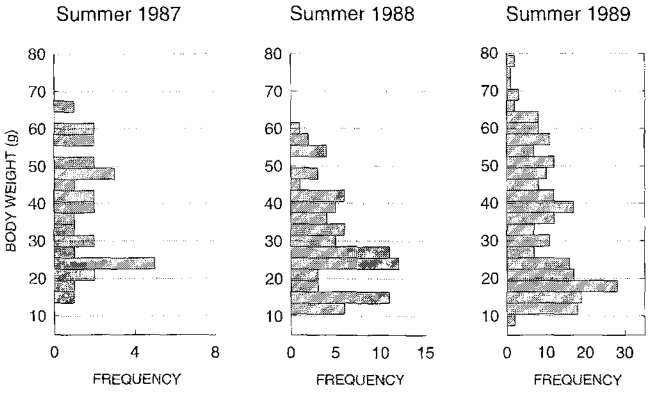

Fig. 4 Body weight distributions for all collared lemmings captured of both sexes (excluding pregnant females), all areas combined, 1987–1989. Adult lemmings tended to be larger in the summer of 1989

Growth and body size

Growth rates were measured on individual lemmings and voles with sequential captures less than 4 weeks apart. Growth rates were not calculated for obviously pregnant females. Because of the low densities and high mortality rates, few data are available in each summer. We did an analysis of covariance on instantaneous relative growth rates with weight as a covariate, and analyzed for the effect of year, summer month, sex, and grid (n=214). We could detect no effects of grid (P=0.27) or sex (P=0.45) on growth rates. There was a tendency for June growth rates to be higher than July and August rates, but these differences were not significant (P=0.12). The main source of variation in growth rates for collared lemmings was year (P=0.005, Fig. 3). The average-sized lemming (40.6 g) grew much faster in 1989 than in 1987 or 1988. On average for these collared lemmings growth ceases at 50 g. But some individuals did not grow and some larger individuals did grow beyond 50 g. We are able to explain about 35% of the variance in growth rates, so there is considerable variation yet to be explained statistically. Spring-born lemmings were often stunted in their growth. Individuals caught in June around 30 g would typically gain only a few grams during the summer.

Body mass varied significantly between years in lemmings. We utilized the weight at first capture for each individual in this analysis and discarded all subsequent weights taken on the same individual. We did an analysis of variance with year and grid as factors. Only the year-to-year variation was significant. Adult lemmings averaged a larger body size in 1989 than they did in 1987 or 1988 (Fig. 4) (ANOVA, P<0.01). Maximum body size in 1987 was 65 g, in 1988 75 g, and in 1989 79 g.

The body mass of tundra voles was analysed in the same manner. Tundra voles also showed a tendency for larger body size in the summer of 1989 (ANOVA, P<0.001). The largest vole in 1987 was 46 g, in 1988 49 g, and in 1989 63 g. Weight distributions for tundra voles were qualitatively similar to those shown in Fig. 4 for lemmings.

Mortality

Methods of radiocollaring were developed in 1987 and survival data were obtained for 1988 and 1989 summers (Table 5). Only collared lemmings were radiocollared. There was no significant difference in survival between the 2 years, and on average the probability of survival for 14 days was 0.726 for male lemmings and 0.770 for female lemmings, which means that approximately half of the population was disappearing each month.

Many radiocollared lemmings were found dead during our daily checks on or near the grids, and for these we tried to determine the immediate cause of death from clues left at the site. We could determine the cause of death for 70–85% of the individuals found dead (Table 6). In 1988 a pair of red foxes *(Vulpes vulpes)* raised a litter near our study area and approximately half of the losses were caused by red fox predation. In 1989 rough-legged hawks *(Buteo lagopus)* killed many adult lemmings and red fox predation was minimal. Both red fox and arctic ground squirrel *(Spermophilus parryii)* (Boonstra et al. 1990) may have favored female over male lemmings as prey because these predators concentrated on nesting females with litters.

Tundra voles were not radiocollared and we estimated their mortality rates from Jolly-Seber mark-recapture models. We pooled all data from 1987–1989 for all grids and both sexes since we could not distinguish any significant differences in mortality rates among these (three-way ANOVA without replication, P>0.25 for all main effects). The pooled summer survival rate of female tundra voles was 0.811 per 2 weeks, and for male tundra voles 0.802 per 2 weeks. These survival rates for tundra voles

Table 5 Survival rates per 14 days for collared lemming adults in the summers of 1988 and 1989 at Pearce Point. Data combined from four study areas (95% confidence limits in parentheses)

	1988		1989	
	Males	Females	Males	Females
SURVIVAL RATE				
June	0.87 (0.74–0.99)	0.91 (0.83–0.99)	0.47 (0.27–0.61)	0.7 (0.59–0.80)
July	0.74 (0.57–0.87)	0.64 (0.52–0.73)	0.75 (0.60–0.88)	0.86 (0.80–0.91)
August	0.92 (0.44–1.00)	0.81 (0.64–0.97)	0.72 (0.47–0.99)	0.85 (0.52–1.00)
Total	0.83 (0.62–0.98)	0.75 (0.60–0.91)	0.63 (0.50–0.77)	0.8 (0.57–0.89)
NO. OF RADIO DAYS				
June	181	413	326	668
July	453	1007	315	1484
August	253	533	111	629
Total	887	1953	752	2781

Table 6 Proximate causes of death of adult and spring-born collared lemmings in the summers of 1988 and 1989. Total mortalities include deaths from unknown causes. Each tally represents one radiocollared lemming found dead on the study area

	1988		1989	
	Males	Females	Males	Females
AVIAN PREDATORS				
Rough-legged hawk	1	1	18	20
Peregrine falcon	0	0	3	2
Unknown raptor	0	1	2	7
MAMMAL PREDATORS				
Red fox	7	16	1	1
Arctic ground squirrel	2	4	2	7
Weasel	1	0	1	0
Caribou	1	1	0	1
UNKNOWN PREDATOR[a]	6	9	4	10
ACCIDENTAL (Human)	1	2	1	2
TOTAL MORTALITIES	19	34	32	50

[a] Radio found on ground, presumed predator kill

were within the observed range for collared lemming survival rates given in Table 5.

Discussion

Collared lemming populations in the Canadian Arctic have frequently been classified as cyclic because their numbers rise and fall dramatically every 3–4 years (Shelford 1943; Krebs 1964; Fuller et al. 1975a; Mallory et al. 1981; Rodgers and Lewis 1986). Cycles may not be clear or even occur in all collared lemming populations (Fuller et al. 1975b). Chitty and Nicholson (1942) noted for the mainland western Arctic of Canada that the lemming cycle was not clearly visible to natural history observers in some settlements. The data presented here cover only 3 years but are consistent with 3 additional years of data at the same site reported by Reid et al. (1995). We conclude from these 6 years of data that cycles are absent from part of the western Canadian Arctic. This is the first detailed study of a non-cyclic collared lemming population. Fuller et al. (1975b) could not determine whether collared lemming populations on Devon Island were cyclic or not. Collared lemmings show well-developed cycles on both Banks and Victoria Islands in the western Arctic (Chitty 1950).

Four features of lemming and vole demography at Pearce Point require explanation:

1. Lemming numbers during summer often decrease or change little. If they increase, the rate of increase is low (doubling every 9 weeks).
2. Vole numbers in summer increase rapidly (doubling every 3–4 weeks).
3. Survival rates of adult lemmings and tundra voles in summer are low.
4. Summer reproductive rates of both species are always high.

How do these demographic features differ from those observed in other lemming and vole populations that fluctuate cyclically? There are very few data on collared lemming populations to which we can compare our results. There is much data on other cyclic *Microtus* species but again relatively little detailed data on *M. oeconomus*.

Collared lemming populations increase rapidly in some summer periods in cyclic populations (Krebs 1964). This never happened on a broad scale at Pearce Point. For example, in 1987 when lemming numbers did increase on Airfield grid, they dropped rapidly on Water Lake area, less than 600 m away (Fig. 1). Since reproductive rates in lemmings appeared to be high, low survival is the immediate cause of summer declines at Pearce Point. Every summer on a regional scale lemmings suffer high losses, and our results suggest that predation is the cause of these losses. Lemmings at Pearce Point may be trapped in a predator-pit.

But tundra vole numbers did increase rapidly each summer at rates typical of cyclic Microtus species (Krebs and Myers 1974, p. 281). These voles apparently do not fluctuate cyclically because of winter conditions. All cyclic *Microtus* have the ability to extend the breeding season into the autumn, winter or early spring, and this "winter breeding" is necessary to reach high numbers (Nelson 1987). We do not know why tundra voles cannot breed in winter at Pearce Point, although we note that they are near their geographic range limit and might be limited by cold temperatures or low snow cover.

But how can tundra voles at Pearce Point increase rapidly in summer when they have the same rate of adult mortality as collared lemmings? We suspect that voles reproduce at a much higher rate than lemmings because of higher litter sizes and better juvenile survival in the nest. We suspect also that young-of-the-year voles begin reproducing in their first summer at 3 weeks of age, while young lemmings do not reproduce in their first summer at Pearce Point. There must be some reproductive advantage of tundra voles over lemmings, given that there is no apparent survival advantage.

At least five hypotheses can be offered to explain these observed demographic trends at Pearce Point for collared lemmings and tundra voles. We summarize these hypotheses briefly and then discuss which are more likely to apply to our data.

1. *Food limitation* If the quality and quantity of food available to these rodents is low, population growth may be restricted by food shortage. This was the original explanation for lemming cycles in northern Alaska (Batzli et al. 1980). It could be tested by fertilization of the vegetation or supplemental feeding.

2. *Predator limitation* If summer predation rates are high because of the influx of seasonal predators (raptors and foxes), population growth could be prevented. This idea could be tested by excluding predators from an area of tundra. If this idea is correct, vole and lemming populations are trapped in a "predator-pit" (Boutin 1992; Sinclair 1989).

3. *Habitat limitations:* If burrowing sites or overwintering sites are severely limited, lemmings or voles might be limited by shelter requirements. This idea could be tested by providing artificial shelter sites for animals (such as winter nest boxes).

4. *Landscape limitations:* If suitable habitat patches are a minor fraction of the landscape, lemmings and voles could be limited in a metapopulation context by the difficulties of dispersal across uninhabitable terrain.

5. *Intrinsic limitations:* If the Chitty hypothesis (Chitty 1960) is operative in these rodents, social mortality might be sufficient to prevent population growth through territorial strife and infanticide (Mallory and Brooks 1978, 1980). This hypothesis requires that these populations be fixed for the hypothetical „low-density genotype" in which spacing behaviour limits numbers (Krebs 1985). Alternative intrinsic hypotheses like the Charnov-Finerty hypothesis (Charnov and Finerty 1980) rely on kin-selection and might apply to this low density system. The social mechanisms discussed by Lambin and Krebs (1991) based on matrilineal kin groups could also potentially operate in this system to restrict population growth.

We can provide here only a preliminary evaluation of these five hypotheses. The *landscape hypothesis* (4) is the most difficult one to test. The simplest metapopulation model for lemmings at Pearce Point would consider each patch as an isolated fragment with exchange through dispersal. The dynamics of each patch could be driven largely through internal processes, and from this one would expect differences in population trends in different patches, as we have observed in lemmings (Fig. 1). If dispersal is hazardous, these losses could be sufficient to restrict population growth in summer. In the presence of abundant generalist predators this simple model would predict for summer that high losses of lemmings would occur during dispersal movements. All patches of lemming habitat seemed to be occupied at Pearce Point, although at very low densities. Not all patches however contained tundra voles, and the metapopulation model may apply more closely to these voles than it does to lemmings.

Suitable habitats for voles and lemmings are very patchy along the arctic coast near Pearce Point but they become more connected as one moves 10 km or more inland. We have searched the inland sites around Pearce Point on foot and have not seen any signs of higher rodent densities in the inland areas (based on visual evidence of active burrows and runways). This evidence is not quantitative but it leads us to conclude that it is not primarily the landscape that limits population outbreaks in this region of the western arctic, at least for lemmings. Areas of Banks Island that have regular lemming cycles appear less fragmented than those at Pearce Point (R. Boonstra, personal observations), and it is possible that habitat fragmentation has some effect on lemming and vole dynamics at Pearce Point. We note that predation mortality occurred in most cases on a lemming's home range and did not seem to operate mostly on dispersing individuals. Dispersal however may be very risky in tundra habitats with little vegetative cover, and if dispersal is largely accomplished by juvenile lemmings and voles, which were not radio-collared, we would not have data relevant to test for this effect. We think the landscape hypothesis is worthy of more research in this part of the Canadian Arctic.

Habitat limitations (3) through shelter also do not appear to be a reasonable explanation for the lack of cycles in this region. Snowbanks at the end of winter typically have lemming and vole winter nests in moderate abundance in areas where the forage is only partly utilized. In summer we searched all areas for burrows to set out powder slides (Boonstra et al. 1992). We typically set out 40 or more slides per hectare in our study areas and we ignored the majority of burrows present because they were overgrown with vegetation or had partly collapsed. Several areas judged by the habitat to be highly suitable for lemmings and voles were searched for possible live-trapping grids and we could find no evidence of lemmings or voles. These areas were continuous with occupied patches and were not isolated, but they were always at the base of cliffs that held nesting raptors. It is possible that summer habitat limitations of burrow sites occur at Pearce Point but all our natural history observations argue against it. We do not have any information on the availability of winter burrows or winter nest sites that would allow us to test for winter shelter limitations.

Intrinsic limitations (5) could be operating on lemmings and voles at Pearce Point but in order to invoke this hypothesis we would have to explain why these populations are locked into the state of “aggressive, low-density types“ without being able to change to the “docile, increase-phase types” (cf. Stenseth and Lomnicki 1990). We have completed breeding studies in the laboratory to estimate the heritability of social behaviours and body size in collared lemmings from Pearce Point (R. Boonstra and C.J. Krebs, unpublished work), and these data may shed some light on the feasibility of invoking the Chitty hypothesis for the Pearce Point collared lemmings. The observation that there are many areas of empty habitat at Pearce Point suggests that intrinsic limitations are not the primary limitation for these rodents.

The two most plausible explanations for demographic trends at Pearce Point are *food* (1) and *predators* (2). We tested these two models at Pearce Point from 1990 to 1992 (Reid et al. 1995). The high rate of loss over summer to predators (Tables 5 and 6) points more in the direction of predation than food, but it is important to analyze the possible interactions between predators and food more explicitly (McNamara and Houston 1987). Fox predation was a dominant cause of death in 1988 but foxes were rarely seen during 1989 and avian predators took most of the lemmings in that year.

We have assumed in this analysis that the same hypothesis applies to both rodent species at Pearce Point. It is possible that different hypotheses explain the dynamics of collared lemmings and tundra voles in this region. Tundra voles are at the northern edge of their geographic range at Pearce Point and Fuller et al. (1975b) argue that *Microtus* cannot breed during the winter at this latitude because of physiological limitations. We have observed the paucity of winter breeding in our populations of tundra voles, and if this is due to their physiological limitations, one could explain vole demography at Pearce Point with an intrinsic limitation hypothesis based on the energetics of winter breeding. Lemming demography would have to have another explanation, since winter breeding is their forte. Tundra voles in summer (Table 3) increased at rates near the maximum possible for lemmings and voles (Krebs and Myers 1974, p 281).

Body size in lemmings and voles changes systematically over a population cycle. Individuals from peak populations are typically 20% larger than animals from increasing, declining, or low phases of the cycle (Chitty and Chitty 1962; Krebs 1964; Mallory et al. 1981). Even though we found no evidence of a cycle in population density at Pearce Point, we did observe a shift in adult body size in 1989 to larger lemmings and voles (Fig. 4). Adult lemmings averaged 10% larger in body weight in 1989 and tundra voles averaged 26% larger than they had been the previous year. We do not know why this occurred, and in particular why it occurred in both species. In lemmings virtually all the animals present every spring must have been born under the snow in the previous winter. None of the lemmings we marked in one summer were found alive in the following spring. Body size differences in this case are unlikely to be an age effect or a photoperiod effect, as claimed by Mallory et al. (1981) and Malcolm and Brooks (1993). For tundra voles the larger individuals of 1989 must have been born the previous summer, since winter breeding was rare in this species at Pearce Point.

Density levels in our populations of the collared lemming were significantly lower than those studied by Fuller et al. (1975b) on Devon Island and appeared lower than those studied by Rodgers and Lewis (1986) on Igloolik Island. Our lemming densities at Pearce Point were one-tenth to one-hundredth of those reported by Shelford (1943) at Churchill and Krebs (1964) at Baker Lake. We suggest that these are the lowest densities of lemmings yet studied in detail. Comparisons among the few studies of lemming demography are hampered by the difficulties of estimating absolute densities from a variety of sampling techniques.

Acknowledgements We thank Dean Cluff, Don Garnier, and Joe Serensits for their assistance in the field in 1987, and Michelle Kanter for assistance in 1988 and 1989. We thank Don Reid for his help in improving this manuscript. This research was supported by the Polar Continental Shelf Project of the Department of Energy, Mines and Resources, and by the Natural Sciences and Engineering Research Council of Canada through grants to R. Boonstra and C.J. Krebs. We are grateful to the Inuvialuit of Paulatuk for allowing us to do this research on their lands.

References

Batzli GO, White RG, MacLean SF, Pitelka FA, Collier BD (1980) The herbivore-based trophic system. In: Brown J, Miller PC, Tiezen LL, and Bunnell FL (eds) An Arctic ecosystem. Dowden Hutchinson and Ross, Stroudsburg, Pennsylvania, pp 335–410

Boonstra R, Krebs CJ, Kanter M (1990) Arctic ground squirrel predation on collared lemmings. Can J Zool 68:757–760

Boonstra R, Kanter M, Krebs CJ (1992) A tracking technique to locate small mammals at low densities. J Mammal 73:683–685

Boutin S (1992) Predation and moose population dynamics: a critique. J Wildlife Manage 56:116–127

Charnov EL, Finerty JT (1980) Vole population cycles: a case for kin selection? Oecologia 45:1–2

Chitty D (1960) Population processes in the vole and their relevance to general theory. Can J Zool 38:99–113

Chitty D, Nicholson M (1942) Canadian Arctic wildlife enquiry, 1940–41. J Anim Ecol 11:270–287

Chitty H (1950) Canadian Arctic wildlife enquiry, 1943–49: with a summary of results since 1933. J Anim Ecol 19:180–193

Chitty H, Chitty D (1962) Body weight in relation to population phase in *Microtus agrestis*. Symp Theriol Brno:77–86

Fuller WA, Martell AM, Smith RFC, Speller SW (1975a) High arctic lemmings *(Dicrostonyx groenlandicus)*. I. Natural history observations. Can Field Nat 89:223–233

Fuller WA, Martell AM, Smith RFC, Speller SW (1975b) High arctic lemmings *(Dicrostonyx groenlandicus)*. II. Demography. Can J Zool 53:867–878

Jolly GM, Dickson JM (1983) The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can J Zool 61:922–927

Krebs CJ (1964) The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. Arct Inst N Am Techn Pap 15:1–104

Krebs CJ (1966) Demographic changes in fluctuating population of *Microtus californicus*. Ecol Monogr 36:239–273

Krebs CJ (1985) Do changes in spacing behaviour drive population cycles in small mammals: Symp Br Ecol Soc 25:295–312

Krebs CJ (1989) Ecological methodology. Harper and Row, New York

Krebs CJ, Myers JH (1974) Population cycles in small mammals. Adv Ecol Res 8:267–399

Lambin X, Krebs CJ (1991) Can changes in female relatedness influence microtine population dynamics? Oikos 61:126–132

Lambin X, Krebs CJ, Scott B (1992) Spacing system of the tundra vole *(Microtus oeconomus)* during the breeding season in Canada's western arctic. Can J Zool 70:2068–2072

Leslie PH, Perry JS, Watson JS (1945) The determination of the median body-weight at which female rats reach sexual maturity. Proc Zool Soc Lond 115:473–488

Malcom JP, Brooks RJ (1993) Cyclic variation in skull-body regressions of collared lemmings: differential representation of seasonal cohorts. In: Stenseth NC, Ims RA (eds) The biology of lemmings. Academic Press, London, pp 135–155

Mallory FF, Brooks RJ (1978) Infanticide and other reproductive strategies in the collared lemming, *Dicrostonyx groenlandicus*. Nature 273:144–146

Mallory FF, Brooks RJ (1980) Infanticide and pregnancy failure: reproductive strategies in the female collared lemming *(Dicrostonyx groenlandicus)*. Biol Reprod 22:192–196

Mallory FF, Ellioot JR, Brooks RJ (1981) Changes in body size in fluctuating populations of the collared lemming: age and photoperiod influences. Can J Zool 59:174–182

McNamara JM, Houston AI (1987) Starvation and predation as factors limiting population size. Ecology 68:1515–1519

Nelson RJ (1987) Photoperiod-nonresponsive morphs: a possible variable in microtine population-density fluctuations. Am Nat 130:350–369

Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival analysis in telemetry studies: the staggered entry design. J Wildlife Manage 53:7–15

Reid DG, Krebs CJ, Kenney AJ (1995) Limitation of collared lemming population growth at low densities by predation mortality. Oikos 73 (in press)

Rodgers AR, Lewis MC (1986) Diet selection in arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): demography, home range, and habitat use. Can J Zool 64:2717–2727

Shelford VE (1943) Abundance of the collared lemming in the Churchill area, 1929–1940. Ecology 24:472–484

Sinclair ARE (1989) Population regulation in animals. In: Cherrett JM (ed) Ecological concepts. Blackwell, Oxford, pp 197–241

Stenseth NC, Ims RA (1993) The biology of lemmings. Academic Press, London

Stenseth NC, Lomnicki A (1990) On the Charnov-Finerty hypothesis: the unproblematic transition from docile to aggressive and the problematic transition from aggressive to docile. Oikos 58:234–238