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

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 (66°48'N, 122°45'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
Lemmings populations in many parts of the Canadian Arctic fluctuate cyclically in abundance, reaching peak numbers every 3–4 years (Sheffield 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 (Fulher et al. 1975b, 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 (1947) 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
this paper we address three demographic questions which form the backdrop for all these other studies:

1. Do lemming and vole populations at Pearl Point show dramatic population fluctuations?

2. What life stage changes occur in reproduction and growth in different years?

3. What are the major mortality factors affecting small rodents at Pearl 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 x 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 mleming 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 do not use our method allowed us to capture >95% of all lemmings on the study area. During 1988 and 1989 we fitted all collared lemmings x4 g with radio Teats (Biotrack model S11). Radio-collared 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 weather always precluded this activity. We located the nests of breeding female lemmings from their radio signals and in 1988 we dug out 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.

Unmarked 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 ear tags.

We live-trapped four main areas east Pearl 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. Dryas integrifolia heath with upland sedge (Carex rostrata) mixed and small amounts of Salix spp.
4. Sedge hummock, dominated by C. truncatae but with some D. integrifolia
5. Sedge marsh, principally with C. aquatilis. These habitats 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 t was used as a measure of preference (Krebs 1989, p. 396).

Results

Table 1 Habitat available and habitat utilized by collared lemmings at Pearl 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 t 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. 399)

<table>
<thead>
<tr>
<th>Grid area</th>
<th>Habitats</th>
<th>Rock-mud</th>
<th>Dryas heath</th>
<th>Sedge hummock</th>
<th>Sedge marsh</th>
<th>Sample size</th>
<th>No. of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>AIRFIELD</td>
<td>Available</td>
<td>21.99</td>
<td>38.81</td>
<td>21.96</td>
<td>16.83</td>
<td>0.42</td>
<td>187</td>
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<td></td>
<td>Utilized</td>
<td>2.58</td>
<td>14.16</td>
<td>40.40</td>
<td>39.60</td>
<td>0.03</td>
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<tr>
<td></td>
<td>Manly's t</td>
<td>0.02</td>
<td>0.07</td>
<td>0.40</td>
<td>0.48</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>WATER LAKE</td>
<td>Available</td>
<td>28.61</td>
<td>14.50</td>
<td>42.55</td>
<td>14.34</td>
<td>0.00</td>
<td>1218</td>
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<tr>
<td></td>
<td>Utilized</td>
<td>3.12</td>
<td>7.63</td>
<td>50.16</td>
<td>39.98</td>
<td>0.00</td>
<td></td>
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<tr>
<td></td>
<td>Manly's t</td>
<td>0.02</td>
<td>0.12</td>
<td>0.26</td>
<td>0.60</td>
<td>0.00</td>
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<tr>
<td>OLD ROAD</td>
<td>Available</td>
<td>9.74</td>
<td>45.55</td>
<td>21.35</td>
<td>22.11</td>
<td>1.24</td>
<td>1096</td>
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<tr>
<td></td>
<td>Utilized</td>
<td>0.82</td>
<td>18.80</td>
<td>29.56</td>
<td>49.09</td>
<td>1.73</td>
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<tr>
<td></td>
<td>Manly's t</td>
<td>0.01</td>
<td>0.08</td>
<td>0.25</td>
<td>0.40</td>
<td>0.25</td>
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<tr>
<td>POTENTILLA</td>
<td>Available</td>
<td>6.54</td>
<td>72.94</td>
<td>11.68</td>
<td>5.44</td>
<td>0.40</td>
<td>1170</td>
</tr>
<tr>
<td></td>
<td>Utilized</td>
<td>2.31</td>
<td>43.42</td>
<td>34.44</td>
<td>19.8</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Manly's t</td>
<td>0.06</td>
<td>0.00</td>
<td>0.41</td>
<td>0.32</td>
<td>0.15</td>
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the shortage of moses, a principal winter food for brown lemmings (Batelli et al. 1980), may make the wetter habitats in this region unsuitable for the brown lemming. The collared lemming the highest preferred 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 2). 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). Rogers 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 Drays 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 changed 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.

Lemmings densities were almost never above 2ha in any habitat at Pearece Point (Table 4). Maximum densities recorded were 3.2ha 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 Pearece 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.

Tundra voles were common only on two areas, Pozertilla and Water Lake. Vole numbers increased during the summer months and declined over winter (Fig. 2). On average tundra voles increased at a rate of 0.193 per week in summer and declined at 0.027 per week in winter (Table 2). 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 Pointe Pelee. Even in the better wet habitats the local density never exceeded 10–20 voles per hectare.

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 both 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 Micromys that must have originated from spring breeding under the snow in April or May.

Lemmings and voles at Pointe Pelee seemed to be reproducing at near-maximal rates throughout the summer. For microtine rodents with a 20–21-day generation 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.
On average for these collared lemmings growth ceases at 30 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 only a few grams growing during the summer.

Body mass varied significantly between years in lemmings. We utilized the weight at first capture for each individual to this analysis and discarded all subsequent weights taken on the same individual. We ran an analysis of variance with year and sex 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 vores in 1987 was 46 g, in 1988 49 g, and in 1989 63 g. Weigh 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 (Table 5). Only collared lemmings were radially collared. 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 0.776 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 (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 night-egged hawks (Buteo jamaicensis) killed many adult lemmings and red fox predation was minimal. Both red fox and arctic ground squirrel (Spermophilus parryii) (Hopcraft et al. 1990) may have eaten male over male lemmings as prey because these predators concentrated on nesting females with litters.

Tundra voles were not radio-collared and we estimated their mortality rates from July-September 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<0.05 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

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**Fig. 3** Instantaneous relative growth rates (and SE) for collared lemmings at Peace 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 for both sexes (excluding pregnant females); all rats 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>0.21) 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.
Table 5 Survival rates per 14 days for collared lemming adults in the summers of 1988 and 1989 at Peace Point. Data combined from four study areas (95% confidence limits in parentheses).

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<tbody>
<tr>
<td><strong>SURVIVAL RATE</strong></td>
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<tr>
<td>June</td>
<td>0.87 (0.74-0.99)</td>
<td>0.91 (0.83-0.99)</td>
<td>0.47 (0.27-0.61)</td>
<td>0.7 (0.59-0.89)</td>
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<tr>
<td>July</td>
<td>0.74 (0.56-0.87)</td>
<td>0.64 (0.41-0.73)</td>
<td>0.73 (0.50-0.88)</td>
<td>0.6 (0.50-0.77)</td>
</tr>
<tr>
<td>August</td>
<td>0.92 (0.64-0.97)</td>
<td>0.51 (0.38-0.64)</td>
<td>0.82 (0.55-0.91)</td>
<td>0.72 (0.50-0.91)</td>
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<tr>
<td><strong>Total</strong></td>
<td>0.83 (0.62-0.98)</td>
<td>0.75 (0.60-0.91)</td>
<td>0.63 (0.50-0.77)</td>
<td>0.8 (0.57-0.89)</td>
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Table 6 Proximate causes of death of adult and spring-born collared lemmings in the summers of 1988 and 1989. Each tally represents one radio-collared lemming found dead on the study area.

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<tbody>
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<td><strong>AVIAN PREDATORS</strong></td>
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<tr>
<td>Rough-legged hawk</td>
<td>1</td>
<td>1</td>
<td>18</td>
<td>20</td>
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<tr>
<td>Peregrine falcon</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>2</td>
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<tr>
<td>Unknown raptor</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>7</td>
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<tr>
<td><strong>MAMMAL PREDATORS</strong></td>
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<tr>
<td>Red fox</td>
<td>7</td>
<td>16</td>
<td>1</td>
<td>1</td>
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<tr>
<td>Arctic ground squirrel</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>7</td>
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<tr>
<td>Weasel</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
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<td>Carrion</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
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<tr>
<td><strong>UNKNOWN PREDATOR</strong></td>
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<td><strong>ACCIDENTAL (Human)</strong></td>
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<td>6</td>
<td>9</td>
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<tr>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><strong>TOTAL MORTALITIES</strong></td>
<td>19</td>
<td>34</td>
<td>32</td>
<td>50</td>
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* Radio found on ground, presumed predator kill

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 (Sheldford 1943; Krebs 1969; Fuller et al. 1975a; Mallory et al. 1981; Rodgers and Lewis 1986). Cycles may not be clear or even occur in small 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 Peace 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 4–8 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 response to increasing snow cover (Krebs 1983). This has been observed in a broad area at Peary 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 Peary Point. Every summer a regional on a seasonal scale systems suffer high losses, and our results suggest that predation is the cause of these losses. Lemmings at Peary Point may be trapped in a predator-pit.

But tundra voles 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" in tree to reach high numbers (Nelson 1987). We do not know why tundra voles cannot breed in winter at Peary 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 Peary 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 Peary 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 Peary 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. Predation limitations: 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 (Batellier 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 (e.g., 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" (Bothin 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 nests).

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 movement of dispersal movements.

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" that allows for group living. Alternative intrinsic hypotheses like the Chernov-Finney hypothesis (Chernov and Finney 1980) fit the low density systems. The social mechanisms discussed by Lambin and Krebs (1991) based on linear and kin groups could also potentially operate in this system to restrict population growth.

We can provide 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 Peary 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 harrassed, 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 Peary Point, although at very low densities. Not all patches were colonized by tundra voles, and the metapopulation model might apply more closely to tundra voles than to lemmings.

Suitable habitats for voles and lemmings are very patchy along the arctic coast near Peary Point but they become more connected as one moves 10 km or more inland. We have searched the inland sites around Peary 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 Peary Point (R. Boostra, personal observations), and it is possible that habitat fragmentation has some effect on lemming and vole dynamics at Peary Point. We note that predation mortality occurred in most cases on a lemming's home range and did not seem to operate mainly on dispersing individuals. Dispersal however may be very risky in tundra habitats with little vegetative cover, and if dispersal is largely accomplished by 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 ap-
pear to be a reasonable explanation for the lack of cycles in this region. Snowbanks at the end of winter typically have lenmings and voles winter nests in moderate abun-
dance in areas where the forage is only partly utilized. In the summer we searched all areas for burrows to set out powder slides (Boostra et al. 1992). We typically set out 40 or more slides per hectare in our study areas and we failed to find evidence of burrows present because they were overgrown with vegetation or had partly collapsed. Several features judged by the habitat to be slightly suitable for lenmings and voles were searched for possible live-
trapping grids and we could find no evidence of len-
mings or voles. These areas were generally not covered and voles were not isolated, but were always at the base of cliffs that held nesting rabbits. It is poss-
ible that winter habitat limitations of burrow sites occur at Pearl Point but not at our natural history observations argue against it. We do not have any information on the availability of winter burrows or winter new sites that would allow us to test for winter shelter limitations.

Intrinsic limitations (3) could be operating on len-
mings and voles at Pearl Point but in order to invoke this hypothesis we would have to explain why these pop-
ulations are locked into the state of “aggressive, low-
density types” without being able to change the “doc-
ile, increase-phase types” (cf. Smith and Lonnwick 1999). We have completed breeding studies in the labo-
ratory to estimate the heritability of social behaviour and body size in collared lemminings from Pearl Point (R. Boostra and C.J. Krebs, unpublished work), and these data may shed some light on the feasibility of in-
voking the Chitty hypothesis for the Pearl Point col-
lered lemminings. The observation that there are many ar-
ces of empty habitat at Pearl Point suggests that intrin-
sic limitations are not the primary limitation for these ro-
dents.

The two most plausible explanations for demographic trends at Pearl Point are food (1) and predators (2). We tested these two models at Pearl Point from 1990 to 1992 (Reid et al. 1995). The high rate of loss over sum-
er to predators (Tables 5 and 6) points more in the di-
rection of predation than food, but it is important to an-
yze the possible interactions between predators and food more explicitly (McNamara and Houston 1987). Fox predator was a dominant cause of death in 1989 but foxes were rare; seen during 1989 and avian predators took most of the lemminings in that year. We have assumed in this analysis that the same hy-
pothesis applies to both rodent species at Pearl Point. It is possible that different hypotheses explain the dynam-
ics of collared lemminings and tundra voles in this region. Tundra voles are at the northern edge of their geographic range at Pearl Point and Fuller et al. (1975b) and

Microtus cannot breed during the winter at this latitude because of physiological limitations. We have observed the paucity of winter breeding in this population of tundra voles, and if this is due to their physiological limi-
tations, one could explain vole demography at Pearl

Point with an intrinsic limitation hypothesis based on the energetic of winter breeding. Lenmiting 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 len-

mings and voles (Krebs and Myers 1974, p. 281).

Body size in lemminings and voles changes systemati-
cally over a population cycle. Individuals from peaks pop-
ulations are typically 26% larger than animals from in-
creasing, declining, or low phases of the cycle (Chitty and Chitty 1962; Krebs 1965, Mallory et al. 1981). Even though we found no evidence of a cycle in population density at Pearl Point, we did observe a shift in adult body size in 1989 to larger lemminings and voles (Fig. 4). Adult lemminings 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 oc-
curred, and in particular why is occurred in both species. In lemminings virtually all the animals present every spring must have been born under the snow in the previ-
ous winter. None of the lemminings we marked in one summer were found alive in the following spring. Body size differences in this case are unlikely to be an age ef-
fect 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 Pearl Point.

Density levels in our populations of the collared lem-
ning were significantly lower than those studied by Full-
er et al. (1975b) on Devon Island and appeared lower than those studied by Rodger and Lewis (1986) on Ig-
lool Island and lemmining densities at Pearl Point were one-tenth to one-thirteenth of those reported by Sheffold (1943) at Churchill and Krebs (1964) at Baker Island. We suggest that these are the lowest densities of lemminings yet studied in detail. Comparisons among the few studies of lemmining demography are hampered by the difficulties of estimating absolute densities from a variety of sampling techniques.

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References

Batai GO, White RG, MacLean SF, Pasin FA, Collier BD (1990) The herbivore-based trophic system: in Brown J, Mill-
er PC, Trettin LL, and Busnell PL (eds). An Arctic ecosystem. Doward Hutchinson and Ross, Scrub Hill, Pennsylvania, pp 335-410


Lambin X, Krebs CJ, Scoe B (1992) Seasonal pattern of the tundra vole (Microtus arctulus), during the breeding season in Cana

OECOLOGIA 103 (1995) © Springer-Verlag


Stenström IC, Lutnicki A (1990) On the Chamae-Finley hypothy

Squirrel RM, De Vincente J, Mill- xenon J, Avinna J, P

vdosn MP 750